1 Cortical columns

It has been hypothesized that small vertical structures called *cortical columns* are the basic units of sensory and motor information processing in the cortex. How can such a structure emerge from the complexity of the cortex?

1.1 Cortex composition and organization

The cortex is the superficial part of the encephalon and represents the biggest part of grey matter in the brain. It has a horizontal organization in layers of different types of cells (figure 1). The number of layers, their cell composition, their thickness and organization are not the same over the surface of the cortex. Those differences led neurophysiologists to divide the cortex into small regions a few square centimeters large (figure 2) where those characteristics were homogeneous and that corresponded to different functions, e.g., vision or motion. Nevertheless most of the cortex is made up of six layers of neurons, from layer I at the surface of the cortex to layer VI that lies next to the white matter. Its thickness varies from 3 to 6 mm.

About fourty types of neurons have been identified through the cortex but they can essentially be divided into only two classes: *projection neurons* and *local inter-neurons*. Projection neurons (also called *principal neurons*) are excitatory cells, most of them having a pyramidal cell body and being situated in layers III, V and VI of the cortex. Inter-neurons can be found in all layers but they just amount to 20 up to 25% of cortical neurons and are often inhibitory. Information processing in the cortex is multi-step and the axons of projection neurons carry information from one stage to the next, sometimes in distant groups of neurons. Inter-neurons can receive the same input as principal neurons but just convey it to local cells implied in the same stage of information processing. More detailed information about cortical structure and function can be found in [21, 1, 22].

1.2 Cortical columns

Neurons one runs across perpendicular to the cortex tend to be connected to each other and to respond to precise stimulations with similar activities throughout the layers, we say they form a *cortical column*.

Anatomical basis

Many cortical neurons throw their axons and dendrites from the cortex surface to the white matter thereby forming the anatomical basis of the columnar organization in the cortex (figure 3-B). Nervous fibers from the thalamus mostly end in layer IV where they are connected to stellate neurons. These neurons throw their axons towards the surface of the cortex, parallel to apical dendrites of neighboring pyramidal neurons, and establish connections with them (figure 3-C). The thalamocortical input is therefore conducted within a thin column of pyramidal cells so that the same information is shared throughout the depth of the cortex perpendicular to its surface [22].

Several studies have shown biological evidences for such small aggregates of about one hundred neurons, 20 up to 50 μm wide, called *minicolumns* [8, 30]. However the minicolumn hypothesis

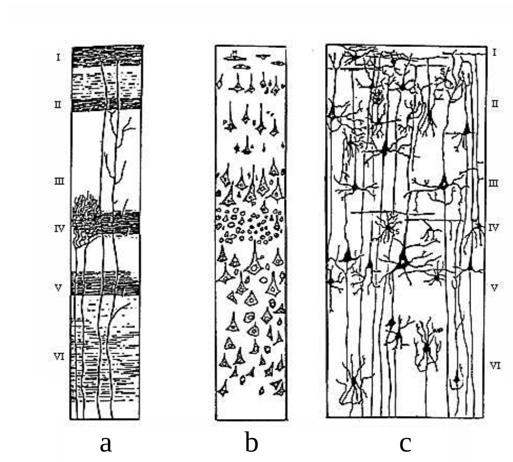

Figure 1: *Layer organization of the cortex (a) Weigert's coloration shows myelinated fibers (axons) and so the connections inside and between layers, (b) Nissl's coloration only reveals cell bodies (c) Golgi's coloration shows the whole cells (From [31]).*

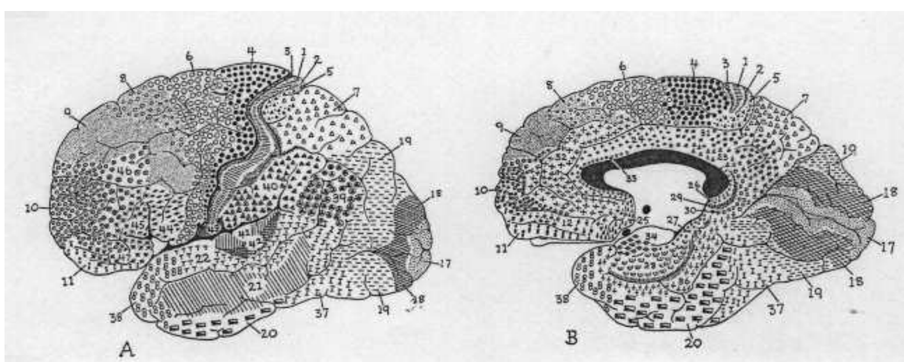

Figure 2: *In 1909, Brodmann [5] divided the cortex into 52 cytoarchitectonic areas according to the thickness of the cortical layers. For example, layer IV is very thin in the primary motor cortex (area 4) while it is very thick in the primary visual cortex (area 17).*

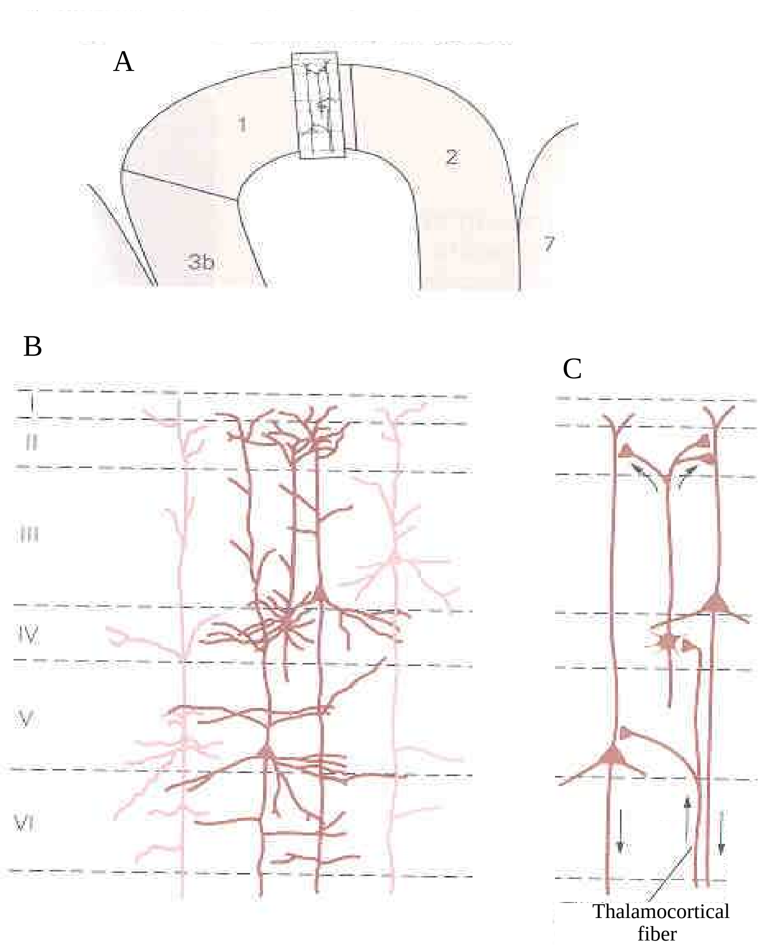

Figure 3: *(A) Sagittal section of the primary somatosensory cortex of the monkey (S-I) (B) Morphology of relay cells from layers III to V. Stellate neurons (layer IV) receive information from the thalamus and transmit it to neighboring pyramidal cells in superficial layers of the cortex. Pyramidal cells throw their axons towards deep layers of the cortex and other cortical or sub-cortical regions. They also establish horizontal connections with neighboring columns sharing the same physiological properties (C) Diagram of intra-cortical excitatory circuitry (From [22]).*

does not solve the problem of defining cortical colunms: minicolumns behaviour is not well known and horizontal connections between them tend to blur the anatomical description of larger units made up of them.

Cortical columns as physiological units

In 1957, Mountcastle discovered a columnar organization in the cortex [29] (see figure 4). With electrode recordings, he showed that neurons inside columns of 300 to 500 μm of diameter displayed similar activities. Those physiological units are usually called *macrocolumns*. In figure 5, we see physiological columns obtained from the diffusion of a radioactive substance. Some of them are spatially well defined while some ohers are more difficult to distinguish from one another. What is the meaning of such units?

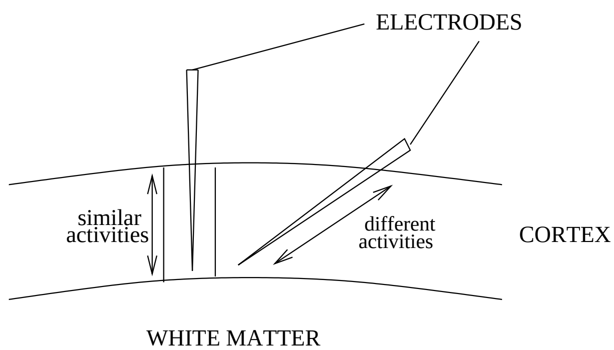

Figure 4: *Mouncastle's pioneering experiment. When he moved an electrode perpendicular to the cortex surface, he encountered neurons with similar electrical activities while moving the electrode obliquely gave him different types of recordings. So he showed the existence of 300-500 μm wide columns in the cortex.*

From physiological to functional units

Many experiments on somatosensory and visual cortices made it possible to relate physiological columns with sensory functions [22, 29, 17, 16, 28]. In some cases the processing site for a given function is clearly defined like in rat's sensory cortex where every whisker is associated with a sharply bounded cortical site in layer IV (see figure 6). In other cases, the information processing sites move continuously across the surface of the cortex when stimulation varies so that it is not possible to define a size for columns. It is the case of the *orientation columns* in the primary visual cortex (figure 7) [17, 16, 14].

So there are several non-equivalent ways to speak of a cortical column, the relevance of which strongly depends on the problem we want to tackle. For instance in the macaque monkey primary

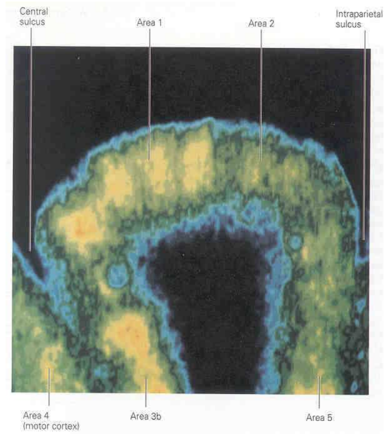

Figure 5: *Columns from the primary somatosensory cortex shown by auto-radiography after 45 minutes of stroking a hand with a brush. On this sagittal section of the cortex a high activity (proportional to the concentration of a radioactive substance) can be viewed in areas 1 and 3b. Columns are well defined in area 1 and form a continuum in area 3b (From [22]).*

visual cortex, [28] gives a very interesting discussion about both the anatomical and functional basis for columnar organization.

We now present Jansen's model of a cortical column. This model considers columns as tightly connected excitatory/inhibitory populations of neurons able to produce EEG-like activities. So if we want to link this model to biology we should consider Jansen's columns as physiological macro-columns (0.2 to 1 millimeter wide, containing tens to hundreds of thousands cells).

2 Jansen's model of cortical columns

Jansen's model of cortical columns is based on the work of Lopes Da Silva *et al.* and Van Rotterdam *et al.* [26, 27, 35]. They developed a biologically inspired mathematical framework to simulate spontaneous electrical activities of neurons assemblies recorded by EEG, with a particular interest for alpha activity. In their model, populations of neurons interact by excitation and inhibition and can in effect produce alpha activity. Jansen *et al.* [20, 19] discovered that this model was also able to simulate evoked potentials, *i.e.* EEG activities observed after a sensory stimulation (by a flash of light, a sound, etc...). More recently, Wendling *et al.* used this model to synthesize activities very similar to those observed in epileptic patients [37].