

Cortical Columns and Planning Models

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Abstract—The cortical column hypothesis is described along with backing evidence. Proposals for the functional properties of columns are reviewed, namely those based on construction of columnar models and networks of columns. An attempt is made to tie this knowledge into that of an existing model of planning, the TELOS model.

Index Terms—cortical column, minicolumn, macrocolumn, neural model, PFC

I. INTRODUCTION

In all regions of cortex, it appears that a columnar organization of cells exists. The computational significance of this is not well understood, especially in associational regions of cortex. To approach the question of whether the columnar organization has a role in serial plan formulation and goal directed behavior, it is necessary to understand the current body of knowledge on cortical columns. This article attempts to summarize what is known, and the evidence that backs it, and follows with an overview of existing models of columns and their networks. Then, a modern model of goal directed behavior, constructed from columns, is reviewed. A brief consideration of the TELOS model of reactive and planned behavior is made in light of the proposed columnar properties.

II. WHAT IS KNOWN ABOUT CORTICAL COLUMNS?

Vernon B. Mountcastle formulated the column hypothesis in neuroscience based upon physiological observations made during cat and monkey single neuron recordings of the somatosensory cortex (1957). A great number of anatomical and physiological experiments have been conducted since that time documenting the columnar and modular organization of neocortex in many species, including mice, rats, cats, rabbits, monkeys and humans, in visual, somatosensory, motor, auditory, and homotypical cortical regions. Mountcastle (1997; 2003), Buxhoeveden and Casanova (2002), and Jones (2000), review the modern day generally agreed upon formulation of the vertical cell column model of cortical organization, summarized next.

The *minicolumn* is the basic anatomical and functional unit of cortical operation. Consisting of about 80-100 neurons in the mature cortex (twice this number in primate visual cortex),

the minicolumn is roughly 40-50 μm in diameter, with cell-sparse regions (filled with unmyelinated axon fibers, dendritic arborizations and synapses) separating minicolumns. Density is on the order of 1000 minicolumns per mm^2 .

Bundles of approximately 60-80 minicolumns are found to bind together with short-range horizontal connections to form a larger unit known as a *macrocolumn*, varying between 300 to 600 μm in diameter. Such columnar organization appears across many species, and it is believed that evolution has favored cortical expansion by increasing surface area via greater numbers of columns, with relatively little change in cortical thickness. The macrocolumn in somatosensory cortex is known as a *segregate*. In visual cortex, the macrocolumn is known as a *hypercolumn*.

Minicolumn cells extend perpendicular to the pial surface and stack in cellular layers, accounting for the laminar structure of cortex from which the cytoarchitectonic regions were demarcated by early brain researchers. While minicolumns show a great deal of similarity between different regions of cortex, they are differentiated by connectivity, synaptic transmitters, and relative numbers of cell types in the traversed lamina. The most typical form of cortex contains six layers, numbered from the pial surface to the white matter, defined primarily by the presence or absence of cell bodies and connectivity (Amaral, 2000):

- 1) Layer I consists of dendrites of cells located deeper in the cortex, and axons that travel through, or form connections, in this layer.
- 2) Layer II is composed of small, spherically-shaped, *granule* cells.
- 3) Layer III contains a variety of mostly pyramidally-shaped cells. Cells from layers II/III receive callosal and cortical input, and project to other cortical areas. Layer IIIb cells receive some thalamic input. Within a minicolumn, layer II/III cells project to layers V and VI.
- 4) Layer IV consists of stellate and granule cells, and receive thalamic, callosal and cortico-cortical input. Within a minicolumn, layer IV cells typically project to cells in layers II/III.

- 5) Layer V consists of pyramidally-shaped cells. Layer V sends projections to the spinal cord, pons, medulla, tectum, thalamus, red nucleus and striatum.
- 6) Layer VI is a heterogenous layer of cells, blending into the white matter. Cells from layers V/VI project to subcortical structures.

A minicolumn has all cortical cell phenotypes. The basic cell types that appear in minicolumns include the spiny (having spines on their dendrites) pyramidal cells, the spiny stellate cells, and the non-spiny interneurons. Excitatory pyramidal cells constitute 75-80% of cortical neurons, inhibitory interneurons composing the remaining 10-25%. The output pathways of a minicolumn are derived only from pyramidal cells. Large and small basket cells, the chandelier cell, and the double bouquet cell are the three best known types of inhibitory cells.

In summary, the hypothesis of the column as the fundamental processing unit of the cerebral cortex 'requires that nerve cells in middle layers of the cortex, in which thalamic afferents terminate, should be joined by narrow vertical connections to cells in layers lying superficial and deep to them, so that all cells in the column are excited by incoming stimuli with only small latency differences. The columns form a series of repeating units across the horizontal extent of the cortex. (Jones, 2000)'

III. WHAT IS THE EVIDENCE FOR CORTICAL COLUMNS?

In visual, somatic sensory, auditory, motor and homotypical cortical areas, a number of experimental techniques have been used to provide evidence for the minicolumn and macrocolumn: microelectrodes and evoked potentials, Nissl-staining, 2DG metabolic labelling, nerve regeneration, optical recordings, and developmental studies (Mountcastle, 1997; Buxhoeveden and Casanova, 2002; Jones, 2000). A relatively new technique, *in-vivo* voltage-sensitive dye imaging (VSDI), may offer the possibility to gather evidence of columnar dynamics, as this technique operates at a spatial resolution of 200 μm and millisecond time resolution (Grinvald and Hildesheim, 2004).

The earliest evidence may be attributed to Lorente de N3 (1938), who observed 'vertical cylinders' in Nissl-stained cells, and commented that 'it may be called an elementary unit (of the cortex)' (Buxhoeveden and Casanova, 2002).

In somatic sensory cortex, single neuron electrophysiological studies in anaesthetized cats and monkeys conducted by

Mountcastle (1957; 1959) found that electrode penetrations parallel to the pial surface and crossing through the radial axis of the cortex passed through 300-500 μm sized blocks of cellular structure sharing the same receptive field properties. The blocks were found to have sharp transitions across properties, defined as the response of a cortical cell to stimulus of a particular zone on the body surface. Since that time, the minicolumn-columnar organization of the somatic sensory cortex for place has been confirmed in microelectrode mapping experiments in cats and monkeys (Mountcastle, 1997).

Favorov and Diamond (1990), using receptive field mapping techniques on cats, were able to find honeycomb-shaped macrocolumns (300-400 μm width) containing about 80 minicolumns (of 40-50 μm diameter and 50-60 μm spacing).

Further evidence for the minicolumn structure was provided by Kaas (1981; 1983) in nerve regeneration studies in monkeys, where receptive nerves of the hand were severed, swapped with an adjacent digit, and reattached. Cortical zones of 40-60 μm width having sharp receptive field transitions were clearly identified.

Evidence from 2-deoxyglucose (2DG)-based experimental techniques also exists. In primary somatosensory cortex of monkey and cat, investigations into the distribution of tactile stimulus-evoked 2DG labelling found narrow, translaminal minicolumns separated by narrow zones of decreased activity (ie. distinguishable from their neighbors on the basis of labeling intensity), with a spatial period of 18-33 cycles/mm (30-56 μm width) (Tommerdahl et al., 1993).

In visual cortex, perhaps the most well-known evidence of macrocolumnar structure is found in the work of Hubel and Wiesel (1959). Microelectrode penetrations made perpendicular to the pial surface exposed a columnar organization in the primate V-1 defined by the neuronal properties of ocularity (neurons preferentially driven by stimuli delivered to one eye or the other) and place (a particular locus in the visual field) imposed by input from LGN, and by line-orientation specificity generated by intracortical processing. Orientation selectivity, where a full sequence of 180° line rotation is covered in columnar distances that vary from 500-750 μm , came to be termed an *orientation hypercolumn*. Pairs of columns containing neurons whose activity graded systematically from full dominance by one eye to full dominance by the other, were termed *ocular dominance hypercolumns* (Mountcastle, 1997). Optical imaging experimental techniques have since

identified orientation and ocular dominance macrocolumns in visual cortex (Blasdel, 1992).

In auditory cortex, many studies on cats and monkeys of evoked potentials due to frequency stimulus have provided direct evidence for columnar organization (Mountcastle, 1997).

In human primary motor cortex (area 4), Meyer (1987) used the Golgi method to show that in layers IIIb/c, the somata and dendritic trees of pyramidal and nonpyramidal cells are grouped into columnar aggregations approximately 100-300 μm wide and separated by 50-100 μm wide cell-sparse zones.

Anatomical and electrophysiological studies by Keller (1993) of the synaptic circuitry of the motor cortex demonstrate that columnar aggregates of neurons related to different aspects of the same movement compose the motor cortex.

Homotypical (association) areas of cortex also show columnar structure, although not in the relatively clear manner demonstrated in the visual and somatosensory areas. Response properties in homotypical areas do not reflect any single sensory input, nor do they correspond in an unconditional way to peripheral output. Modular organization in posterior parietal cortex of monkey has been found via electrophysiological experiments, where neurons with similar properties are arranged in vertical modules extending across cellular layers (Mountcastle, 1997).

In the medial temporal (MT) visual area of the macaque monkey, Albright, Desimone, and Gross (1984) found that neurons with similar axes of motion preference are arranged in vertical columns. Axis of motion columns appeared to exist in the form of continuous slabs, such that 180° of axis of motion are represented in 400-500 μm of cortex.

From both optical and extracellular recordings, Tsunoda et al. (2001) found that complex objects are represented in macaque inferotemporal (IT) cortex by the combination of feature columns. The columns measured approximately 400 μm in the horizontal dimension. Their results suggest that objects may be represented not only by simply combining feature columns, but also by using a variety of combinations of active and inactive columns for individual features. The individual columns represent component visual features of an object. Objects are represented by combination of multiple columns in a sparsely distributed manner.

Buldyrev et al. (2000) applied quantitative techniques derived from condensed matter physics to the study of Nissl-stained tissue taken from the STS association cortex region.

The findings show a cortical structural element, which they call a microcolumnar ensemble, perpendicular to the pial surface, composed of roughly 11 tightly-packed neurons with periodicity of 80 μm .

Lastly, perhaps the most compelling evidence for the basic columnar organization of the cortex comes from its mode of generation. Studies of neocortical development by Rakic and colleagues (1988; 1998) resulted in the *radial unit hypothesis* and the idea of an *ontogenetic unit* of the neocortex:

One remarkable feature is that neurons that constitute cerebral cortex are not generated in the cortex itself; rather, they migrate from the site of their origin to proper laminar and areal positions. In primates, including humans, cortical neurons are generated during the first half of gestation in the ventricular zone of the developing brain near the surface of the cerebral ventricle. In addition to cortical neuronal progenitors, this region contains a population of elongated radial glial cells whose projections span the entire cortical thickness. These cells are attached to the ventricular surface by their end feet and have radial processes that protrude toward the pial surface, spanning the cortical width. These radial processes form the scaffolding for neuronal movement into cortex and exist only transiently, during this phase of cortical formation. The cerebral cortex is built below the cerebral surface by migration of neurons that are produced at the margin of the cerebral ventricle. Successively generated neurons migrate along the radial glia guides and settle in an inside-to-outside order within the developing cortex. Each successively generated neuron must bypass predecessors that migrated along the same glial fiber, before ultimately settling at the outermost level of the cortical plate. The neurons become arranged radially in stacks named ontogenic columns. A column consists of cells that originate from several clones but share the same birthplace, migrate along the common pathway, and settle within the same ontogenic column. (Rakic, 1998)

Emerging from the exploration of this radial unit hypothesis is the question: which is an emergent property and which is a morphological reality, columnar organization, or lamina? Or is it a mixture? Karten (1997) favors the dual phylogenetic origin hypothesis, where the cerebral neocortex may derive from two groups of founder cells. The work of Kuan et al. (1997) is cited, who demonstrate that the neurons of the deeper layers of cortex arise as a tangential (laminar) population from a common source, whereas those of the more superficial layers arise from a different source and appear to arise as radial units.

Corbin, Nery, and Fishell (2001) provide evidence that not all radially migrating cells follow a direct route, rather, some cells can migrate tangentially for long distances.

in cortical processing of thalamic input (Read, Winer, and Schreiner, 2002). However, the idea of local amplification of thalamic input seems to remain.

IV. WHAT ARE SOME OF THE FUNCTIONAL PROPERTIES OF COLUMNS?

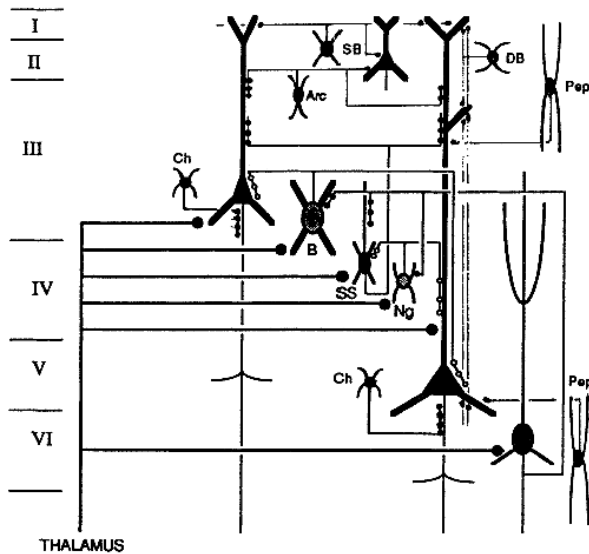


Fig. 1. From Jones (1991) and Mountcastle (1997): 'Schematic outline of neuron cell types in the monkey neocortex. Cells that receive synapses of thalamocortical fibres include the pyramidal cells of layers III, V and VI, and three types of non-pyramidal cells: B = large basket cells, SS = non-pyramidal, nonspiny (stellate) cells, Ng = neurogliform cells. The non-pyramidal cells not known to receive thalamocortical afferents directly are also shown: Arc = arcade cells, Ch = chandelier cells, DB = double bouquet cells; Pep = peptidergic cells; and SB = small basket cells.'

Cortical column anatomy and cell physiology provide some basic information on minicolumn functional properties. Input from the thalamus projects to excitatory interneurons of layers IV and IIIb (see Figure 1). These excitatory interneurons extend axons vertically up and down, connecting to pyramidal cells and inhibitory neurons, creating a re-entrant circuit (Mountcastle, 1997). The largely columnar organization of dendrites and axons of layer IV spiny stellate and star pyramidal neurons, combined with the preferential and dense projections within cortical layers IV and II/III, suggests that these two cell types serve to amplify thalamic input and relay excitation vertically within a single cortical column (Lübke et al., 2000) (see Figure 2). It is important to note that columns in different cortical regions are differentiated by specifics of thalamic input. Smith and Populin (2001) show that, in cats, layer III/IV pyramidal cells in auditory cortex are the main thalamic target, whereas in visual cortex spiny stellate cells are mainly postsynaptic, implying modality specific differences

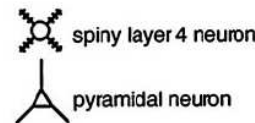
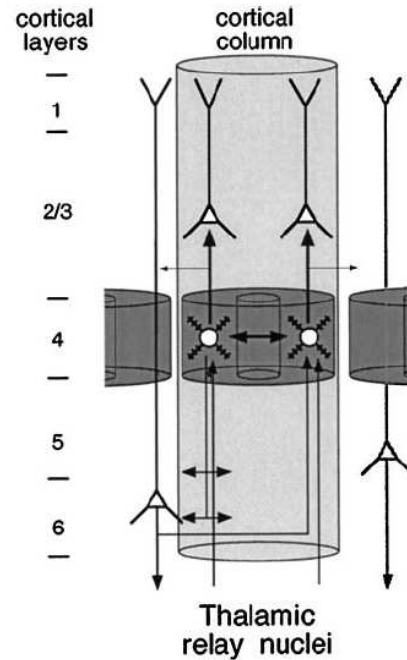


Fig. 2. From Lübke et al. (2000): 'Simplified schematic diagram of the flow of excitation within a cortical macrocolumn of rat barrel cortex. In layer IV, individual minicolumns are shown in dark gray. A macrocolumn (barrel) is shown in light gray. Excitatory input from the thalamus is relayed and amplified in layer IV by excitatory spiny neurons with strong synaptic connections as indicated by the thick arrow. Excitation is transmitted to layer II/III pyramidal cells and distributed throughout the barrel cortex via the long-range tangential axons of layer II/III pyramidal cells. Thickness of arrows indicates the preferential projections of the axons, in particular for the spiny layer IV neurons.'

The real 'work' performed by a column is found in the interplay of the excitatory and inhibitory circuits. 'Understanding how columns work depends on knowledge of the functioning of local inhibitory circuits (Buxhoeveden and Casanova, 2002)'. The plentitude of types of inhibitory interneurons (some 50 anatomically-electrically defined types) ensures immense complexity in forms of columnar processing. This is true both within columns, and between neighboring and distant columns. The function of interneuron diversity is very likely a balancing mechanism, automatically scaling stimulus intensity. (Markram et al., 2004), (Dantzker and Callaway, 2000)

Columnar properties are subject to dynamic physiological

mechanisms, meaning that afferent inflow or intracortical constructions set columnar defining properties, and varies between cortical areas (Mountcastle, 1997). Evidence of this comes the rewiring of auditory and visual input of ferrets. Sur and Leamey (2001) have shown that if retinal inputs are forced to innervate the auditory cortex at birth, auditory cortex develops in a way that is much more like visual cortex than auditory cortex, and behavioral tests show that visual stimulation percepts appear to be 'seen' rather than 'heard' (Swindale, 2000).

V. WHAT INSIGHT DO MODELS OF COLUMNS OFFER?

An understanding the computational properties of columns can be gained through neural models, accounting for the level of model abstraction, and model suppositions. In the review of models of cortical columns that follows, models of visual cortex were not included due to their lack of generality, and specificity in describing ocularity and line-segment selectivity. Also, models deemed too abstract were excluded from this review, such as the *trion* model (Shaw, Silverman, and Pearson, 1985), and the cortical column as autonomous oscillator model (Hoppensteadt and Izhikevich, 1998).

Lücke and von der Malsburg (2004) study a model of the macrocolumn consisting of a collection of inhibitorily coupled minicolumns, composed of spiking neurons with refractory period, interconnected randomly and with excitatory interconnections within the minicolumn, shown in Figure 3.

'A stability analysis of the system's dynamical equations show that minicolumns can act as monolithic functional units for purposes of critical, fast decisions and learning. Oscillating inhibition (in the gamma frequency range) leads to a phase-coupled population rate code and high sensitivity to small imbalances in minicolumn inputs. The result of a decision is identified with the active state of the macrocolumn at the maximum of the inhibitory oscillation. Minicolumns are shown to be able to self-organize their collective afferent fiber inputs without supervision by Hebbian plasticity into selective receptive field shapes. The macrocolumn model is shown to be able to classify input patterns and extract basic features from the input. The network owes it's computational abilities to the properties of the internal macrocolumnar neuron dynamics, which itself is emergent from the columnar interconnection structure, the spiking nature of neurons, and background oscillation.' (Lücke and von der Malsburg, 2004)

Seriès and Tarroux (1999) constructed a cortical column

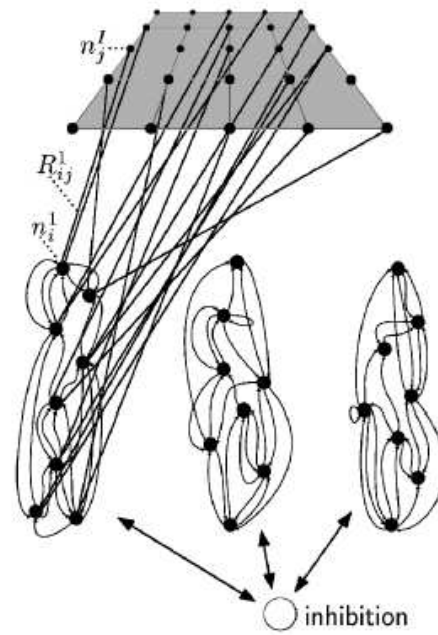


Fig. 3. From Lücke and von der Malsburg (2004): 'Sketch of a macrocolumn with 3 minicolumns connected to an input layer of 25 neurons. The 8 neurons per minicolumn are randomly interconnected; each minicolumnar neuron receives 3 synapses from within its minicolumn. The inhibition is sketched as one inhibitory neuron receiving input from all minicolumns and projecting back to all of them. Each minicolumnar neuron receives 2 synapses from neurons of the input layer. The randomly initialized receptive field of one of the three minicolumns is shown. Lines within the input layer are displayed only for visualization purposes. There are no connections of neurons within the input layer.'

model which proposed a realistic mechanism (consistent with experimental data) accounting for synchrony and delay activity observed in associational cortex. A column was composed of 100 excitatory bistable neurons and 25 fast-spiking inhibitory neurons. The neurons were based on the Hodgkin-Huxley model, with the excitatory neurons possessing an additional sodium current, known to exist in pre-frontal cortical (PFC) neurons, and capable of producing a plateau potential giving rise to bistability. Within a column, excitatory cells contacted about 10% of the other excitatory cells, whereas they contacted between 60-100% of the inhibitory cells. Between column connectivity was much sparser. Transmission delays varied from a few milliseconds within a column, up to 15 ms between columns. The modelling results demonstrated sustained oscillatory activity, both within a column and between columns, following the injection and removal of a spike train input. The variance of an inhibitory controlling parameter was found to affect the oscillation frequency and mean columnar firing rate, and to induce a competition process between columns. They suggest this mechanism could act in PFC as a selective

working memory of a stimulus.

Fransén and Lansner (1998) constructed and simulated a network of model columns also composed of Hodgkin-Huxley model neurons. They chose to model the lamina II/III cells in cortical columns, paying special attention to incorporating biologically realistic asymmetric and dense connectivity between excitatory and inhibitory cells, and sparse connectivity between columns. Accuracy in somatic and dendritic contact was maintained in the multi-compartment neuron models. Their goal was to explore the associative memory characteristics of such a network model. The results demonstrated that columns acting as single units can operate as an associative memory, showing attractor-like behavior. The network demonstrated pattern completion, pattern rivalry, and noise suppression capabilities. The pattern completion process was found to occur in 30-60 ms, comparable to psychophysical reaction time experiments. Later work (Cürüklü and Lansner, 2001) using the same network model proposed that neuron spike and burst synchronization of activities over distances of several millimeters of cortical surface can occur due to the long-range horizontal connections and local connections that exist in layer II/III of minicolumns.

Pinto et al. (2003) describe a biologically-based integrate-and-fire model of a rat whisker barrel, whose important circuit features include: 1) strong thalamocortical input to excitatory and inhibitory cells, 2) reciprocal connectivity between excitatory and inhibitory cells, 3) dominant inhibition, and 4) recurrent connectivity. Results suggest that barrels are cortical dampers (essentially high-pass filters) rather than cortical amplifiers:

A (thalamic) signal with high initial synchrony rapidly engages positive feedback among interconnected excitatory neurons, generating a strong excitatory response; inhibitory cells are driven in a more linear fashion by their thalamic inputs. The nonlinear buildup in the excitatory population is subsequently transferred to the inhibitory neurons that, because inhibitory synapses are strong and long-lasting, quickly dominate network activity, bringing the system back to its resting state. The time delay between the arrival of a thalamic signal in the cortex and the development of network inhibition represents a window of opportunity during which strong excitatory responses can be generated. Low temporal contrast signals, which generate smaller responses, are able to engage excitatory feedback mechanisms only weakly before the window is forced shut by a wave of inhibition. Thus it is the mechanism by

which barrel circuits process arriving signals that render them more sensitive to the initial synchrony of a thalamic input and less sensitive to the input magnitude. (Pinto et al., 2003)

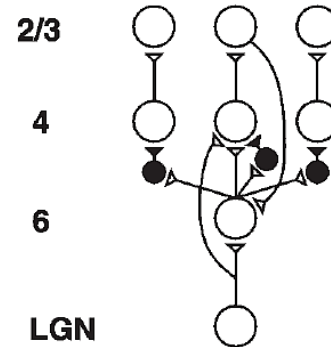


Fig. 4. From Grossberg and Williamson (2001): 'Cortical feedback loop between layers IV, II/III and VI: LGN activates layer VI as well and layer IV. Layer VI cells excite layer IV cells with a narrow on-center and inhibit them using layer IV inhibitory interneurons that span a broader off-surround. Layer IV cells excite layer II/III cells, which send excitatory feedback signals back to layer VI cells via layer V (not shown). Layer II/III can hereby activate the feedforward layer VI-to-IV on-center off-surround network.'

The *laminar computing* models (Grossberg, 2003) propose how the circuitry of the six main layers of cortex help to realize processes of development, learning, perceptual grouping, attention and 3-D vision through a combination of bottom-up, horizontal, and top-down interactions. As such, the columnar organization is just part of these models, and the focus is instead on investigating the functional utility of organizing cortex into layers. In the model, a process called *folded feedback* is predicted to be a mechanism that binds cells in layers II/III, IV, V and VI into functional columns (Grossberg and Williamson, 2001). This is illustrated in Figure 4. Layer II/III signals feed back via connections to layer VI (via layer V, not shown). Layer VI cells activate the on-center off-surround network from layer VI to IV. The feedback signal is 'folded' back into the new feedforward flow entering layer IV, thus reinforcing stronger groupings. The VI-to-IV folded feedback pathway is predicted to 1) maintain contrast sensitivity to bottom-up thalamic inputs, 2) help to select the strongest groupings that initially get formed in layer II/III, 3) receive top-down attentional modulation from other cortical areas, and 4) deliver top-down attentional signals to the thalamus (Grossberg and Williamson, 2001). The LAMINART model of visual processing (Grossberg, 1999) includes this mechanism, along with a considerable amount of inter- and intra-layer circuitry necessary to account for different visual phenomena.

Underlying this model are Adaptive Resonance Theory (ART) principles:

Adaptive Resonance Theory, or ART, proposes a solution of how attention solves the stability-plasticity dilemma by modelling how bottom-up signals activate top-down expectations whose signals are matched against bottom-up data. Both the bottom-up and top-down pathways contain adaptive weights, or long-term memory traces, that may be modified by experience. The learned top-down expectations focus attention upon information that matches them. They select, synchronize, and amplify the activities of cells within the attentional focus, while suppressing the activities of irrelevant cells, which could otherwise be incorporated into previously learned memories and thereby destabilize them. The cell activities which survive such top-down attentional focusing rapidly reactivate bottom-up pathways, thereby generating a type of feedback resonance between bottom-up and top-down signal exchanges. Such resonances rapidly bind distributed information at multiple levels of brain processing into context-sensitive representations of objects and events. These resonances are also proposed to support slower processes of learning; hence the name adaptive resonance. (Grossberg, 1999)

VI. WHAT ROLE DO CORTICAL COLUMNS PLAY IN GOAL-DIRECTED BEHAVIOR?

Koene, Cannon, and Hasselmo (2004), of the Boston University Center for Memory and Brain, incorporated minicolumns based on integrate-and-fire neurons in a model of goal-directed behavior. The minicolumns, modelling prefrontal cortex (PFC), were intended to enable the learning of conditional relationships and task planning in working memory. The simulation, conducted in the Catacomb2 environment (Cannon, Hasselmo, and Koene, 2003), replicated the results of the experimental work of Schultz, Tremblay, and Hollerman (2000), where monkeys were trained to perform goal-directed behavior in response to random visual cues.

PFC subserves the cognitive control capability of coordinating thoughts or actions in relation with internal goals (Koechlin, Ody, and Kouneiher, 2003), although the mechanisms of rule encoding and retrieval are not known. Koene, Cannon, and Hasselmo (2004) hypothesize that 'networks of prefrontal minicolumns encode associated knowledge that is retrieved by a process of converging activity of a forward spread and spread of activity from the goal concept.' They make the following presuppositions in their model:

- Substrate presuppositions:
 - A PFC minicolumn consists of neurons in multiple layers with extensive intracolumnar connectivity and less extensive intercolumnar connectivity.
 - PFC activity is correlated with learning goal-directed behavior.
 - Long-term potentiation (LTP) strengthens connections within and between minicolumns during learning of specific goal-directed routes. However, LTP elicited as spike time dependent plasticity cannot associate spikes at arbitrary intervals, so a short-term buffer based on persistent spiking enables encoding with LTP.
- Mechanistic presuppositions:
 - Rules are learned by associating states and actions represented by individual minicolumns.
 - Spread of activity from the minicolumn representing a goal through the minicolumns of associated concepts gates a forward spread from the current state. This convergence governs goal-directed behavioral responses.
 - One concept may have multiple roles associated with different rules that lead to different behavior, so there are separate sets of neurons for each role in I/O populations of a minicolumn.

Koene, Cannon, and Hasselmo (2004) simulate the task protocol of Schultz, Tremblay, and Hollerman (2000), where cues indicate three possible trials (shown in Figure 5):

- **Srm** - reward is given if monkey performs a movement
- **Srnm** - reward is given if monkey does not perform a movement
- **Surm** - a movement is required, but no reward is given

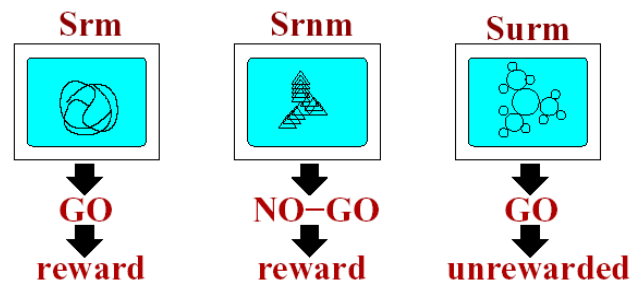


Fig. 5. From Koene, Cannon, and Hasselmo (2004): Visual cues indicating three possible behavioral trials in the Schultz, Tremblay, and Hollerman (2000) task protocol.

These three trials are called 'states' in the model, and minicolumns are mapped to each of these states. Also, mini-

columns are mapped to two possible actions: movement (go), and non-movement (no-go). So, in this PFC model, sensory input states and motor actions are represented by individual cortical minicolumns composed of spiking neurons. Rules are encoded as LTP-driven associations between state-action spike pairs. This is illustrated in Figure 6.

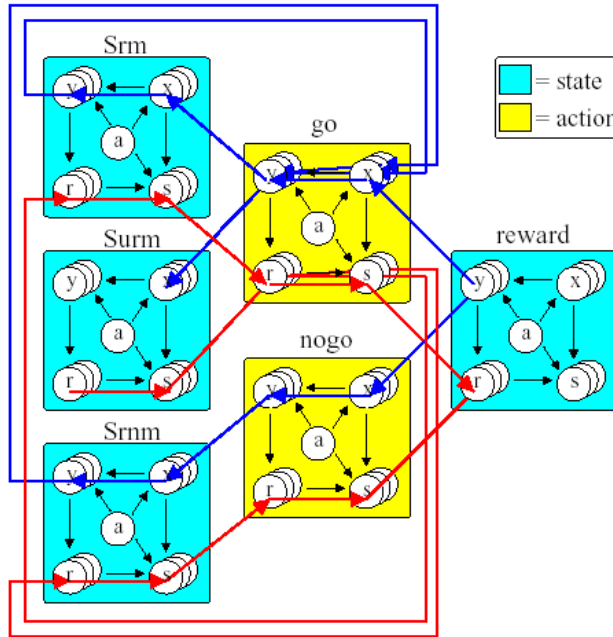


Fig. 6. From Koene, Cannon, and Hasselmo (2004): Forward associations (clockwise loops) and associations from the goal (counter-clockwise loops) between state and action minicolumns that must be learned during training. x , y , r and s are populations of neurons necessary so that an item can fulfill multiple roles as in the case of "go", with its (minicolumn) connections to possible rewarded trials following an unrewarded move trial.

During task performance, a desire for a reward (a 'goal') causes the spread of spiking activity from a goal minicolumn. The current state causes a forward spread of activity along prior LTP-encoded state-action associations. These activities converge when, referring to Figure 6, the goal spread in x and y populations gates the forward spread in s and r populations. Thus, only routes that lead to the goal can propagate activation. Neurons on such routes in the s population of the current state compete, so that only the first to reach threshold spikes. The first spike in the s population of the current state indicates the next goal directed action. (Koene, Cannon, and Hasselmo, 2004)

In summary, 'an associative spread of activity from the goal representation enables retrieval of a learned sequence of states and actions, so that a goal-directed action is selected for the current state. Encoding and retrieval take place in distinct phases of network oscillations. The model corresponds to a

biological implementation of reinforcement learning.' (Koene and Hasselmo, 2004)

VII. DISCUSSION

In this paper, an overview of the body of knowledge gathered on cortical columns and their functionality, as well as a sampling of columnar models, has been provided. What generalizations can be made in order to begin to propose a role for columns in models of serial plan formulation, choice and learning? It seems that a great deal more experimental work is necessary, particularly in frontal and associational cortex, before the characteristics of minicolumns, macrocolumns, and columnar networks, becomes clear. Columns have been proposed to be both amplifiers and bandpass filters of thalamic input, feature selectors, maintainers of contrast sensitivity, decision units, and a form of short-term working memory. Networks of columns have been shown to act as an associative memory, where columns behave as single units, where the network exhibits attractor behavior. Whereas other columnar network models behave like a state machine, and where subpopulations of neurons within a column play distinct and critical roles.

Now with these ideas in mind, the TELOS model will be briefly considered, proposing where columnar functions could enhance the models of frontal circuits in this model. The TELOS model (Brown, Bullock, and Grossberg, 2004) proposes to explain how laminar circuitry of the frontal cortex, exemplified by the frontal eye fields (FEF), interacts with the basal ganglia (BG), thalamus, superior colliculus, and inferotemporal and parietal cortices to learn and perform reactive and planned eye movements.

Figure 7 illustrates the elements of the models, composed of multiple interacting brain regions. An FEF region input layer takes input from visual cortex regions. FEF layer III/Va cell activities model 'plans', that is, representations of potential motor responses to input signals. FEF layer Vb and VI cells act in concert with the thalamus and BG to gate plan execution. FEF output activates posterior parietal cortex (PPC), subthalamic nucleus, and the superior colliculus. The FEF also has cells which delete plan activity. It is clear that this architecture takes a laminar approach, and it is difficult to decide where to fit a columnar organization. One observation is that this FEF model is broken into retinotopically organized zones gated by an associated BG channel. Perhaps this corresponds to a macrocolumn. If so, then the question

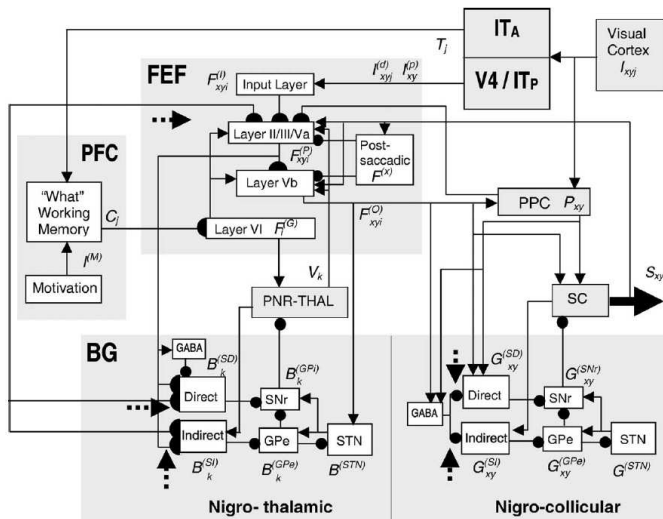


Fig. 7. From Brown, Bullock, and Grossberg (2004): TELOS, a laminar model of basal ganglia interactions with the frontal eye fields and the superior colliculus.

arises as to what sort of interaction takes place within the macrocolumn between the minicolumns. If the FEF were to be organized into macrocolumns, then another question is how to model the interaction with the 'what' working memory of prefrontal cortex. Perhaps the arousal signal from PFC to FEF is a complex dynamic that unfolds over time. Within a macrocolumn or set of macrocolumns, whichever composes a gateable control zone, the dynamics occurring between the excitatory and inhibitory cells is another aspect that could be modelled. Another columnar mechanism that could be incorporated into the FEF model is the state machine-like mechanism seen in the model of goal directed behavior. Perhaps a starting point is to model the TELOS model of a canonical plan-execute episode in this manner.

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