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Possible Functional Roles of the Bipartite Dendrites of Pyramidal Cells

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Abstract

A theory about the possible functional roles of the bipartite dendrites of cortical pyramidal cells is presented that tries to fuse aspects of both Cardinal Cell Theory and Assembly Theory. The article treats resulting functional differences of both dendritic pathways in conjunction with an hypothesis concerning the existence of two activity ranges. The model includes a three–rule system of self–organization.

1 Cortical architecture

The main cortical cell type are pyramidal cells. These cells show a typical dendritic morphology. An *apical* dendrite originates from the top of the cell body and runs perpendicular to the cortical surface into direction of the pia mater. These dendrites are contacted by synapses from cortico–cortical fibres that enter an areal from the white matter. *Basal* dendrites form a local plexus around the cell body. Synapses at basal dendrites are mainly set up by pyramidal cells in the neighbourhood. *Figure 1* shows this simplified picture of the cerebral cortex called 'skeleton cortex' according to BRAITENBERG, who also introduced the terms A- and B–system for the non–local apical path and the local basal path [2].

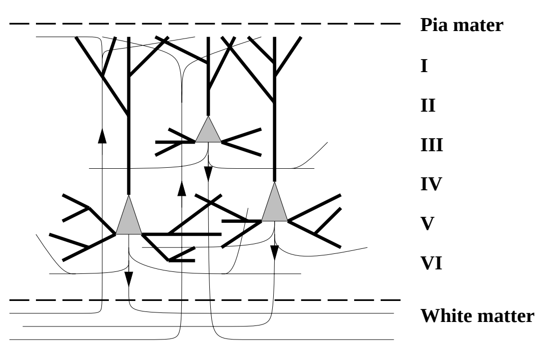

Figure 1: *A(pical)- and B(asal) system of pyramidal cells.*

2 Cardinal Cell and Assembly Theory

Figure 2 compares Cardinal Cell Theory and Assembly Theory. *Cardinal Cell Theory* as proposed by BARLOW [1] assumes a purely *unidirectional hierarchical structure* of neural systems. Low level neurons coding sensory signals feed higher level neurons that respond to complex features up to complete objects in the visual case. The neural system probably forms an inverse pyramide, because there has to be a vast number of complex cells at the top level of the hierarchy. Only few active cells represent a sensory situation. The function used to combine responses of low level neurons into the activity of high level neurons should be *conjunctive* in order to preserve the specialization of cells. Combinatorial explosion is one of the major drawbacks of this theory. *Assembly Theory* that goes back to HEBB [3] on the contrary concentrates on *lateral connections* between neurons. It avoids combinatorial explosion by 'cutting' the hierarchy at a much lower level — hierarchical structure is neglected in most cases. Sensory situations are represented by simultaneous activity of a large number of cells each coding a rather simple feature. Lateral connections between neurons of one level serve for the formation of cell assemblies, i.e. groups of cells that are active due to excitatory interactions. If one neuron can participate in more than one cell assembly, coding space enlarges drastically [5]. Therefore, (weak) *disjunctive* effect of lateral presynaptic cells is necessary, so different cell groups are able to excite one neuron.

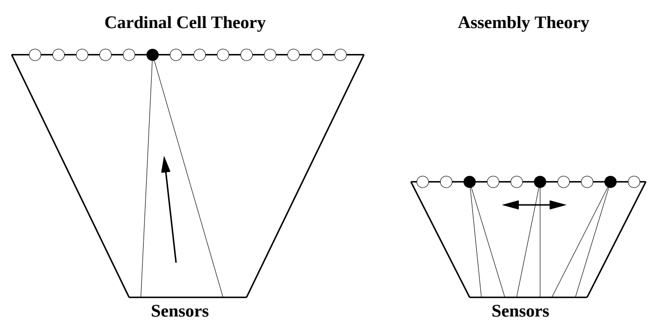

Figure 2: *Comparision of Cardinal Cell Theory and Assembly Theory.*

3 Functional interpretation

In difference to BRAITENBERGs interpretation of the two dendritic pathways of pyramidal cells [2] we try to fuse Cardinal Cell Theory and Assembly Theory by the assumption, that the *hierarchical structure* of the Cardinal Cell Theory corresponds with the *A–system* of pyramidal cells, whereas the *lateral structure* of the Assembly Theory finds its biological counterpart in the *B–system*. A neuron can either be activated from a specific input combination through the hierarchical A–system or can take part in different assemblies through the B–system. Following this, synaptic effects of *apical synapses* onto the postsynaptic neuron have to be *conjunctive* and effects of *basal synapses disjunctive*.

We further assume *two separate ranges of activity*: *high firing frequencies* for signals originating from 'real' *external inputs*, and *low frequencies* that code *hypotheses* about signals. Real signals are only mediated by the A–system, hypotheses by both systems. A pyramidal cell signals real activity, if enough parts of the apical represented conjunction are activated, otherwise the neuron fires at the hypotheses level. Independent of the activity level of presynaptic cells the basal dendrite is only able to cause hypotheses activity in the postsynaptic neuron. This can be explained from the point of learning. Lateral connections reflect statistical relations between conjunctions of signals. High basal weights between two neurons that resulted from frequent coincident activation via the A–system, could never be reduced if the basal pathway could evoke 'real' activity in the case of a 'real' conjunction of the basal partner neuron.

4 Self–organization

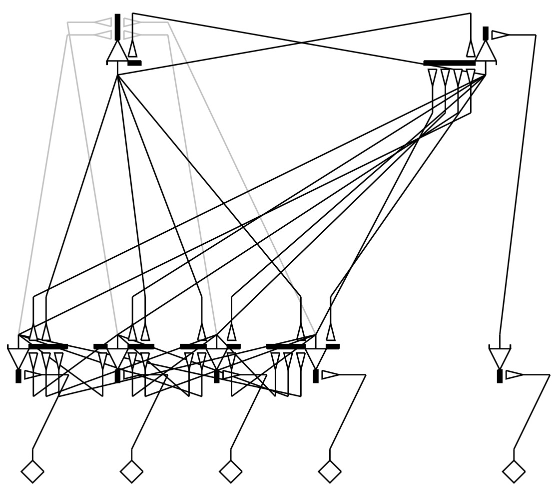

Figure 3: *Diagram of all connections of a simple test network.*

Self–organization of synaptic weights in both the A- and B–system requires a learning rule system of three rules. The *apical learning rule* is HEBBian with normalization of the weight sum reflecting conjunctive properties of the apical path. The rule connects 'real' pre- and postsynaptic activity and a term expressing real activity at a number of *basal* partner neurons. In the consequence, a conjunction is only represented in apical weights, if the conjunction often takes part in one ore more assemblies in the basal path. A *sensitivation rule* temporarily dissolves the conjunctive character of the apical path to allow for the alteration of the represented conjunction — without this rule, no other conjunction could ever excite the neuron up to the level necessary for learning. A 'pre–not–post–LTD' rule [4] has to be used for the *basal learning rule*, because asymmetric relations between two channels should create weights

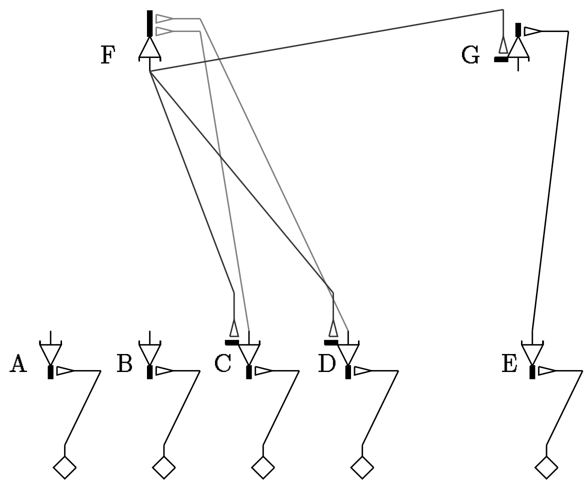

Figure 4: *Final weight state of the test network. Gray levels depict weights.*

in the direction from premise to conclusion. Related problems stated in [4] are avoided by the assumption of separate activity ranges. All learning rules are influenced by 'real' activity only.

Figures 3 and *4* show the effect of the learning rule system with a simple network. An asymmetric complex coincidence between the conjunction of channels C and D on one side and channel E on the other side was presented together with random activity on all channels. The learning rule system leads to the specialization of neuron F to the apical conjunction of C and D, and F and G are connected by asymmetric basal weights.

References

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