NEURONAL TREPHOCYTES

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There are, empirically speaking, 3 major, functionally differentiated types of neuronal trephocytes, or cells which play a significant part in the nutrition of nerve cells. The proposed types of neuronal trephocytes are Schwann's cells, which form the neurilemma of medullated fibers and the mantle, or perineuronal cells, of the capsule enveloping the cyton of spinal ganglionic neurons; the satellite cells, which are tangent to or lie near the cytons of large nerve cells in the central nervous system; and the granule cells, which form a layer characteristic of the folia in the cerebellum in various animals and man.

The interchangeable or synonomous use of such terms as neuroglia, glia, and neurogliocyte or gliocyte, is exasperating but, apparently, unavoidable. The terms neuroglia and, more recently, glia had the connotation of a tissue or plexus of neuroglial cells (as proposed by Virchow (147)); the suffix "-cyte", as in gliacyte, or gliocyte, is used to direct attention to the individual cell (140, 414).

Neurons are highly specialized cells which have lost the ability to reproduce themselves and, like certain intestinal columnar epithelial cells that seldom or never undergo mitosis, these cells have a rather high functional activity which they alone are unable to sustain.

There are several types of neuronal trephocytes. The neuroglial trephocytes, or satellite cells, are associated with the large neurons, such as the stellate nerve cells. Trephocytes of ganglionic neurons are modified neurilemma, or Schwann, cells and by prolongation of the neurilemma sheath form a capsule enveloping the body of ganglionic cells, such as those in spinal ganglia. The cells forming the neurilemma capsule present the appearance of a syncytium (414) and are individually designated mantle cells. It is also possible that granule cells in the cerebellum and cells other than neurogliocytes or lymphocytes, may serve as trephocytes for nerve cells.

Some, if not all, neurogliocytes, or gliocytes, are not only trephocytes for neurons in the brain and spinal cord, but also have the important function of binding the components of the central nervous tissue together. It appears that all of the neurogliocytes, except the microgliocytes, are derived from the ectoderm, as are the neurons (58). The fact the neurogliocytes may function as trephocytes of neurons does not preclude these recipient cells from obtaining nutritive material from the tissue fluid as other cells commonly do. Since it has been shown that

the cerebral cortex has intercellular substances, "Nissl's cerebral gray matter", which has physical and physiological characteristics of those found in plasma proteins, the conclusion is deduced that these substances function in supplying the osmotic and part of the nutritional needs of the nerve cells (570).

By use of the electron microscope, Hartman (246) shows that in rats the nuclear membrane of both normal motor cells and of those having had the axons severed is a wide band "made up of submicroscopic granules" instead of having a "system of regularly arranged pores". Hartman (246) also found that sectioning the axon of a motor neuron was followed by an increase in the number of normal mitochondria. This increase appears to indicate an increase in RNA in conjunction with the regeneration of the severed nerve fibers.

Perivascular infiltration of small lymphocytes and plasmacytes occurs in the brain in certain inflammatory conditions of the central nervous system of man, including polio-encephalitis and epidemic encephalitis (encephalitis lethargica) (625). Lymphocytes and plasmacytes which form perivascular infiltrations may serve as trephocytes in a manner similar to that in other organs with the exception that the lymphocytes and plasmacytes are further removed from the source and that the intercellular substance plays, therefore, a greater part than the localized, immediate contacts occurring in many other sites of inflammation, such as in Aschoff nodules of the heart.

Schwann Cells

The capsule of spinal ganglionic neuron bodies is continuous with the neurilemma of the cell. Since the trephocytes of the capsule and Schwann's cells forming the neurilemma have a common origin in the embryonic neural crest (534), these relations lend significance to the Schwann cells as trephocytes. The cells which form, and probably gave rise to, the neurilemma, or sheath of Schwann (562), are generally conceded to have essential, nutritive relations with both myelinated and unmyelinated peripheral nerve fibers (239, 448, 562). Ortiz-Picón (418) suggests that the Schwann cells may "represent the neuroglia of the nerves"; Speidel, 1950, holds that "there is a reciprocal nutritive relationship between the sheath cell and nerve fiber", each exerting a significant trophic influence on the other (448). Schwann and endoneurial cells probably supply most of the nucleic acid for peripheral nerves in mammals (491). Three to 24 canals in a single Schwann cell, which are known as incisures of Schmidt-Lantermann, through which sheet-like protoplasmic processes of the Schwann cell penetrate the myelin sheath and reach the axon (289, 562) are commonly recognized. These protoplasmic processes, although they do not appear in every sheath cell, apparently aid the Schwann cells in supplying the axon with nucleic acid components, adenosinetriphosphate, and other indispensable substances for its maintenance. However, Schwann cells

are not totipotent, for it has been shown that the nucleus is the trophic unit and "regenerative center of the cell", as is shown by the fact that when a process is cut in two, the distal portion dies, while regeneration proceeds from the nuclear end of the transected process (562).

Electron microscopic studies of bull frog sympathetic nerves revealed a striking array of vesicles or globules in the cytoplasm of Schwann cells. These vesicles closely resembled those in capillary cells of mice, had an average diameter of 510 Å, were most numerous at the convex surface of the Schwann cells and are supposed to function in mediating exchange of materials (134). De Robertis and Bennett (134) think that the 'circles' and 'holes in the neurilemma as it inflects at the node', which were described by Hess and Lansing in 1953, probably were the vesicles in Schwann cells which they (134) describe in frogs. These vesicles and the actual contact with the axon at the nodes of Ranvier afford effective means for direct, trephocytic relations of Schwann cells with the nerve fiber, particularly with the axon. A plausible support for the idea that there is a nutritional relation between the Schwann cell and the neurofibrillae is indicated by the contacts of these cells with the axon, which in turn is in intimate contact with the cytoplasm of the nerve cell body. Several investigators have verified the fact that there is peripherad movement of material within the axon and from without into the axon (448). Parker, 1929, holds that neurofibrils are especially concerned with metabolism of the more distant parts of the cell and thus implies that nerve fibrils are actually trophic elements (289).

Del Rio-Hortega, 1922 to 1928, postulated that Schwann cells in their relations to nerve fibers are homologous with certain oligodendroglial, or oligoglial, cells which envelop nerve cells in the white matter of the central nervous system (418). Ortiz-Picón in 1932 (and later the works of other investigators) supports Rio-Hortega's contention and also established that "the reality of the existence of a ganglionar neuroglia is beyond doubt". Thus, Schwann cells and ganglionic gliocytes (subcapsular trephocytes) fundamentally represent "peripheral glia" and form a part of the true neuroglia (418).

The presence of Schwann cells appears to be essential for the regeneration of severed axons (239) although regeneration in the axon precedes that in the sheath (49); that is, the tip of the bare, regenerating axon projects much beyond the distal boundary of the sheath. Ham (239) states that regeneration of axons does not occur if the Schwann cells are deficient, and is limited to the proximal part of the transected axon (562).

Perineuronal Satellite Cells

Two types of glial cells are recognized on the basis of Golgi preparations: the ependymal cells and the astrocytes, or gliocytes (289). The ependymal cells,

although they extend from the central canal through the cord to the pia mater (289, 438), apparently have limited trephocytic functions, especially as regards nucleoproteins, but all the glial cells appear to have important trephocytic relations at some time with certain cells in the nervous system.

The perineuronal satellites, other than ganglionic amphicytes, are chiefly oligodendrogliocytes, but one or more, usually 2 to 5 in number, are sometimes microglia (239, 289, 373, 438). Some of these perineuronal satellites of stellate nerve cells are found close, tangent, or attached to the body or expansions of the neuron. Cajal came near exposing the trephocytic nature of satellite cells when he suggested that they are symbionts of nerve cells and are comparable to the subcapsular cells (amphicytes) of spinal ganglionic cells (418, 438).

The cyton, or body, of each ganglionic cell in the spinal, cranial, and autonomic ganglia is surrounded by a layer of cells showing up to a dozen nuclei in a single central section which in turn are enclosed within a connective tissue capsule, as shown by von Möllendorff (534), while Jordan (289) and Nonidez and Windle (414) state that all ganglionic cells, except those of the acoustic ganglia, are encapsulated.

Apparently these subcapsular cells have not been definitely identified as to type, but it has been suggested that they are oligodendroglial (289) satellites. They are commonly called amphicytes or capsule cells (140), but these cells are also known as perineuronal satellites, Mantelzellen (418), satellite cells (534), peripheral neuroglia (562) and by other terms which may confuse one in determining whether the reference is to trephocytes of ganglionic or other neurons. Ortiz-Picón (418) describes a photomicrograph of spinal ganglionic amphicytes of a goat as "perineuronal satellite-cells" and as "perisomatic gliocytes". Thus, apparently, he considers amphicytes and perineuronal satellites as being very closely related and as having essentially the same trephocytic functions, while Singer (534) points out that both the satellite cell (amphicyte of ganglionic cells) and its sheath arise from cells which developed from the neural crest in the embryo. Jordan (289) supports Penfield's (438) view by stating that the amphicytes "and the neurilemma represent neuroglia (oligodendroglia)" in ganglia.

Bourne (69) states that the perineuronal satellite cells form a capsule composed of fibroblasts and fibers of connective tissue cells around the cyton. Inside this is a layer of "spindle-shaped cells pressed against the surface of the neurone", the capsule cells. He calls these capsule cells, which are believed to have the same embryological ectodermal origin as the neurons (438), and "amphicytes" and states that "their function is unknown". Singer (534) points out the significance of the thin film of fluid "between the sheath of the satellite cells and the surface of the neuron", which serves to cushion the cyton and to exchange metabolic substances by diffusion between the capillary bed and the nerve cells, especially in ganglia.

The cells forming the nucleated capsule of ganglionic cells (5, 289) bear the same nutritive relation to the cyton of the neurons as the oligodendritic satellite cells bear to neurons in the brain and spinal cord. The nucleic acid relations of these nucleated capsular cells, or amphicytes, resemble ovarian follicular cells and oligodendroglia which form satellite cells of the neurons in the brain as shown by the Feulgen and the DNAase-toluidin blue O reactions (289, 305, 534).

Neurogliocytes

The lengthy synonomy of the various types of cells which are grouped as neuroglia, glia (gliocytes) or interstitial tissue of the central nervous system (438) and of the sensory ganglia (418), as well as certain of the sensory ganglia (418), and several other things greatly increase the difficulties encountered in grasping the various functions of these and related cells.

The neuroglia (neurogliocytes) include the various types of astroglia, or macroglia; oligodendroglia; microglia, or mesoglia; and ependymal cells (562). All, with the possible exception of the microglia, arise from the spongioblasts of His (438). The astrocytes, of which at least 2 types, protoplasmic and fibrous astrocytes, are currently recognized (240), arise from embryonic ependymal cells and migrate to all parts of the central nervous system (289).

The perivascular glial membrane, which is formed by the foot plate, or terminal expansion, of certain specialized processes of the fibrous and protoplasmic astrocytes, is the chief component of the "blood-brain barrier" (414). The blood-brain barrier appears to have a highly developed capacity for inhibiting the passage of certain substances from the blood stream into the brain while admitting free passage to certain other substances. A much-cited illustration of this function is the inhibition of the passage of parenterally administered serotonin while admitting the free passage of its precursor (5-hydroxytryptophan) into the brain (591, 632, 633).

Since some of the gliocytes have been compared to small lymphocytes as trephocytes, Jordan's (289) statement that the small glial cells have so little cytoplasm that it forms scarcely more than a rim about the nucleus, is significant. The importance of this cellular adaptation becomes apparent when the gliocytes are considered in the light of the similarities in chromatin arrangement and staining qualities with small lymphocytes.

Some neurogliocytes are phagocytic under certain conditions. For example, microgliocytes (Hortega cells) in the ameboid form (276, 438), especially under conditions of degenerative processes in the central nervous system (276, 414), are actively phagocytic.

The binding and nutritive cells within the brain and spinal cord are usually conceded as belonging to three distinct subdivisions: the astrocytes, oligodendrocytes, and microgliocytes. These cells differ somewhat from the connective-

nutritive cells in other parts of the body because they serve also as a delicate network of support in the brain and spinal cord (562).

The electron microscope has provided information suggesting that neurogliocytes classified as protoplasmic astrocytes do not have typical protoplasmic expansions, but that the glial cytoplasm is extensive and is bounded by a cell membrane and that "nerve fibers extend through the cytoplasm of the glial cell between its nucleus and outer membrane" in rats (600).

Astrocytes

Functionally, astroglia, macroglia, the body of which may be called an astrocyte (562), are generally considered as being a type of connective tissue cell. However, several writers state that one characteristic of protoplasmic and fibrous astrocytes is the presence of a "sucker foot", or "vascular foot plate" (58), which terminates a process and is attached to a blood capillary. The functional relations of this foot-like process are similar to those of the multiple protoplasmic processes of astrocytes and of odontoblasts in young osseous or in active odontonal tissue in providing a transportation mechanism for nutritive materials (58). The sucker foot is believed to carry nutrients from the capillaries to certain neuron bodies in the brain and spinal cord. They are also credited with supporting, especially the fibrous types, repair and/or replacement (58).

Oligodendrocytes

The oligoglia are held by some authors to be nutritive, especially for myelin (58), and at times phagocytic cells (276, 289, 373, 438). The relations of these cells as perineuronal satellites to the cell body of neurons in the gray matter of the brain and spinal cord (58, 414) and their high nucleocytoplasmic ratios suggest that oligodendrocytes may function as rich DNA-bearing trephocytes (305) which, with the perinuclear rim of RNA, deliver components of DNA, RNA, and probably ATP directly to the cyton of the neuron to which they are frequently attached (289, 438). De Robertis and Bennett (132) show from electron microscopic studies of leopard and bull frogs that perineuronal cells of sympathetic ganglion cells have vesicles averaging 680 Å in diameter within the cytoplasm which pierce the membrane of the satellite. This provision is thought to favor the passage of trephones from the satellite to the neuron.

The close proximity of these satellite cells to the cyton is especially significant in view of the RNA and DNA-relations within the nerve cell body. The nucleus in the cyton is usually characterized by having relatively little DNA, an extremely large RNA-rich nucleolus, and a great amount (305) of RNA in the cytoplasm. This extremely high cytoplasmic content of RNA in the cyton is recognized by Caspersson (91) as indicating that these large neurons have an exceedingly high

rate of protein synthesis. Although most of the satellites are oligogliocytes and appear throughout both the white and the gray substance, many are microgliocytes (438) and some are held to be astrocytes (289).

Microglia

The microglia cells (mesoglia, mesogliocytes, Hortega cells) differ from other glial cells in that they are derived from the mesenchyme, probably from the forming pia mater (240). Del Rio-Hortega (131) warns that although the microglia which he describes arise from the meninges, they do not correspond to the mesoglia of Robertson. Microglia are considered to be part of the reticulo-endothelial system (92, 240, 438, 534) which, after assuming the form of large phagocytes, called neurophages or "compound granular corpuscles" (240), localize at sites of degeneration, necrosis, or other injury and phagocytize the degenerated cells and replace them in the neural lesions (190, 289, 393, 414, 438, 562). These cells occur throughout the central nervous system (58, 414) but are most numerous in the gray matter (58).

Del Rio-Hortega (131) considers microglia as not being strictly glial cells since they are derivatives of mesodermal cells in contrast with the oligodendrocytes which are of ectodermal origin (289, 438, 562), specifically of ependymal cells (131, 414). However, the mesodermal origin of microglia (58) is not universally accepted (373). Functionally, microglia and oligodendroglia appear to have certain trephocytic relations to nerve cells similar to those existing between small lymphocytes and fibroblasts with other cells. Penfield (438) shows that the microglia cells, like the fibroblasts, have very small, deeply staining nuclei with a concentration of chromatin in certain states. The arrangement and distribution of the chromatin material in microglia resemble that in lymphocytes, in oligodendrocytes and in the nuclei of fibroblasts, as indicated in various reproductions of these cells.

The presence of numerous fine cytoplasmic processes of microglia should not confuse the significance of the function of these cells, because within the central nervous system the arrangement of the microglial processes has two functions not found in other organs: to form a matrix which reacts as an argentaffine, supporting network, and to serve in conduction of nutritives to the recipient cells. Oligodendrocytes, as shown above, apparently have a trephocytic relation to certain large nerve cells, for they commonly occur in the white matter of the central nervous system (414) and, especially, in the gray matter, where they lie in proximity, or tangent, to the cytosome of large nerve cells (414). The relatively few, moniliform processes of these glial cells appear to have the special function of mechanical agitation, as was shown by experiments using explants from rat or human embryonic brain (632), which is held to favor the passage of nutritional material

from the capillaries to and from the nerve cell by agitating the surrounding fluid (632).

Whatever the function of these cells and their processes, it is interesting to know that they normally "pulsate", or extend and contract, rhythmically with a systole of 3 minutes and a diastole of 2 minutes (632). Serotonin (5.0 μg/ml) applied directly to and drained off of the preparation after a latent period of about 30 minutes, produced maximal tetanic contraction lasting 2 to 3 hours before the processes of the oligodendrocyte began to relax (632).

Granular Layer of the Cerebellum

The function of the granule layer in the cerebellum has not been established. It has been pointed out that granule cells may function in transmission of stimuli by affording an alternate passageway, or link, for passage of impulses and thus establish a circuit for extensive, transversal diffusion in the cerebellar folia (562). The abundance of DNA in the granule layer suggests the possibility that the granule cells may synthesize and store DNA and histone for use of other cells. This region of the cerebellum may have a most important function in storage of nucleoproteins.

The granular layer of the cerebellum appears to be composed chiefly and characteristically of closely packed cytons of small nerve cells (240, 562), most conspicuous in the cortex of cerebellar folia when stained by ordinary methods, such as cresylviolet, Nissl, toluidin blue (562), and hematoxylin and eosin (240). The nuclei in the granular layer are closely packed and very chromatic and in general appearance resemble those of closely packed lymphocytes (562). The individual granule cell is a small, multipolar nerve cell (240, 414, 562) having a deeply staining nucleus, but very scanty cytoplasm (119). Material from normal hamsters in which sections were stained with toluidin blue and consecutive sections were stained by the Feulgen method verifies the paucity of cytoplasm of granule cells (117). However, Cajal depicted these cells as having an appreciable amount of cytoplasm and 3 or more dendritic processes with claw-like endings (562).

The granule layer of the cerebellum represents a concentration of DNA which is comparable in density to that in sections of the thymus gland. The DNA in this layer is readily visible macroscopically when sections are stained by the Feulgen method for DNA. The abundance and close proximity of these cells in addition to the small amount of cytoplasm results in concentration of DNA and probably also a concentration of histone. The presence of DNA was confirmed by use of DNAase treatment. The DNA in nuclei of granule cells occurs in clumps that often protrude from the nuclear membrane and that are larger than those in nuclei of small lymphocytes.

Granule cells differ from small lymphocytes in being more resistant to several conditions that cause chromatolysis and pycnosis of small lymphocytes. No alteration in amount or location of DNA and RNA or in rate of cytolysis was observed in granule cells of normal adult male or female Syrian hamsters of various ages or of those receiving cortisone (116), parenterally administered atropin or pilocarpin, total-body X irradiation (995 r) (303), low (2%) protein diet, or subjected to prolonged hunger (117).

Comparisons of sections stained for RNA after treatment with DNAase with sections treated with RNAase to confirm presence of RNA show that the cytoplasm consists of a very thin shell around the nucleus. The physiological significance of this small shell of cytoplasm should not be overlooked in view of the importance of ribose adenylic acid in ATP. In addition, one function of the granule cells may be the formation of adenylic acid or ATP for metabolism of the Purkinje cells.

Factors Affecting Neural Trephocytes

The process of aging reduces the efficiency of trephocytes of neural cells very much the same way that it depletes lymphoid tissue and reduces the number of circulating lymphocytes. Brownson (81) holds that glial satellite cells show definite signs of age changes in relation to ventral horn neurons of the spinal cord in mice and in the motor cortex of both rats and mice. He (81) reports finding 56–58 per cent satellitosis in young and 32 to 40 per cent in senile mice, and 72 to 76 per cent in young immature rats; markedly senile rats had only 32 to 50 per cent satellitosis.

Hyden and Hartelius (272) found that subcutaneous or intravenous injections of 3 to 4 mg/k body weight of malononitrile (d (+) Maltose (Hydrate), N.B. Corp., 1955) doubled the ribose polynucleotide content and considerably increased the amount of protein in the cytoplasm of motor and spinal ganglionic cells in dogs and rabbits. They (272) also found that psychic disorders were attended by considerably decreased amounts, or absence, of protein substance and polynucleotides in some of the cerebral cortical ganglionic cells in patients.

Gliosis, as it pertains to conditions associated with development of neuroglial tissue following many pathological conditions, such as certain types of paresis, which may show "massive glia hypertrophy" (393), general paralysis of the insane (90) and hemorrhagic pseudo-encephalitis of Wernicke (642) may be accompanied by lymphocytic infiltration (90, 642). Also, in encephalitis periaxialis diffusa, (Schilder's disease), there may be perivascular infiltration of lymphocytes accompanied by a variable infiltration of phagocytic "round cells chiefly of neuroglial origins" (90). Boyd (70) describes a neuroglial reaction to trauma in man and also in experimental animals in which the three types of glial cells

have a function. The microglia reacted to the destruction and disintegration of tissue; some became scavanger cells and remained throughout the duration of the disintegration products. The second step in the reaction to trauma is enlargement in vacuolization of the oligodendroglial cells which persists for weeks (70).

The hormones in general have only an indirect effect on the nutrition of nerve cells, as, for instance, would be expected from administration of somatotrophin, adrenalin, or sex hormones. There is considerable evidence in support of the contention that adrenocortical hormones have important effects on the brain and spinal cord. However, a considerable part of the experimental work with these hormones has been directed toward producing chromatolysis and generally destructive effects in various neural structures with the result that investigators have paid little attention to the less obvious effects these substances may have had on trephocytes of the neurons.

Cortisone appears to be more potent than ACTH, but either may produce various pathologic changes in the brain, and it has been shown that administration of cortisone causes inflammatory lesions in the blood vessels and edema in the brain in sensitized rats, and psychotic reactions, euphoria, and convulsions in human patients (92). However, Spirtos (553) failed to find any evidence of cytohistologic changes, such as vacuolization, chromatolysis, hyperemia, glial proliferation, hemorrhage, or edema in the brain or meninges of cats subcutaneously injected daily with 50 mg/k of cortisone for 10 days or in rats receiving 5 mg daily for 20 days.

Effects of cortisone and ACTH on neurons in the hypothalamus of rats appear to follow very closely the general pattern produced by ischemia or chronic inanition (92). The cytological findings in rats thus treated indicate that cortisone and, to a lesser extent, ACTH deplete the DNA and RNA-content of cerebral cells. However, it is pointed out that the hormones may not have acted specifically upon the central nervous tissue but indirectly by causing an unfavorable general condition in the animals (92, 553); Scharrer and Scharrer found cytological evidence of reduced secretory activity in the hypothalamus (92).

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