Number of Neurons and Synapses in Primary Visual Cortex

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1. Introduction

Of all cortical areas, primary visual cortex has been the one to attract the overwhelming attention of neurophysiologists, largely because the stimuli necessary to activate it can be readily offered to an animal in a reproducible fashion to evoke well-defined responses from the constituent neurons. This activity on the part of neurophysiologists has induced neuroanatomists, and more recently neurophysiologists themselves, to examine the neurons present in visual cortex in attempts to ascertain how the various neuronal types are synaptically related to each other and to the extrinsic inputs that impinge upon them. In addition, visual cortex, and in particular area 17 of the rat, has been a favorite object for those interested in the neurotransmitters used by various neuronal types, while in cat visual cortex others have tried to determine how different transmitters affect the response properties of neurons. Much of these data have been presented in Volume 2 of this series.

This concentration of attention on visual cortex has also provided the stimulus for a somewhat milder effort to attempt to analyze its neuronal composition, to determine how many neurons are available for processing the information received by the cortex, what proportions of pyramidal and nonpyramidal cells

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are present, and how many synapses are involved. The purpose of the present chapter is to summarize and examine the results of the numerical analyses of area 17, some of which have been reviewed previously by Colonnier and O’Kusky (1981).

2. Concentration of Neurons

2.1. Monkey

The most recent analysis of the composition of macaque visual cortex is that of O’Kusky and Colonnier (1982). They used material from adult monkeys that had been fixed by perfusion, after which the tissue was osmicated and embedded in plastic. The counts of neurons were made from semithin sections. Neuronal nuclei were used as the test objects and account was taken of the shrinkage that occurred during tissue processing. As shown in Table I, O’Kusky and Colonnier (1982) estimated that in area 17 of both Macaca mulatta and M. fascicularis there are about 120,000 neurons per mm$^3$ of tissue and about 200,000 neurons beneath 1 mm$^2$ of cortical surface, 28% of which are in layers I–III, 45% in layer IV, and 27% in layers V–VI.

In another study, Rockel et al. (1980) used a different approach, and counted the number of neurons contained in a 30-μm-wide strip of cortex in a 25-μm-thick paraffin section passing through the depth of the cortex. This was part of a comparative study of the numbers of neurons in different cortical areas of a variety of species, and the brains, except for the human ones, were fixed by perfusion with 10% formalin. Blocks were further fixed in 70% alcohol and 2% acetic acid before being embedded in paraffin. In those preparations from visual cortex of the macaque, Rockel et al. (1980) estimated there are 267.9 ± 13.7 neurons contained in a 30 x 25-μm strip. From this it can be calculated, as shown in Table I, that there are some 357,000 neurons beneath 1 mm$^2$ of cortical surface. This is higher than the figure calculated by O’Kusky and Colonnier (1982), but Rockel et al. (1980) did not take into account the shrinkage produced by tissue processing, although they estimated the linear shrinkage to be 18%. Powell and Hendrickson (1981) have subsequently taken this shrinkage into account, and determined that corrections for shrinkage lead to an estimated 218 neurons in a column of macaque area 17 measuring 30 x 30 μm. This would give a figure of 240,000 neurons beneath 1 mm$^2$ of cortical surface. By comparison, in frozen sections of macaque visual cortex in which they believe no shrinkage to occur, Powell and Hendrickson (1981) find 175 neurons in a 30 x 30-μm strip, equivalent to 194,000 neurons beneath 1 mm$^2$ of cortical surface. As can be seen in Table I, these values are compatible with those of O’Kusky and Colonnier (1982).

Chow et al. (1950) have also calculated the numerical density of neurons in macaque area 17, using the brains of two immature specimens fixed in 10% formalin and embedded in nitrocellulose. They estimated the number of neurons per 0.0005 mm$^3$ of area 17 to be 79. This gives 160,000 neurons/mm$^3$.

Other data on macaque area 17 come from the comparative study of Cragg (1967), who determined the densities of neurons in the visual and motor areas