ON THE NATURE OF INTRANUCLEAR RODS

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INTRODUCTION

Siegesmund, Dutta, and Fox (1) have recently demonstrated, in an electron microscope study, that the intranuclear rods described by Ramon y Cajal (2) correspond to a compact bundle of fine fibrils. These rods and corresponding fibrils are found only in some nerve cells and in some species. Although Cajal refers to these structures as Roncoroni's rodlets, Siegesmund, Dutta, and Fox point out that Roncoroni (3) described them in a wide number of cells and in a great variety of species in which Cajal was unable to demonstrate them and in which the fibrils are not found. They suggest that the Roncoroni rodlets may be folds of nuclear membrane. This may seem surprising since Roncoroni described the rods as sometimes passing from one pole of the nucleus to the other, and in some cases as bipartite and tripartite. Such extensive nuclear folds have not been described by electron microscopists in neurons where Roncoroni rodlets can be demonstrated, for example in the pyramidal cells of gyrencephalic cortices. In the course of a study on the compara-

tive ultrastructure of cells in the cat cerebral cortex, it was possible to confirm the interpretation of Siegesmund, Dutta and Fox.

MATERIAL AND METHODS

The material studied was cat visual cortex fixed by perfusion with glutaraldehyde (4). Small blocks from this material were then washed in buffered sucrose, immersed in osmium tetroxide, counterstained with phosphotungstic acid, and embedded in Araldite. The cut sections were further stained with lead citrate (5).

RESULTS

The slightly curved or spiral-shaped intranuclear rods in neurons are evident in thick (0.5 μ) sections under phase-contrast microscopy and closely correspond to Roncoroni's description (Fig. 2; Fig. 6, inset; Fig. 9, inset). They are present in a very large number of nuclei and are attached to the nuclear membrane or lie free within the nucleoplasm. Some are relatively small; others course right through the nucleus; *i.e.*, diametrically from nuclear membrane to nuclear membrane. They are single, double, bipartite, or tripartite. Some assume outlandish forms of intriguing complexity (Fig. 6, inset). These rods may come very close to the nucleolus, seem to end upon it (Fig. 9, inset) or bypass it completely (Fig. 2, cell *a*).

In low-power electron micrographs dark bands are seen coursing through the nucleus in a curved (Figs. 3 and 4) or spiral (Fig. 8) manner. These dark bands are tongues of cytoplasm deeply invaginating the nucleus. They sometimes extend from one pole of the nucleus to the other (Fig. 4). Some are double (Fig. 1); others branch into many parts (Fig. 6). A few can be seen to come into intimate contact with the nucleolus (Figs. 7 and 9). The dark appearance of the invaginations is due to an extremely dense packing of ribosomes in this region (Fig. 5).

The number of pores per unit length of nuclear membrane seems to be greater within the invaginations than around the rest of the membrane (Figs. 5, 6, 9), although quantitative data would be necessary to prove this point.

Transverse sections through the invaginations reveal that at least some of them are in the form of tubes rather than sheets (Fig. 5).

DISCUSSION

The morphology of the cytoplasmic invaginations within the nuclei of neurons corresponds to Roncoroni's description of the nuclear rods and confirms Siegesmund, Dutta, and Fox's suggestion as to the nature of these rods.

It has been suggested (6) that nuclear indentations permit greater nucleocytoplasmic interactions by increasing the nuclear membrane surface. The presence of a large number of ribosomes within the indentations is consistent with the hypothesis that RNA particles from the nucleus are being liberated into the cytoplasm at this site.

The work of several recent authors (7, 8) implicates the nucleolus in the synthesis of ribosomal RNA. If such a mechanism is present in neurons, the close relations between the cytoplasmic invaginations and the nucleoli would permit a direct interaction between them.

Although finger-like indentations have been described in other cell types, as in Ehrlich's ascites tumor cells (9), extensive invaginations such as those described here have not been shown in electron micrographs of the normal cerebral cortex. They were very numerous and constant in the glutaraldehyde-perfused material used in this study. Most previous observations and reports on these neurons are from osmium tetroxide–immersed material. Perhaps osmium tetroxide immersion does not permit a wide enough sampling of complete cell bodies to see these invaginations (especially to see them reaching the nucleolus), or else the time of penetration of the fixative into the block is so slow that it allows a rounding of the cell nucleus as an early postmortem change. This would be expected as one of the very first changes if, as it seems, the invaginations are related to RNA and protein synthesis.

SUMMARY

Examination of glutaraldehyde-perfused cerebral cortex has revealed, in neurons, deep cytoplasmic invaginations within the nucleus, some of which come into direct contact with the nucleolus. These correspond to the intranuclear rods as described by Roncoroni and are probably related to nucleo- and/or nucleolocytoplasmic interactions.

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FIGURE 1 Neuron of cat visual cortex with two cytoplasmic processes (*CI*) invaginated within the nucleus (*N*). *CYT*, cytoplasm. × 5500.

FIGURE 2 Phase-contrast photomicrograph of two neurons (*a* and *b*) showing nuclear rods (*NR*). × 1500.

FIGURE 3 Neuron of cat visual cortex with a dark, slightly curved cytoplasmic process (*CI*) invaginated within the nucleus (*N*). *CYT*, cytoplasm. × 8000.

FIGURE 4 Neuron of cat visual cortex with a dark cytoplasmic process (*CI*) extending right through the nucleus (*N*). *CYT*, cytoplasm. × 8000.

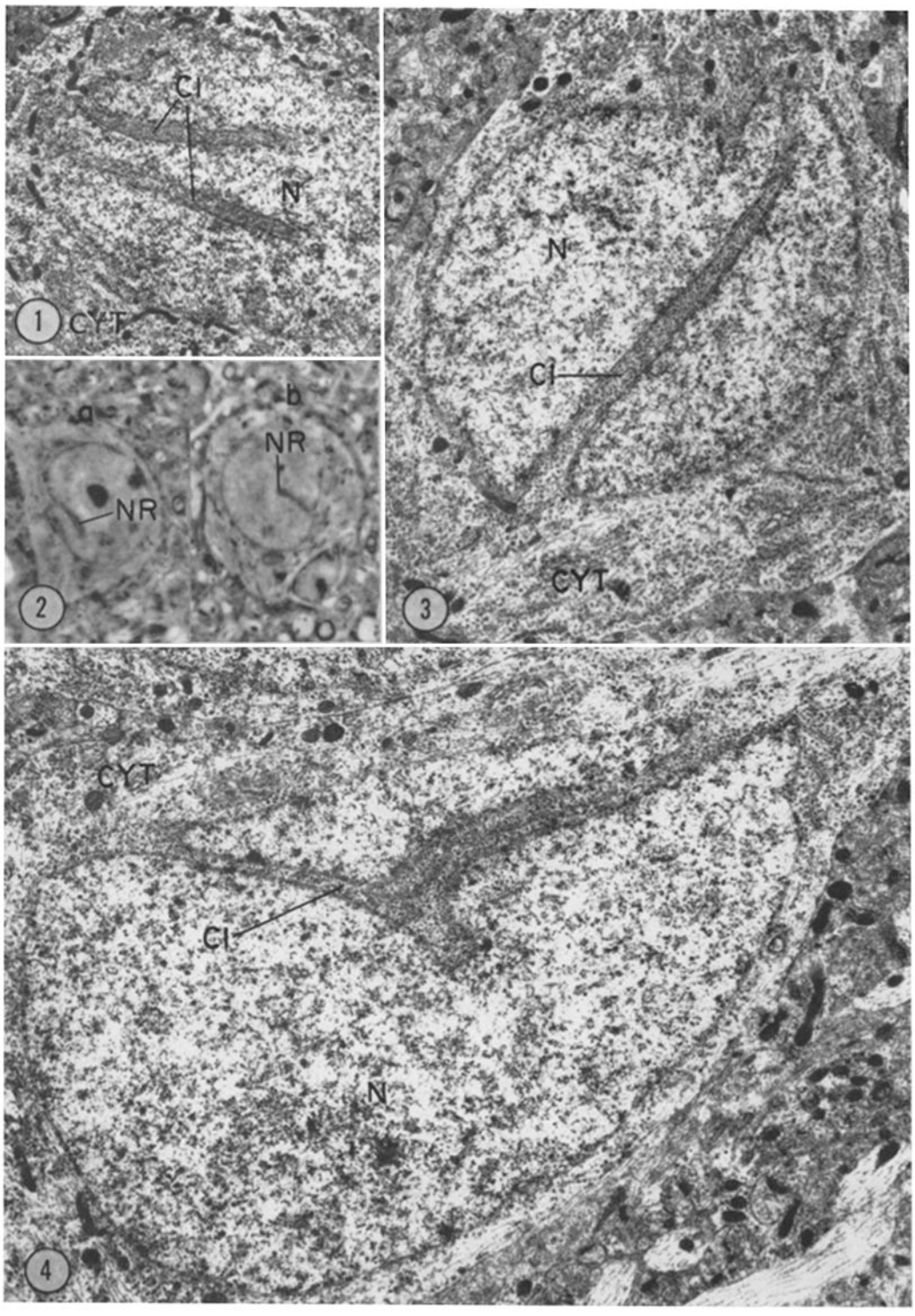

FIGURE 5 Cross-section through a cytoplasmic invagination (*CI*) in the nucleus (*N*). *CYT*, cytoplasm; *NL*, nucleolus; *r*, ribosomes. Arrows point to nuclear pores. × 16,000.

FIGURE 6 Complex cytoplasmic invagination (*CI*) within the nucleus (*N*). *CYT*, cytoplasm. Arrows point to nuclear pores. Inset: Phase-contrast photomicrograph of complex nuclear rod (*NR*). × 22,000; inset, × 1500.

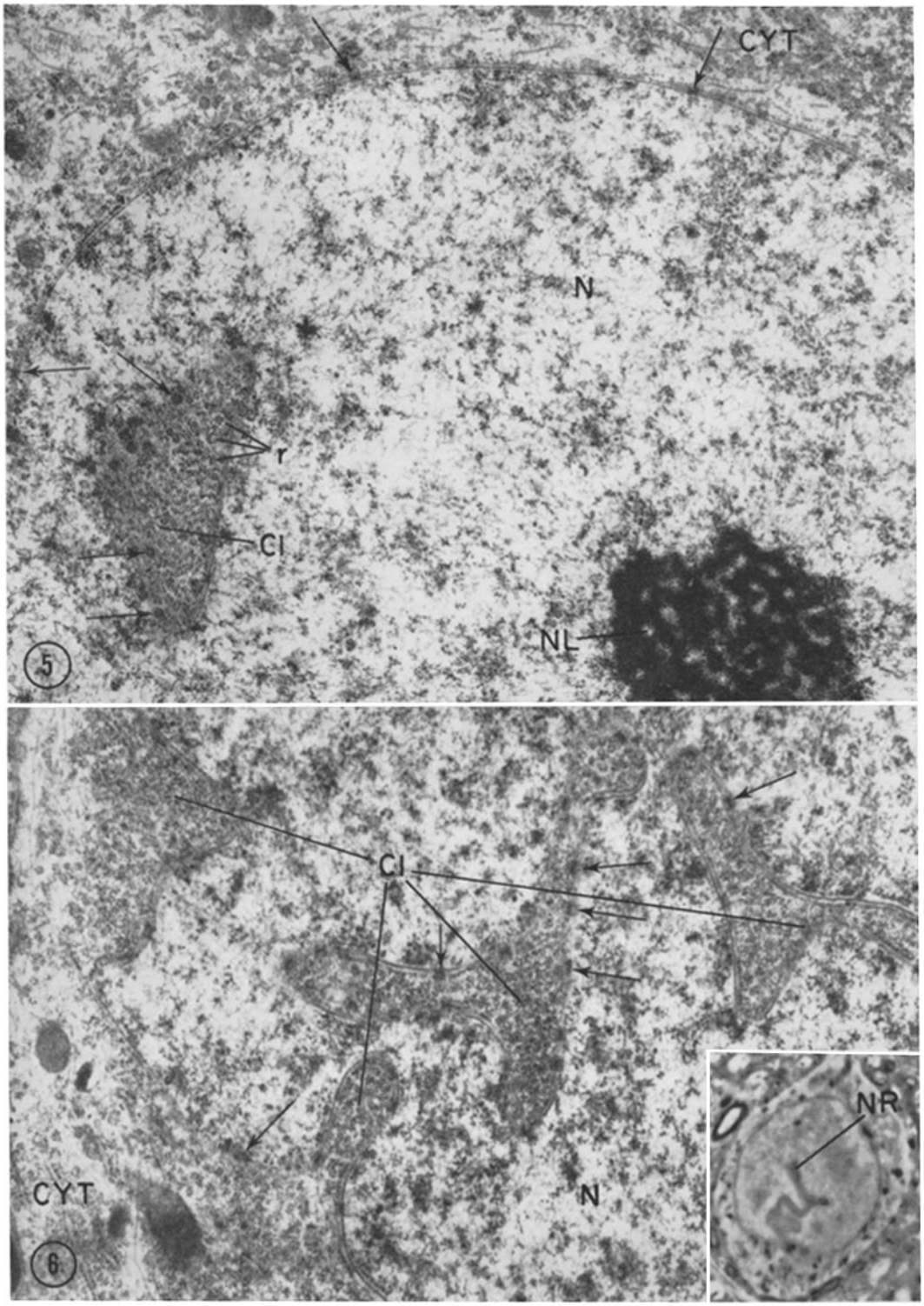

FIGURE 7 Cytoplasmic process (*CI*) within the nucleus (*N*) coming into contact with the nucleolus (*NL*). × 20,000.

FIGURE 8 Neuron of cat visual cortex with a spiral-shaped invagination (*CI*) within the nucleus (*N*). × 14,000.

FIGURE 9 Cytoplasmic process (*CI*) within the nucleus (*N*) coming into contact with the nucleolus (*NL*). *CYT*, cytoplasm. Arrows point to nuclear pores. Inset: Phase-contrast photomicrograph of nuclear rod (*NR*) touching nucleolus. × 21,000; inset, × 1,500.