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Computations in the deep vs superficial layers of the cerebral cortex

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A B S T R A C T

A fundamental question is how the cerebral neocortex operates functionally, computationally. The cerebral neocortex with its superficial and deep layers and highly developed recurrent collateral systems that provide a basis for memory-related processing might perform somewhat different computations in the superficial and deep layers. Here we take into account the quantitative connectivity within and between laminae. Using integrate-and-fire neuronal network simulations that incorporate this connectivity, we first show that attractor networks implemented in the deep layers that are activated by the superficial layers could be partly independent in that the deep layers might have a different time course, which might because of adaptation be more transient and useful for outputs from the neocortex. In contrast the superficial layers could implement more prolonged firing, useful for slow learning and for short-term memory. Second, we show that a different type of computation could in principle be performed in the superficial and deep layers, by showing that the superficial layers could operate as a discrete attractor network useful for categorisation and feeding information forward up a cortical hierarchy, whereas the deep layers could operate as a continuous attractor network useful for providing a spatially and temporally smooth output to output systems in the brain. A key advance is that we draw attention to the functions of the recurrent collateral connections between cortical pyramidal cells, often omitted in canonical models of the neocortex, and address principles of operation of the neocortex by which the superficial and deep layers might be specialized for different types of attractor-related memory functions implemented by the recurrent collaterals.

1. Introduction

1.1. Conceptual introduction

A key architectural feature of the cerebral neocortex is the presence of short-range recurrent collateral excitatory connections between pyramidal cells (Harris & Shepherd, 2015; Lefort, Tomm, Floyd Sarria, & Petersen, 2009; Rolls, 2016). With their associatively modifiable synapses, there is considerable evidence that this recurrent collateral connectivity implements autoassociation or attractor networks that are fundamental in learning and memory (Rolls, 2016). The maintenance of activity in the local recurrent networks provides the basis for short-term memory, and planning (Goldman-Rakic, 1996; Rolls, 2016). The autoassociation aspect of the local connectivity provides for long-term memory, in which the whole of a memory can be recalled from one part (Rolls, 2016). Competition between the representations in cortical attractor networks provides the basis for decision-making, and for maintaining the neuronal activity in the winner to guide the implementation of the decision (Deco, Rolls, Albantakis, & Romo, 2013; Rolls, 2016; Rolls & Deco, 2010).

However, the superficial and deep pyramidal cell layers of the cerebral neocortex have somewhat different sets of recurrent collateral connections (Harris & Shepherd, 2015; Lefort et al., 2009; Rolls, 2016). A key issue that therefore arises in understanding the operation of the neocortex, in for example learning and memory, is whether the deep layers (especially layer 5) perform somewhat different computations to the superficial layers (2 and 3). The aim of this paper is to consider some of the different types of computation that may be performed in the superficial and deep layers in the light of their anatomy and physiology; and then to explore the implications of these issues using simulations of the operation of the attractor networks in the superficial and deep layers of the neocortex. The aim here is to formulate and then to explore some concepts about how the different connectivity of the superficial and deep layers may contribute to the major issue of how the cerebral neocortex computes, and how its computations contribute to learning and memory.

The issues that are explored here are whether different attractor dynamics implement somewhat different computation in the time

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domain (e.g. longer in the superficial layers to promote slow learning useful for learning transform-invariant representations of objects (Rolls, 2016, 2012b; Wiskott & Sejnowski, 2002) vs more temporally precise and limited for the deep layers to support precise motor function); and in the spatial domain with for example more continuous spatial representations in the deep layers which may be useful for smooth motor outputs from the neocortex. Further, if the deep layers operated more as a continuous attractor network, this could facilitate smooth transitions between outputs that would be useful especially in low-dimensional motor spaces; could facilitate the feedback of a more general rather than very discrete signal for top-down attention and recall to previous cortical areas; and might be quite stable even with stochastically spiking integrate-and-fire neurons.

1.2. Cortical connectivity, and recurrent collateral connections within the superficial and deep layers

1.2.1. Partially separate attractor networks in the superficial and deep layers of the cerebral cortex?

Both the superficial and the deep layers of the cerebral cortex have a highly developed excitatory recurrent collateral system, with thousands of synapses on the dendrites of each neuron for the recurrent collaterals from nearby neurons (Harris & Shepherd, 2015; Lefort et al., 2009; Rolls, 2016) (see Fig. 1). Evidence that these recurrent collaterals can support attractor states that help to implement short-term memory, long-term memory, and decision-making has been described (Rolls, 2016).

A fundamental question is why there are somewhat separate superficial and deep layers of the cerebral cortex. The advantages include the different outputs that may be appropriate for sending to the next stage of the cortical hierarchy to build higher level representations (with their origin in the superficial layer 2 and 3 pyramidal cells), whereas the deep layer pyramidal cells in layer 5 may provide an output more suitable for driving the often motor-related target systems such as the striatum and in the case of V1 the superior colliculus (Rolls, 2016). For example, the representations in the superficial pyramidal cells (L2/L3) may be more sparse than the deep pyramidal cells (L5/L6) (Harris & Shepherd, 2015), and Rolls (2016) hypothesizes that this helps the neocortex to increase the memory capacity of what can be stored in discrete autoassociation networks in the superficial layers. The superficial cortical layers are hypothesized to perform the main computationally useful functions of the cerebral neocortex, which involve feedforward operations to form non-linear combinations of the inputs from previous cortical areas utilizing the convergence from stage to construct useful combinations essential for cortical computation, and to implement using the attractor properties of the recurrent collaterals useful functions such as information storage and retrieval (long-term memory, short-term memory, decision-making, etc.). According to the hypotheses being developed, these feedforward competitive learning computations performed by the superficial layers are the computationally useful aspects of the design of the neocortex for building new representations (Rolls, 2016).

The L5A pyramidal cells have a well-developed recurrent collateral system, and the hypothesis has been proposed that the deep layers may operate as a partly separate attractor from that in the superficial layers, for the L2/L3 pyramidal cell dendrites do not descend into the deep layers of the cerebral cortex in which the deep layer neuron recurrent collaterals make their main local connections with nearby layer 5 pyramidal cells (Rolls, 2016) (Fig. 1).

1.2.2. The connectivity of the superficial and deep layers of the neocortex

Quantitative evidence is now becoming available on the distribution of cortical connections within and between cortical laminae (Hooks et al., 2011; Holmgren, Harkany, Svennenfors, & Zilberter, 2003; Lefort et al., 2009). Some of the evidence is shown in Fig. 2, obtained by multiple simultaneous single neuron recording in the mouse whisker barrel cortex (Lefort et al., 2009). Fig. 2a shows that there is a relatively high probability of a connection between pyramidal neurons in layer 3 (0.19), and between neurons in layer 5A (0.19), and that this is higher than the connection probability from L3 neurons to L5A neurons (0.06). Fig. 2b estimates the overall strength of the synaptic effects from neurons in one layer (the columns) to neurons in another layer (the rows), by weighting the probability of synaptic connections between pyramidal cells in different laminae by the strength of the synaptic connections between neurons in the different laminae, based on data from Lefort et al. (2009). The quantitative aspects of this connectivity are

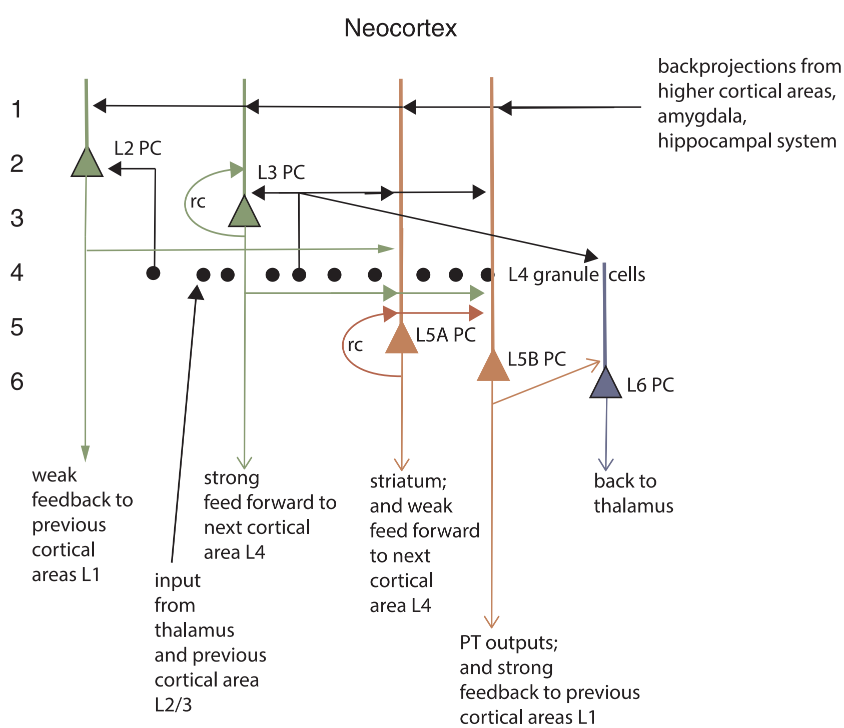

Fig. 1. Functional canonical microcircuit of the neocortex (see text). Recurrent collateral connections (rc) are shown as a loop back to a particular population of cells, of which just one neuron is shown. The dendrites are shown as thick lines above the cell bodies. It should be noted that the dendrites of the superficial (L2 and L3) pyramidal cells do not descend into the deep layers (L5, L6) of the neocortex. In primates the cortico-cortical feedforward projection neurons are concentrated in L3; and the main cortico-cortical feedback projection neurons are in Lower L5 (L5B), and there is weak cortico-cortical feedback from some L2 neurons. Some L6 cortico-thalamic neurons send a projection to L4. Further information is provided in the text and by Rolls (2016).