THE ARRIS AND GALE LECTURES ON THE NEUROLOGY OF VISION.

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The Arris and Gale Lectures

ON

THE NEUROLOGY OF VISION.

LECTURE I.

THE AFFERENT VISUAL PATHS.

THE nerves which deal with the special senses are specially differentiated sensory nerves. In the process of differentiation, however, the analogies which they present to the ordinary spinal sensory nerves are greatly obscured, and may be easily overlooked. Just as the segmental arrangement of the central nervous system is most manifest in the cord, becomes obscured in the medulla oblongata, and is scarcely appreciable in the higher parts of the brain, so the cranial nerves assume that increased complexity which is characteristic of the evolutionary process wherever it occurs.

Considering first the mechanism of transmission and transmutation of an ordinary sensory impulse, we find that the physical stimulus is received by an end-organ, and is there transformed into a nervous impulse. This is carried by a nerve fibre along the sensory nerve and the dorsal spinal root to the cord. It travels up in the posterior columns of the cord to the nucleus gracilis or the nucleus cuneatus as the case may be. The whole of this course is along the processes of a single cell or neurone, which has been called the neurone of the first order. The impulse is taken up in the nucleus gracilis or nucleus cuneatus by a second cell, and is carried along the nucleo-thalamic tract or mesial fillet to the opposite optic thalamus; other fibres, especially those derived from the nucleus cuneatus, pass to the superior colliculus or corpus quadrigeminum. These cells in the nuclei gracilis and cuneatus are the neurones of the second order. A third cell, the neurone of the third order, situated in the thalamus or colliculus, carries on the impulse to the cortex cerebri. Here the nervous impulse is transformed into a psychic impulse, a change which is not, and probably never can be understood. This is the simplest path of an afferent impulse, though by no means the only one; it best serves our present purpose, since it is the most typical.

Returning to the genesis of the impulse in some physical stimulus, there is, as far as we are aware, no preparation of the physical forces before they fall upon the sentient surface. This applies to all sensory nerves, with the exception of the nerve of vision, and to a less extent, the auditory nerve. In the former case, with which we are immediately concerned, the whole eye, with the exception of the retina, is a complicated mechanism for preparing the physical force, light, so that it may produce specific and complex sensations. It is well, therefore, to emphasise the fact that in dealing with visual sensations the stimuli themselves are composite, and for all we know, each component may be provided with its own transmitting apparatus.

At the outset of our comparison of the anatomical structures for the transmission of visual and common sensations, we are met with difficulty. The so-called optic nerve is in no sense comparable with an ordinary sensory nerve. Morphologically and physiologically it is part of the brain. Careful investigation shows that the true optic nerve, corresponding with the sensory neurone of the first order, must be sought in the retina itself. Even so, the analogy is not absolutely complete, for the dorsal root ganglion cell, which forms the first neurone, emigrates at an early stage of development from the neural crest and loses its connection with the cord, only to regain it at a later stage. The retina, on the other hand, develops entirely in the invaginated primary optic vesicle.

THE MORPHOLOGY OF THE RODS AND CONES.—If we seek the analogues of the successive sensory neurones in the optic system, we are met with further difficulties. Histological investigations of the retina have shown that the conducting elements may be divided into three orders: (1) The rods and cones, with their nuclei, which form the main mass of the outer nuclear layer and their processes, which contribute to the outer reticular layer; (2) The rod and cone bipolars, which form the main mass of the inner nuclear layer, with their axones, which contribute to the inner reticular layer; (3) The ganglion cells, the axones of which form the nerve fibre layer, and the main mass of the so-called optic nerve. We shall see later that the ganglion cells and their processes behave exactly like the second order of sensory neurones, a fact which affords further evidence that the optic nerve belongs essentially to the central nervous system. The neurones of the first order, therefore, must be either the rods and cones, or the bipolars. In the former case an extra neurone is intercalated in the visual afferent path; in the latter no such assumption is necessary, but it remains to explain the nature of the rods and cones.

There can be no doubt that the second view is the simpler and more probable. If we adopt it, the rods and cones will be epithelial ependymal cells, corresponding with Merkel's *Tastzellen* or touch cells and the epithelial cells of end-organs, with the neuro-epithelial cells of taste buds, the epithelium of the organ of Corti, &c. The olfactory nerve will prove the sole exception to such a scheme, the sensory neurones of the first order being here situated actually upon the surface, like the sensory cells of some invertebrata.

If we consider the position of the retinal pigment epithelium and the rods and cones from an embryological standpoint, it will be seen that they correspond with the lining of the primary optic vesicle, *i.e.*, with a part of the central neural canal. This is itself an invagination from the surface epiblast, and its lining epithelium, therefore, will correspond with the superficial epithelium of the body. In the neural canal these cells become ciliated ependymal cells, so that their condition in the retina is merely a specific differentiation.

Evidence in favour of the ependymal nature of the rods and cones has been brought forward by Krause. This tends to show that the outer limbs are really coiled up cilia.

Verhoeff, working in the laboratory at Moorfields, supports and extends this theory by further observations. If the rods and cones are ependymal cells we might reasonably expect to find the pigment epithelium also showing traces of the same origin. By bleaching and special staining methods, *e.g.*, Mallory's phosphotungstic acid hæmatoxylin, a membrane, resembling the external limiting membrane, can be made out surrounding the internal ends of the pigmented epithelial cells. The appearance in transverse sections is that of a delicate line running along near the inner margins of the cells. The latter project beyond it in the form of processes of variable length, showing that the line does not represent the inner contour of the cells. Black dots occur at regular intervals along the line, each occurring at the line of junction of two cells. On careful focussing it can be seen that the line is not always at the same level, evidently passing sometimes behind and sometimes in front of the cells. Hence it is difficult to photograph the membrane. In oblique sections the true structure is made more apparent, the membrane appearing not as a straight line, but as a series of hexagonal loops, which are fused together at the lines of contact so as to form a screen into the openings of which the pigment cells project. The little dots are the points of junction of the loops, *i.e.*, the sections of the lines of contact.

It would take too long to discuss the bearing of these observations upon the generally received idea that the membrana limitans externa is formed by Muller's fibres, *i.e.*, by neuroglia. Reference must be made to the original paper in the Royal London Ophthalmic Hospital Reports. Suffice it to say here that there is reason to think that neuroglia is absent in this situation in glioma retinæ.

There are other staining reactions which tend to show that the rod and cone cells differ essentially from the bipolar cells of the retina. In some specimens, more particularly in cases in which the nutrition of the retina has suffered from some cause, the rod and cone nuclei stain differently from the nuclei of the bipolars. This may be seen with the ordinary hæmatoxylin and eosin staining, but as shown by Verhoeff, it is brought out much more clearly by Mallory's acid hæmatoxylin after hardening in 4 per cent. formaldehyde for 4 days or longer. The inner nuclear layers then remain unstained. The contrast between the two layers may be further intensified by staining for 24 hours in lithium carmin after differentiating in ferric chloride solution. The inner nuclei then take on the carmin stain. In some specimens only portions of the retina show this differentiation. It occurs most frequently in cases of detachment of the retina or choroiditis, but it also occurs in apparently normal retinæ. The condition is present also in the retina of the guinea-pig and in that of the frog.

The other theory—that the rods and cones are true peripheral neurones—is supported chiefly by observations on lower types. This has been shown particularly by van Lenhossék in cephalopods. Thus, in eledone, the retina consists entirely of complicated rod cells. From these the retinal fibres pass through the cartilaginous sclerotic to the visual lobe, which contains a peripheral or external nuclear layer, followed by a reticular layer, then an inner nuclear layer, and finally a layer of white fibres. These layers are themselves complex, and until the morphology of the individual cells is more accurately determined the evidence in favour of the purely nervous nature of the rod apparatus is not overwhelming.

Phylogeny, indeed gives better support to the theory in the analogy of the ordinary sensory neurones of the first order, though here, too, the other interpretation is not disproved. In man the spinal ganglion cells are bipolar when first developed; only in the cochlear and vestibular ganglia is this condition retained through life. In the fish it is retained in all the posterior root ganglia. In invertebrates transition stages are found in which the cell body lies farther and farther from the central nervous system, until finally, as in the earthworm, it is actually situated in the surface epithelium (Retzius). One vertebrate, amphioxus, has its bipolar sensory cells within the spinal cord, and some animals, in a comparatively limited space, show a number of transitional stages between the peripheral and the central position (Edinger). In only one undoubted instance in man the peripheral situation is maintained, viz., the peripheral olfactory neurones.

THE NEURONES OF THE FIRST ORDER.—We pass on now to consider very briefly the neurones of the first order, viz., the rod and cone bipolars. Ramon y Cayal's work by a modified Golgi method has shown most clearly the relationship between the various cells of the retina. The bipolar cells come into relation peripherally by vertical dendrones with several rods. The dendrones of the bipolar cells for the cones lie in a deeper plane and are horizontal, but similarly come into relation with several cones. The axones of the rod bipolars run centrally to the inner part of the inner reticular layer, whilst the axones of the cone bipolars may form their arborisations at any of the five layers of the inner reticular layer. Over the greater part of the retina there are about a hundred rods and cones to one ganglion cell. The fovea centralis has been investigated only in the bird and chamæleon. In both, cones alone are present; their axones end in knobs without fibrils, or with only a pair of very short rudimentary fibrils. The dendrones of each ganglion cell in this region seem to come into relation with only a single bipolar, and possibly several amacrine cells; so that here each cone has its own bipolar and ganglion cell—it remains, so to speak, "individualisirt" (Cayal).

THE NEURONES OF THE SECOND ORDER.—The neurones of the second order, or the ganglion cells and their processes, will be considered at greater length. Their axones pass into the nerve fibre layer of the retina, thence into the optic nerve; most cross in the chiasma to the opposite optic tract, some only passing along the tract of the same side; from both optic tracts most are distributed to the external geniculate bodies, whilst others pass to the superior colliculi, and yet others to the pulvinar of each optic thalamus. In man probably 80 per cent. pass to the external geniculate body (von Monakow). In lower animals the optic lobes, *i.e.*, the region of the corpora quadrigemina, are the main visual organs. In fish, almost the whole of the optic nerve ends in the mid-brain; in birds, there is a differentiation of a mesencephalic nucleus, the superior colliculus, from a diencephalic nucleus, the lateral geniculate body, and in them for the first time one meets with a genuine occipital cortex (Edinger). This anatomical differentiation is accompanied by a parallel redistribution of function, and is, therefore, of prime importance in analysing the results derived from experiments upon animals.

Most of our knowledge of the arrangement of the fibres of the optic nerves, apart from the broad question of the relative amount of decussation in the chiasma, is derived from clinico-pathological investigation. I propose here to limit myself to a description of my own researches by the experimental method upon monkeys.

Following the ordinary Wallerian law of degeneration, the afferent fibres of the visual paths degenerate on the central side of a lesion which separates them from their cells of origin, the ganglion cells. The method adopted was to introduce a Graefe cataract knife into the eye 4 or 5 mm. behind the corneo-scleral margin, at either the nasal or temporal side, thus avoiding dangerous injury to the ciliary body and minimising injury to the retina. (The monkeys were of course completely anæsthetised.) The knife was passed across the eye through the vitreous to the opposite side, and the retina wounded there to the required extent,