failed because of defective eyesight. Correction by glasses remedied this defect, and on being asked what was the matter with his neck he told the examining doctor that it was a "bit stiff." No detailed examination was made, and he was passed for training. This was completed, and for the last fourteen years he has carried out his work as a van salesman, starting and driving his van and loading and delivering packages himself.

Present Condition

He is now about to give up his present work on account of heart disease, which has incapacitated him on several previous occasions. He has a slight ache in the neck, worse after a heavy day's work. His arms and shoulders are strong (previous to the operation he could hardly push open a door). While sitting no abnormality of the neck is seen, but on being stripped the head is seen to be held slightly forwards, there is a slight kyphosis of the lower cervical region, and slight lateral deviation to the right. Flexion, extension, and rotation of the head are normal, while movements of the lower cervical spine are limited, and there is some thickening over the back of the spine in this region. He has an enlarged and grossly irregular heart.

Remarks

The change from his original condition is striking. Then he had considerable pain, stiffness of the neck, was unable to support his head alone, and able to walk only by supporting it with a hand on the chin and another on the occiput. He has been relieved of most of the pain and deformity, and has done full manual work for fourteen years; he is married and has a family, and but for heart disease would continue as a vanman. It is nearly twenty years since I have seen him, until he reported, at my request, in July, 1936.

Any success must be largely due to my friends, then Captain F. G. Armstrong, who was responsible for the anaesthetics, and Major H. Muir Evans, who assisted me.

ANATOMY OF PERIPHERAL SENSATION*

BY

H. H. WOOLLARD, M.D., D.Sc.

UNIVERSITY PROFESSOR OF ANATOMY, ST. BARTHOLOMEW'S HOSPITAL
MEDICAL SCHOOL

The punctate theory built up by v. Frey has not been seriously challenged; it is that the four elementary cutaneous sensations are distributed over the skin as a mosaic of points, each point being allocated to one of these sensations. It is a part of the punctate theory that there shall be specific receptors for heat and cold, irrespective of whether the temperature is close to that of the body surface or far removed from it.

Head divided the cutaneous temperature sense into an epicritic moiety near to the temperature level of the surface of the body and a protopathic (dyscric) moiety further removed from it. This seems a difficulty, for we would then need receptors for cold, cool, warm, and hot. This is not impossible, though it is difficult to imagine why there should be separate receptors for heat and cold, since these differ physically only in molecular velocity. Some present-day histologists maintain that all neurofibrillae pass at the periphery into a neuroprotoplasmic continuum. Others emphasize that nerve endings are so various and transitional forms so common that form and position have no particular significance. Thus in their view nerve endings are to be regarded merely as devices for securing increased surface. All the real differences between naked and encapsuled endings disappear if these pass into protoplasmic continuity with one another or with the protoplasm of adjacent cells.

* Paper read in the Section of Anatomy at the Annual Meeting of the British Medical Association, Oxford, 1936.

The ideas of Head, even though they conflict with the punctate theory in some degree, are of the greatest importance, for he first enunciated in clear fashion the theory of the dual composition of the nervous system. The evidence upon which Head based this theory was derived mainly from the experiment of dividing one of his own nerves. Though this experiment has been repeated several times, no one has come to the same conclusions as Head. The basis thus rendered unreliable, the whole edifice has been regarded as insecure. The best evidence for Head's dualistic theory, found elsewhere in comparative neurology, has been assembled by Sir John Parsons. For instance, the double conducting systems of the spinal cord for contact, pain, and temperature on the one hand, and the localization of touch, awareness of position, and discrimination of points on the other—a double conducting system whose pattern can be traced in all vertebrates—is convincing evidence that can be obtained from comparative anatomy.

Electrical Investigation

The analysis of peripheral nerves has proceeded apace recently by means of electrophysiology. Anatomical analyses make it quite clear that nerves in passing from the cord to the dermis preserve their morphological characters. It might well be supposed that the diameter of a nerve would depend on the distance it has travelled, upon the number of collaterals given off, and upon whether the nerve itself was an original fibre or a collateral. At all levels, then, the nerve fasciculi contain both thick and thin fibres. If the frequencies of nerves arranged in 2- μ groups are plotted, a curve with two well-separated summits is obtained.

Adrian, from his investigations on the change of potential, rate of adaptation, velocity of conduction, and other features, divides nerves into two groups, while Gasser and others make three or more groups. There is general agreement that the finer fibres which conduct slowly and adapt slowly bear the pain sensation. The difficulty lies in the fact that such fibres cover morphologically those from less than 2 μ up to those of 5 μ or more in diameter, and in rates of conduction from 0.5 metre to 30 metres a second; the pain sensation group includes also exclusive pain fibres, as well as some which bear first the sense of contact and then pain. Thus there are difficulties in suggesting that these two main subdivisions can be fitted to Head's series of protopathic and epicritic nerves.

Histological Investigation

We have made use of large flat spreads of human skin stained while still living with methylene-blue. This has the advantage that a nerve fibre can be traced for long distances and all its subdivisions and endings can be inspected. This method dispels the idea of intermediate and transitional endings. It can be asserted that one nerve fibre bears only one kind of nerve ending, and that these are as uniform and as like each other as the flowers on the same stalk. As many as thirty-seven similar endings have been counted on the collaterals of one nerve fibre. There may have been more.

We are thus reduced to really a small number of endings. It is in the deeper, complex, highly organized, and encapsuled endings that the greatest seeming diversity occurs in different parts of the body, and it is to these that so many names have been applied until one has exclaimed, "So many observers, so many endings!" We would agree that the general observation of large areas of skin and the making of maps of all nerves and nerve endings that can be found therein reduces the anatomical complexity to limits which promise success to the task of associating these endings with the elementary cutaneous sensations.

Organs of Special Sensation

It has been generally assumed that the epidermis is the seat of pain and the dermis the seat of touch. This view, which has hitherto prevailed, has been challenged recently by Waterson. Waterson has emphasized that it is possible to shave off the epidermis, at any rate as far as the deeper layers of the stratum mucosum, without causing pain, while the exposed surface remains sensitive to touch. It has already been remarked that, whether one supposes the epidermis to be the seat of touch or of pain, these sensations are so closely packed at the surface that an abundant innervation must be present to act as their receptors. Such an abundant innervation is not to be found. Here and there, with great difficulty, nerves in the epidermis can be found. Most usually they are branches of medullated nerves continued to the stratum Malpighii, where they end often in the form of Merkel's corpuscles, or they are a continuation of Meissner corpuscles into the epidermis, where, again, they end as Merkel's corpuscles, or, especially in regions like the hand, where tactile acuity is high, large uniform fibres can be traced in the epidermis as far as the stratum granulosum. Thus what can be easily demonstrated in the epidermis is the continuation of endings like Meissner and other medullated nerve endings often regarded as incomplete Meissner endings, these with good reason always having been associated with touch. These are most easily demonstrated in regions where acuity is high and the epidermis well developed. The same observations apply to hairs and special structures, such as Eimer's organ in the snout of certain animals. These special tactile organs are also ones in which it is easy to demonstrate epidermal endings, as in the outer root sheath of the hairs.

That the nerves of the epidermis form an accessory organ of touch is made still more likely by the fact that it is possible to demonstrate the existence of a close mesh-work of naked varicose fine nerve fibres in the sub-epidermal tissue, immediately below the stratum Malpighii. This mesh anastomoses, and also forms endings which terminate sometimes by entering the epidermis—though mainly it is a plexus below the epidermis. This plexus, apparently continuous, has been traced for a distance of six centimetres. It has all the characters that we might expect from the history, the physiology, and the quality of the pain sensation. By the analysis of the areas upon which this sensation has previously been indicated, cold has been found to assume the form of compact terminal subdivisions each of which ends in a blunt expansion. These are borne on the ends of medullated fibres, the diameter of which is about 7 μ . They lie quite superficially and near the stratum Malpighii in the subepidermal tissue.

In regard to heat we have not been so fortunate. The long latent period has made it certain that the heat receptor lies further from the surface. The large gaps between adjacent receptors make it more difficult to discover groups of endings, and the deep situation has rendered it impossible for us to use an *intra-vitam* stain. We have had to resort to sections stained with silver. In thin sections it is very hard to recognize actual endings. To map the heat spots we have used a metal junction and passed a constant current through this for a constant period, so that we have always applied to the skin the same amount of heat. Spots so found have been excised, and after staining with silver have been cut into sections. In such cases we have always found that our prick which marked the heat spot has perforated exactly the hair follicle complex passing into the vicinity of the sebaceous and sweat glands. We have found many nerve bundles and fibres and endings in the course of these pricks, but we are unable to say what type of endings, if any, are

especially associated with heat. Further investigations are in progress.

It is a common enough observation, mentioned by many others, to find a thin fibre entering into a nerve ending, a fibre quite distinct from the medullated nerve that carries the nerve ending. This additional accessory ending has on the ground of its thin non-medullated character been reckoned as sympathetic. It may, however, and in our judgement even more probably, be regarded as an accessory nerve of pain, and may form the anatomical basis of the oft-repeated statement that excessive stimulation of any receptor may end in pain. It is not suggested that a receptor changes its sensation, but that these accessory fibres furnish the protective pain sensation. In the eye this function is supplied by the fifth nerve, which furnishes pain receptors and pain only to the eye itself. In the case of the internal ear the same function is undertaken by the seventh nerve. The accessory fibre exercises the same function for the hairs, Meissner corpuscles, Pacinian corpuscles, and other deep endings.

THE PROBLEMS OF EMBRYOLOGY*

BY

C. H. WADDINGTON, M.A.

FELLOW OF CHRIST'S COLLEGE, CAMBRIDGE

Embryology may be, and often has been, regarded as a branch of comparative anatomy. According to this way of thinking, the fundamental subject of biology is the study of adult organisms; this study can be divided into two main groups of sciences, which we may call the anatomical, which relates to the forms of animals, and the physiological, which relates to the physical and chemical mechanisms by which organisms perform the business of keeping alive. If we confine our attention to adult animals, it is clear that the phenomena dealt with by the anatomical sciences must be studied before those with which the physiological sciences are concerned, since the physiological functioning of any highly evolved organism is founded on the principle of specialization, by which particular organs are set apart to perform particular functions.

Even when we investigate the progress of a relatively simple chain of chemical processes occurring in a restricted region of the body, perhaps in a single cell, more and more evidence is accumulating to show that the progress of the reactions is dependent to a large extent on the morphological arrangement of the particles of the living protoplasm. I need only remind you of the numerous and important researches on the properties of biological membranes and the orientation of protein molecules in muscle cells, and of the recent demonstration of the position effect, by which the effect of a Mendelian factor, or gene, is shown to depend on its position on the chromosome relative to the other genes. In some cases we are already in a position to try to discover the forces which hold the molecules in these microscopic patterns, and we are here approaching one of the fields in which the debt is the other way round, and it is anatomy which must follow in the footsteps of physiological advances.

Among the anatomical sciences embryology is often relegated to a subordinate position. If we attempt to give an account of the facts of comparative anatomy in terms of the theory of evolution, the embryological data come in as interesting additional evidence. In the heyday of comparative anatomy, embryonic development was explained by reference to adult forms; in Haeckel's theory of recapitulation the sequence of embryonic stages was compared with the evolutionary series of ancestors. But

* Paper read in the Section of Anatomy at the Annual Meeting of the British Medical Association, Oxford, 1936.