

Modeling the formation of the visual hierarchy

The human visual cortex is modular, parcellated into a hierarchy of visual areas (V1, V2, V3, etc.) that abut each other in the brain. The areas are each retinotopically organized with several characterizing higher-level organizational features — a notable example is that the polar angle of the retinotopic maps alternates (is mirrored) across area boundaries. Normative (task-trained) models of the dorsal visual stream capture important aspects of neural tuning, but typically only involve feedforward connections and already assume a hierarchical organization of a discrete set of areas. They also do not explain the spatial organization of these areas in the brain. On the other hand, recent work with self-organizing maps has shown that it is possible to explain some of the spatial aspects of the organization of visual areas through multi-scale spatial relationships alone without requiring complex feature tuning relationships [1]. Complementing this approach, here we take a developmental perspective in which the visual cortical connections are grown from simple bottom-up rules [2]. These rules rely on an activity-dependent wiring process driven by spatial relationships implicit in the structure of retinal waves, and a synaptic pruning process dependent on wiring length, both grounded in biological data. Several features emerge as a result of the growth process: First, a discrete set of areas develops, with largely feedforward connections between them, defining a hierarchy. Second, each area exhibits retinotopy and characteristic mirror reversals in polar angle. The global eccentricity map is preserved. Third, connectivity is local: nearby neurons connect to nearby neurons in the preceding level of the hierarchy, together with a small fraction of recurrence. And lastly, receptive field sizes increase along the hierarchy. Altogether, this study demonstrates that many features of brain organization may arise not by direct optimization on particular tasks but as a consequence of low-level biophysical rules which unroll a cascade of developmental processes that determine structure and connectivity.

Supporting information

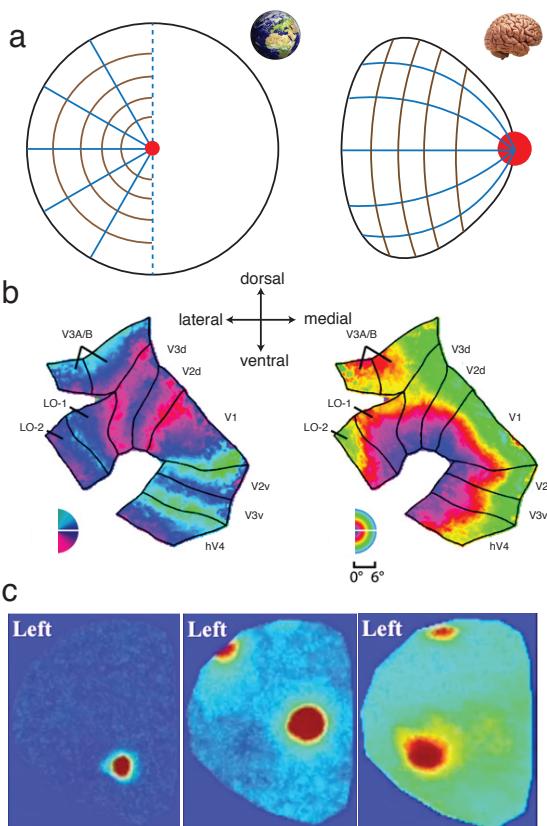


Figure 1: Experimental observations in the visual system: (a) The mapping of the visual hemifield(left) onto the primary visual cortex(right) is distorted [3, 4]. (b) A large area of the human visual cortex laid out onto 2d, showing the structure of retinotopic maps. [4] (c) Snapshots of activity in the retina 10 days before eye-opening (in rodents) shows bump-shaped retinal wave activity [5]

Growth model In mammals, retinal ganglion cells (RGCs) are active and functionally drive their target cells before eyes open, and even before they have functional photoreceptors. In these early stages of development, in the absence of light responses, retinas are spontaneously active. These early activations in the retina are called ‘retinal waves’ [6]. Retinal waves have been implicated in the formation of the initial visual map before eye-opening. Studies have shown that disruptions in retinal wave activity lead to some visual deficits [7].

We begin by assuming a preformed visuotopically wired primitive map and that retinal waves cause corresponding activity in it. Our central paradigm is to recruit new neurons and establish synapses via this spontaneous retinal wave activity. This primitive map will eventually form the primary visual area V1, and the recruited new neurons form the extrastriate visual areas. To further refine the connectivity and formed visual map in the cortex, we introduce a pruning rule based on neural activity and wiring minimization.

The growth model proceeds in the following fashion: First, a set S of neurons with available presynaptic terminals are chosen probabilistically based on the activity induced by the retinal wave at any given time. Then, for this set of neurons S we choose the nearest neuron n with unrecruited postsynaptic terminals as a candidate neuron to form synaptic connections from S . To decide whether the set S will form connections to the neuron n , we define a “synaptic permanence” for each formed synapse, calculated as a function of the axonic length and the neuronal activity when the synapse was formed. Shorter axons and stronger neural activity lead to stronger synaptic permanences, and conversely synapses with longer axons formed through weaker neural activity have weaker synaptic permanences. Connections from the set S to neuron n are then made

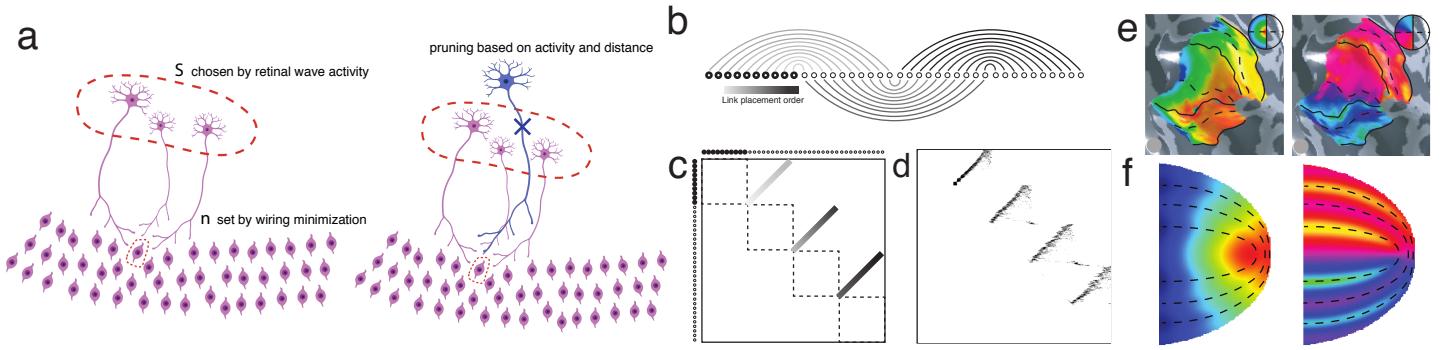


Figure 2: Growth rules and optimal greedy minimization. (a) Growth rules (b) A 1d schematic of the GWM process(c) Weight matrix corresponding to the schematic in (b). (d) Weight matrix from simulating the growth process. (e) Visuotopic maps in the human visual cortex. Mapping of eccentricity (left) and polar angle (right) (top right insets of each figure) onto the visual cortex defines regions V1, V2 and V3. [4] (f) Formed visual map in 2d using GWM captures the structure of the polar angle and eccentricity map.

in priority of synaptic permanence — if creating a new synapse would have a synaptic permanence that would supersede a previously existing connection to n , then the new connection is favored and the older connection with weaker permanence is pruned away; if however all existing postsynaptic terminal synapses at n have a stronger permanence, then the next-nearest neuron with unrecruited synapses n' is chosen to potentially receive synaptic connections from S . This process of comparison of synaptic permanence is then continued until suitable neurons are found to satisfy all presynaptic terminals from the set S . This process then repeats itself by choosing a new set S on the basis of the new induced retinal activity and the next time step, under the constraint of a maximum cap on the number of presynaptic and postsynaptic terminals of any given neuron. We implement a proof-of-principle of this growth model in a one-dimensional analog of the visual cortex, wherein we successfully recreate the emergence of a hierarchy with a small number of discrete areas with largely feed-forward connectivity, apart from a small fraction of recurrent connections (Fig. 2(d)). Further, the formed connectivity results in a retinotopic organization with polar angle alternations due to the emergence of synapses that mirror the map in each preceeding visual area.

Optimal solution: Greedy Wiring Minimization The final connectivity generated by the growth model described above implements an approximation to a sequential version of global wiring minimization, which we refer to as greedy wiring minimization (GWM). GWM leads to the emergence of most large scale features in the formed map. It replaces a global wiring minimization objective by a simple rule: *place the shortest possible connections first and then proceed to longer ones*. This does not lead to a global minimum of wiring lengths in the connectome, but instead at each point in time, the growth dynamics favor the shortest new connection to be created. When coupled with out-degree and in-degree saturation, this very naturally leads to a mirroring of the formed map in each visual area as shown in the schematic Figs. 2(b). The synaptic growth model described above results in the connectivity matrix shown in Fig. 2(d), which is in close agreement with the expected connectivity from a GWM process Fig. 2(c).

The exact mapping of the visual hemifield onto the primary visual cortex (Fig.1a) is known as a logarithmic conformal mapping and occurs due to the non-uniform density of retinal ganglion cells and the connections from LGN to cortex. This distorted map, when coupled with GWM leads naturally to both alternations in the polar angle (Fig.2f (right)), and preservation of the eccentricity map (Fig.2f (left)). Thus, our model suggests that the emergence of polar angle alternations in closely tied to the distortion of the visual field map onto V1.

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