



Review

Inter- and intra-laminar connections of pyramidal cells in the neocortex

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Abstract

The flow of excitation through cortical columns has long since been predicted by studying the axonal projection patterns of excitatory neurones situated within different laminae. In grossly simplified terms and assuming random connectivity, such studies predict that input from the thalamus terminates primarily in layer 4, is relayed ‘forward’ to layer 3, then to layers 5 and 6 from where the modified signal may exit the cortex. Projection patterns also indicate ‘back’ projections from layer 5 to 3 and layer 6 to 4. More recently it has become clear that the interconnections between these layers are not random; forward projections primarily contact specific pyramidal subclasses and intracortical back projections innervate interneurons. This indicates that presynaptic axons or postsynaptic dendrites are capable of selecting their synaptic partners and that this selectivity is layer dependent.

For the past decade, we and others have studied pyramidal cell targeting in circuits both within, and between laminae using paired intracellular recordings with biocytin filling and have begun to identify further levels of selectivity through the preferential targeting of electrophysiologically and/or morphologically distinct pyramidal subtypes. Presented here, therefore, is a brief overview of current thinking on the layer and subclass specific connectivity of neocortical principle excitatory cells.

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Keywords: Neocortex; Pyramidal cell; Axon; Selective innervation; Synapse; Microcircuitry; Excitatory pathways; Paired recording

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1. Introduction

Increasingly sophisticated anatomical, electrophysiological and theoretical techniques have been employed over recent decades to unpick and attempt to understand the intricacies of neuronal interconnections in the mammalian neocortex. Each technological advance has uncovered ever expanding levels of complexity such that the identification of specific ‘rules’ of connectivity presents a bewildering task. First were the Golgi studies used to visualise the dendritic and axonal arbourisation patterns of neurones, unveiling exquisite spatial distribution of their processes and leading to the morphological classification of many neuronal subclasses (Ramón and Cajal, 1911; Lund, 1973). Later, retrograde and anterograde tracers were used to establish which areas project to which and the data generated has led to the identification of cortical ‘feedforward’ and ‘feedback’ pathways thought to indicate the direction of information passage through the cortex (Lund et al., 1975; Rockland and Pandya, 1979) (see Fig. 1). As a result of such studies, it is now apparent that (in simplified terms) the major afferent input to the primary sensory cortices originates from the thalamus and that these primary afferents terminate mostly in layer 4 and to a lesser degree in layer 6. Further studies have led to the proposition that information then progresses within vertically oriented functional processing units termed ‘cortical columns’ (for review see Rockland, 1998) from layer 4 to layers 2/3, from 3 to 5 and from 5 to 6 (Gilbert, 1993). The deeper layers are then proposed to project elsewhere in the cortex via lateral projections or to subcortical regions, relaying information that has been both temporally and spatially modulated by disynaptic inhibition en route (Porter et al., 2001).

However, the modulation and delivery of the cortical code requires the orchestrated activity of many hundreds of neurones spanning all six layers of the cortex and each layer contains a very wide range of cellular subtypes whose individual attributes must have a great influence on the properties of cortical outputs. So precisely which cells are contacting which, and what is the nature of those synaptic connections? Anatomical demonstration of the location of axonal profiles cannot alone accurately reveal which cells are involved in the flow of the cortical code as the dendritic arbours of neurones often span several layers. In other words, axons terminating in layer 2, say, may not necessarily be exclusively contacting layer 2 cells, they have access to the dendritic trees of a great many cells whose dendrites extend into that layer. The use of multiple-field potential recordings has attempted to address these issues by more precisely locating the responses to the activity elicited in identified presynaptic neurones (Bode-Greuel et al., 1987). However, even these combined with anatomical studies can reveal nothing of the electrophysiological subclasses that comprise the postsynaptic, e.g. layer 2 cells that might otherwise appear similar, and nothing of the nature of those connections.

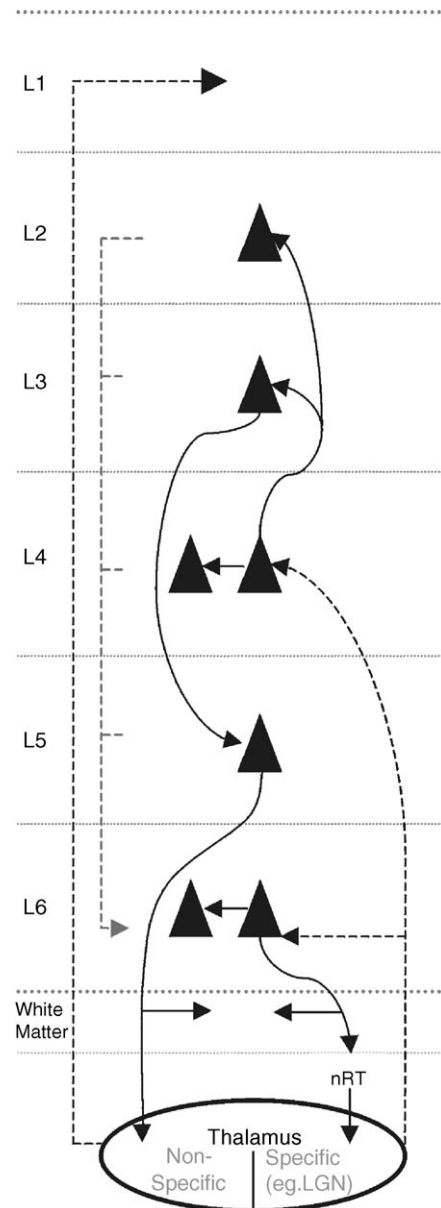


Fig. 1. Excitatory feedforward pathways as derived from anatomical evidence of axonal projection patterns. In this highly over-simplified wiring diagram of a cortical column in the rat primary visual cortex, the cortical information is proposed to enter at layer 4 (and layer 6), progress to layers 3 and 2 then to layers 5 and 6 before exiting the cortex to activate sub cortical regions or reenter and activate other areas of the cortex. Layer 6 does not receive any particularly focussed inputs from any layer, instead it receives weak input from all laminae.

We have used arguably the most labour intensive, but perhaps also the most accurate methods of paired intracellular recordings, biocytin filling, visualisation and axo-dendritic reconstruction of synaptically connected pairs of excitatory neurones to correlate their anatomy and electrophysiological properties. This and related work has allowed the identification of subclasses of excitatory neurones within the general population of each layer, the detection of specific excitatory to excitatory connections

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