OBSERVATIONS ON THE STRUCTURE AND ORGANIZATION OF Olfactory Receptors IN THE RABBIT*

In ordinary histological preparations the olfactory epithelium of mammals appears to have a relatively uniform structure throughout its extent, and, as in Man and the higher Primates, it may be disposed quite evenly in flat sheets which are uncomplicated by folds of turbinal processes. In spite of the apparent homogeneity of its composition, the discriminative potentiality of the epithelium is remarkable, for it permits the distinction and recognition by their odoriferous properties of a seemingly indefinite number of chemical substances (many of which have a comparatively simple molecular structure). The olfactory receptors and their connexions with the olfactory centres of the brain thus present a particularly interesting problem for the study of the morphological basis of sensory discrimination. Presumably the receptors are in some manner capable of functioning as "analysers" which are differentially sensitive to diverse odoriferous substances, for on a priori consideration this seems to be the most likely basis for the discriminatory functions of the olfactory epithelium. Such an hypothesis is also consonant with the phenomenon of selective olfactory fatigue. In recent years direct evidence that the olfactory receptors are not all equally sensitive to specific odorous substances has accrued from the electrophysiological studies of Adrian, Beidler and Tucker, and Ottoson; for example, some receptors are reported to have a higher threshold of sensitivity for a particular chemical substance and other adjacent elements, a lower threshold. According to Adrian, also, these different types of receptor are not uniformly distributed over the olfactory epithelium, though there are some regions in which they are closely intermingled.

This evidence that the olfactory receptors are not functionally homogeneous naturally raises the question whether they show any corresponding differentiation in their morphology and connexions. It was partly with these

* Being an extract from the Ferris Lecture delivered at Yale University School of Medicine, 5 March 1956.
Received for publication May 24, 1956.

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considerations in mind that the investigations here reported were undertaken. Also, with the focus of attention now being concentrated on the electrophysiological phenomena of the olfactory system, and incidentally with a view to providing an orientation for the study of the olfactory receptors and their relationship to other elements of the epithelium by electron microscopy, it has seemed opportune to examine more closely and critically the essential structure and organization of the receptors in so far as these can be elucidated in normal and experimental material by the light microscope. It may be emphasized that the olfactory epithelium offers a particularly challenging problem to the anatomist for the reason that its histological study involves so many difficulties. For example, the receptor elements and their processes are exceedingly delicate and exceptionally difficult to display by ordinary histological methods, and the olfactory nerve fibres which have their origin in the receptors are so fine as to be close to, or even beyond, the limits of the resolving power of the light microscope. Another point which needs emphasis is that laboratory animals (even when kept under the best of conditions) are liable to rhinitic infections which may easily lead to a distortion of normal appearances, and perhaps also (it is to be suspected) to a distortion of electrophysiological records. In our experience much experimental material may have to be discarded because of this disturbing pathological factor, and there seems little doubt that the latter has in the past led to some confusion in the interpretation of the histological picture of the effects of lesions in the olfactory bulb.

The following observations represent a continuation of earlier investigations, and the more extended material now available has led to an amplification of certain of the previous conclusions which were expressed on the basis of that work.

The structure and dimensions of olfactory receptors. The microscopical appearance of the mammalian olfactory receptor has been described in classical studies by a number of histologists (for example, v. Brunn, Cajal, van Gehuchten, and Kolmer). These give an accurate picture of the main features of a receptor and show that it is essentially a bipolar nerve cell, retaining its embryonic position in surface epithelium, and consisting of a small cell body with a rounded or oval nucleus, a fine proximal process (which is actually the commencement of an olfactory nerve fibre) and a coarser peripheral process. To the last named we may conveniently apply the term "olfactory rod"; it terminates at the free border of the epithelium in a small expansion which gives rise to the fine olfactory "hairs." In order to obtain more detailed information regarding the dimensions and structure
of the component parts of the receptor in the rabbit, series of sections have been prepared with Bodian's activated protargol, Cajal's pyridine silver, and Bielschowsky's silver technique. In all cases it has been found an advantage to use different fixatives and to vary the degree of impregnation, for the component parts of each receptor do not all stain equally well with any one procedure. It has also been found useful to study experimental material in which partial or total lesions of the olfactory bulb have led to the atrophy or disappearance of a high proportion of receptors in the olfactory epithelium, thus exposing the "thinned out" residual elements to clearer view.

In Figure 1 is shown a diagram, drawn to scale, which illustrates the relative proportions of olfactory receptors in the rabbit. The dimensions are based on measurements of fixed material impregnated with silver; so far as the finer processes are concerned, therefore, their thickness is likely to be somewhat exaggerated. The cell body is oval with a transverse diameter of approximately 5 μ and a vertical extent of 10 μ. It contains Nissl material in a finely granular form which is mainly concentrated in the upper part of the perikaryon. The olfactory rods appear relatively thick by contrast with the olfactory nerve fibres; in fact, however, they are rather less than 1.0 μ in width. They are refractile as seen under the phase contrast microscope, and stain heavily with protargol (particularly in alcohol-fixed preparations). At the surface of the epithelium the rod shows a local constriction which is less strongly argentophil, and here it penetrates a limiting membrane formed by the contiguity of the cell membranes at the free extremities of the supporting cells of the epithelium. It is, perhaps, of importance from the functional point of view to note that the olfactory rods vary considerably in their length, ranging in continuous gradations from approximately 20 μ to 90 μ (though in the thinner regions of the epithelium near the margins of the olfactory area the rods do not reach the upper limit of their length). In the case of the longer elements the rod becomes very attenuated in the deeper parts of its extent and is here difficult to define in histological sections. The suggestion presents itself that these morphological differences are possibly associated with a differential sensitivity of the re-
ceptors, for it may be surmised that those chemical substances which are less efficient as depolarizers, even if they activate the receptor terminal at its free end, may not be able to fire off the cell of the longer rods, whereas in the shorter elements they may be capable of initiating impulses in the axonal process of the cell.

Superficial to the surface limiting membrane of the olfactory epithelium, that is to say actually projecting into the nasal cavity, is the terminal swelling, a refractile, cup-shaped expansion which reaches a maximum diameter at its upper end of 1-2 μ. Van der Stricht* called this the “olfactory vesicle,” a term which may be misleading for there is no evidence that it is vesicular in the sense that it is hollow. The constructional details of the terminal swelling which are illustrated diagrammatically in Figure 2 are based on the study of many preparations treated with activated protargol, and the diagram shows the appearance seen with moderate degrees of impregnation. The outer wall of the swelling terminates above in a marginal ring to which are attached in radial symmetry a number of olfactory hairs. These are 1-2 μ in length and about 0.1-0.2 μ in thickness. They commonly stain more intensely with silver in their distal two-thirds, and where they are attached to the marginal ring the latter appears to be thickened to form a sort of “basal corpuscle.” However, these local thickenings are not so well defined or sharply stained as the basal corpuscles found at the attachments of the cilia of ordinary ciliated epithelium (seen in adjacent areas of the same sections) and it may be questioned whether they are strictly comparable. Because of their fine structure it is not easy to enumerate the olfactory hairs attached to each receptor. In an attempt to do so, counts have been made under the oil-immersion on sections cut tangentially to the surface of the epithelium (see Fig. 4). The counts were limited to those receptors in which there was no obvious gap in the radial symmetry which might be due to the loss, or the failure of impregnation, of some of the hairs. The results of counts on 100 receptors are as follows:

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Fig. 2. Schematic representation (drawn approximately to scale) of the essential features of the terminal part of an olfactory receptor in the rabbit, based on a study of silver impregnated material. To the right is shown the appearance of the marginal ring, olfactory hairs and “basal corpuscles”, and the central argentophil spot, as seen in sections cut tangentially to the surface of the olfactory epithelium.
Olfactory receptors in the rabbit | LE GROS CLARK

| Number of hairs | Number of receptors |
|-----------------|---------------------|
| 9               | 1                   |
| 10              | 3                   |
| 11              | 8                   |
| 12              | 26                  |
| 13              | 25                  |
| 14              | 20                  |
| 15              | 10                  |
| 16              | 7                   |

This method of computation is obviously open to criticism, but so far as they go the counts appear to show that the number of hairs on a single receptor may vary from 9 to 16, with a mean value of 13. Incidentally, this is more than the number commonly given for mammals in reference books, but of course there may be species differences. Apart from their number, the hairs attached to any one receptor do not always stain with equal intensity, but there appears to be no regularity in this differential staining.

The disposition of the olfactory hairs shows considerable variation in different preparations and, to some extent also, in different receptors of the same preparation. They may be splayed out like the petals of a daisy in full flower (Figs. 4 and 5), or they may be bunched together like the petals of a half-opened bud (Fig. 3). These varying appearances suggest that the hairs, even if not motile, are at least pliable and mobile, and the question naturally arises whether (as usually supposed) they are the actual sensitive terminals of the receptor, or whether they serve some ancillary function facilitating the excitation of the receptor by odoriferous substances. They differ from the cilia of the ciliated ("respiratory") epithelium adjoining the olfactory epithelium in that they are coarser and do not taper finely at their free extremities, as also in the fact that they do not stain so evenly. Incidentally, it may be noted that, near the periphery of the olfactory epithelium, there is some intermingling of olfactory receptors and ciliated epithelial cells of the "respiratory" region, an intermingling which may be much more intimate in some lower vertebrates. This makes easy a direct comparison of the appearance of olfactory hairs and ordinary cilia. But it is also possible that the intermingling may lead to misinterpretations in attempts to study olfactory hairs with the electron microscope.*

* It is not uncommon in cases of mild rhinitis to find some metaplastic conversion of supporting cells of the olfactory epithelium into ciliated epithelial cells. The ciliary process of such cells may also be inadvertently confused with the olfactory hairs of receptors.
When the terminal swelling of the receptor is viewed in tangential sections stained with protargol the marginal ring is found to surround a relatively clear area, the centre of which is usually seen to be occupied by a minute spot which is often strongly argentophil (Fig. 4). This central formation, less than 0.5 μ in size, appears to be continuous below with the argentophil substance of the terminal swelling and thus with the olfactory rod. The possibility suggests itself that the central spot itself represents the ultimate excitable point of the receptor, corresponding, that is to say, to a free nerve terminal. If this should prove to be the case, the olfactory hairs may in some manner act as atypical cilia whose function it is to concentrate odoriferous particles on the essential terminal of the receptor. Such an interpretation may be found difficult of acceptance, however, for the reason that the olfactory receptor is a true nerve cell and the olfactory hairs are thus more likely to be functionally homologous with dendritic processes. On the other hand, it is perhaps equally possible to argue that the hairs are functionally homologous with the ciliary process of ependymal cells which, like nerve cells, are also of neur ectodermal origin.

The terminal swellings of receptors and their hair processes show certain morphological differences. In the first place they differ in magnitude, and in any tangential section occasional receptors here and there stand out conspicuously by their larger size and the intenser staining of the olfactory hairs. It is not possible, however, to determine that there is any regular pattern in the size distribution. The marginal ring varies in diameter from about 1 μ to rather more than 2 μ. As already noted, also, there is a variation in the number of hairs attached to it. The marked contrast which may sometimes be seen in staining properties is shown in the microphotographs in Figure 5, which are taken from sections of septal epithelium stained with the Bielschowsky technique. It will be noted here that occasional receptors have taken up the stain intensely and thus stand out very conspicuously among the faintly impregnated terminal swellings and hairs of adjacent receptors. These intensely stained elements may be seen singly or in pairs, but their relative number shows much variation in different parts of the same section. In some regions, indeed, the receptors appear to show all gradations in the intensity of their staining. Those which stain the more intensely appear to have larger terminal swellings and coarser hairs, but such differences in apparent size may be partly illusory. We do not know whether this differential staining indicates different types of olfactory receptor, or merely reflects different phases of activity in receptors of the same general type. Even if the latter should be the case, however, it suggests a functional differentiation of some sort.
Fig. 3. Section of the olfactory epithelium of a rabbit, stained with protargol, showing the olfactory rods, the terminal expansions, and the olfactory hairs. The nuclei in view are mostly those of supporting cells. x 2100.

Fig. 4. Composite of microphotographs of tangential sections through the olfactory epithelium of a rabbit, stained with protargol, showing the appearance of olfactory receptors seen in surface view, with particular reference to the marginal ring, olfactory hairs, and “basal corpuscles,” and the central argentophil spot. x 3000.
Fig. 5. Bielschowsky section of the olfactory epithelium of a rabbit showing the differential staining of receptors which may sometimes be seen. In a. and b. a single receptor is sharply contrasted by the intensity of its staining with adjacent receptors. In c. two such intensely stained receptors are seen close together. x 1500.

Fig. 6. Composite of microphotographs of tangential sections through the olfactory epithelium of a rabbit, stained with protargol, showing the groups of olfactory receptors disposed in circles round the margins of the free extremities of supporting cells. Since not all the terminal expansions of the receptors with their olfactory hairs are in the same focal plane, it is not possible to show the complete picture of their interrelationships at the surface of the epithelium in a single microphotograph. However, in some places (e.g., the bottom right-hand corner) adjacent terminal expansions are in the same focal plane, and here it can be seen that the hair processes of immediately adjacent elements are in contact or slightly overlapping. x 3000.
Fig. 7. Protargol section of the olfactory epithelium of a rabbit forty-five days after ablation of the olfactory bulb of the corresponding side. Note the olfactory nerve fibres arising from the residual receptors and penetrating the basement membrane. A close examination of the actual sections provides no certain evidence of axonal branching or confluence. x 800.

Fig. 8. Protargol sections of the olfactory epithelium of the normal and operated side of a rabbit six weeks after complete unilateral ablation of the olfactory bulb. Note the residual olfactory receptors on the operated side. x 540.
In summary, the olfactory receptors of the rabbit differ histologically in the length and attenuation of the rod processes, the size of the terminal swelling (as indicated by the diameter of the marginal ring), the number of olfactory hairs attached to each terminal swelling, and their affinity for silver stains. This histological evidence of a morphological differentiation is in conformity with the electrophysiological evidence that the receptors are functionally differentiated, though it has yet to be determined whether there is a direct relationship between the two, and, if so, what the nature of the relationship may be. As we shall see, also, the receptors show a marked differentiation in their reaction to experimental lesions of the olfactory bulb. Lastly, it may be noted that we have not been able to detect any polymorphism of the receptors of the rabbit comparable with that described by Dogiel in the frog. Nor has it been possible to find any large binucleated receptors with coarse axons such as those described by Kolmer in the olfactory epithelium of Man.

The pattern of distribution of the olfactory receptors. Their appearance in vertical sections of the olfactory epithelium invites a comparison between the olfactory rods and the retinal receptors. But, apart from the terminal swellings and hairs of the former, there is an obvious difference in that the retinal rods and cones are densely packed in close apposition to each other, whereas the olfactory rods are separated by intervals of at least 1 μ or more. They are arranged in an hexagonal pattern around the periphery of the columnar supporting cells, the latter at their free extremity having a diameter of approximately 7 μ (Fig. 6). Counts made from microphotographs of tangential sections of the central region of the septal mucosa show that here the average number of rods surrounding each supporting cell is 9·8. From these data it may be calculated that in this part of the olfactory epithelium the density of rods is approximately 127,000 per mm², an estimate which corresponds well enough with the observations of Allison and Warwick who, by direct counts on sections with the aid of an Abbé camera lucida and on microphotographs, computed an average all-over density of 120,000 per mm² (taking into account a gradient of diminishing density near the peripheral margins of the olfactory epithelium). They further showed, from measurements on serial sections of the whole nasal cavity of two rabbits, that the total area of the olfactory epithelium in this animal is of the order of 4·5 cm² on each side. Thus the total number of receptors on each side of the nasal cavity of the rabbit is of the order of 50 million.

While the olfactory rods (and also their terminal swellings) are not in immediate apposition to each other, the olfactory hairs of the adjacent receptors surrounding each supporting cell may, if splayed out, be in contact or even overlap to a slight extent (Fig. 6). Thus through the olfactory
hairs there is an hexagonal mosaic of direct contiguity between olfactory receptors, a chain-mail-like pattern which may possibly provide the basis for an interaction between the receptors which is responsible for the spread of synchronized activity over the olfactory epithelium as described by Adrian and Ottoson.\(^8\) These authors have demonstrated that the synchronized activity occurs independently of connexions with the olfactory bulb and is almost certainly initiated at the receptor level. That the relationship of the olfactory rods to the supporting cells is a very intimate one is evident from sections in which the epithelium has become partly disrupted, leading to a separation and partial isolation of adjacent supporting cells. In such specimens each separate cell is seen to be closely surrounded by its complement of rods firmly adhering to its surface. The precise physical nature of this relationship is only likely to be determined by electron microscopy.

**Olfactory nerve fibres.** According to the classical studies of a number of early histologists using the Golgi technique, each olfactory nerve fibre is a direct continuation of the proximal process of a single olfactory receptor.* These processes, indeed, are the axons of the olfactory cells; they, and their continuations as the olfactory fibres which ultimately terminate in the olfactory bulb, are exceedingly fine, and thus very difficult to visualize in histological preparations. In successful protargol sections, however, it is possible to trace many of them individually with the oil-immersion from their cells of origin into fasciculi within the subepithelial layer of the olfactory mucosa. The most favourable material for their study is provided by experiments in which complete or partial ablation of the olfactory bulb has led (by a process of retrograde degeneration) to a “thinning out” of the receptors, so that the individual processes of those that remain may be more easily followed. Microphotographs of sections taken from one such experiment are shown in Figure 7. A close study of these sections has failed to yield any convincing evidence of the confluence of the proximal processes derived from groups of receptors to form single axons.

In other words, we have found no evidence to dispute the conclusion of earlier histologists that each olfactory receptor gives rise to a single axon which retains its individuality, perhaps as far as its termination in the olfactory bulb. If this is so, it follows that in the rabbit some fifty million

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\(^8\) In a paper published in 1942, Landau asserted that the proximal processes of the olfactory receptors end by breaking up into a plexus of terminals at the base of the epithelium. It seems likely that he mistook for proximal processes the palisade of reticulin fibres which extend vertically between the supporting cells of the epithelium, for these fibres (which can be demonstrated by silver impregnation) split up to form an intricate network of fine fibrils in the basement membrane. Incidentally, it seems not impossible that these reticulin fibres may have also been mistaken by some histologists for terminal ramifications of the trigeminal nerve in the olfactory epithelium.
axons must pass through the small perforations in the cribriform plate of the ethmoid to reach the bulb. On first consideration this might seem unlikely, but (even though it may be difficult to prove, for the reason that most of the fibres are too fine to permit a direct enumeration in whole sections) it does not appear to be an impossible assumption. Thus, in a transverse section taken through the upper part of the septum of one specimen (that is, close to the cribriform plate) we have counted 149 fasciculi of olfactory nerve fibres (excluding the vomero-nasal nerve fasciculi). These septal fasciculi vary greatly in size, but computations show that their total cross-sectional area (excluding that occupied by intrafascicular capillary vessels) is approximately $0.48 \text{ mm}^2$. We estimate, also, that about 80 per cent of the total area of each fasciculus is actually occupied by the subsidiary bundles of axons. If, now, we assume that the axons have a mean diameter of $0.2 \mu$ and are closely packed together in their subsidiary bundles, it follows that the total number of fibres which could theoretically be accommodated in the septal fasciculi would be of the order of 11,000,000. According to our computation of the number of receptors in the area of septal epithelium served by these fasciculi, this would readily permit the acceptance of a one-to-one ratio between olfactory nerve fibres and receptors. Naturally, this estimate can only be regarded as a very rough approximation for, among other things, account has to be taken of shrinkage in the course of histological preparation and of variations in the closeness of packing of the axons in their subsidiary bundles. But, as far as it goes, it does not appear to conflict with the supposition that the axonal processes of all the olfactory receptors retain their individuality up to their termination in the olfactory bulb.

Within the olfactory epithelial layer the axonal processes of a number of neighbouring receptors converge to form a small fasciculus which penetrates the basement membrane. Then, in the subepithelial tissue a series of such tributary fasciculi join the main fasciculi which are coursing upwards and backwards to the cribriform plate. Because of its possible relevance to the interpretation of electrophysiological records, it may be noted that, in the central region of the rabbit’s septal mucosa, the tributary fasciculi pierce the basement membrane at an average interval of about 100 $\mu$. Assuming, then, that the area of epithelium served by a tributary fasciculus is approximately circular, it may be inferred that each one of the latter is made up (on the average) of axonal processes derived from about 1000 receptors. Having pierced the basement membrane, each tributary fasciculus passes down vertically or obliquely to a depth of about 100 $\mu$ beneath the membrane before it joins a main fasciculus extending upwards and backwards parallel to the surface of the epithelium.
The differential reaction of olfactory receptors to lesions of the olfactory bulb. It is known that partial or complete lesions of the olfactory bulb in the rabbit lead to a very rapid degeneration of olfactory receptors.\textsuperscript{6,11} The degenerative process becomes visible in histological preparations as early as 24 hours after the operation, when the olfactory epithelium on the operated side shows a high proportion of pycnolic and fragmented nuclei and some fragmentation of the olfactory rods. Counts of the whole nuclei of receptor cells (in comparison with symmetrically equivalent regions of the epithelium on the normal side) show that by this time about 25 per cent have disappeared. After 48 hours the degenerative process is in its most active phase, and the affected epithelium is thickly strewn with nuclear remnants lying freely in intercellular spaces or enclosed in vacuoles within the cytoplasm of supporting cells (the latter having, it appears, assumed phagocytic properties). By now, about 50 per cent of the normal receptor nuclei have disintegrated. Three days after the operation, the debris of the degenerated receptors has almost all disappeared. So rapid and violent is the process (and so different from the process of retrograde degeneration of nerve cells as it is usually seen after axonal interruption) that some authorities have attributed it to vascular interference following damage to the ethmoidal vessels which pass down into the nasal cavity through the cribiform plate of the ethmoid. However, there are good reasons for supposing that this is not the case, the most convincing of which are (i) the fact that a similarly rapid degeneration, localized in its distribution, follows small lesions limited at the dorsal surface of the bulb (thus avoiding any encroachment on the region traversed by the ethmoidal vessels), and (ii) that rapid disintegration of receptors in the vomero-nasal organ (which is far removed from the territory of supply of the ethmoidal vessels) also occurs after bulbar ablation.

In our earlier studies of the effects of bulbar ablation we relied for our observations on the histological examination of only a limited region of the septal mucosa (i.e., that area of the mucosa which covers the cartilaginous part of the septum and was therefore able to be sectioned without preliminary decalcification). Assuming this to be a representative sample of the olfactory epithelium as a whole, it was then concluded that removal of the bulb is eventually followed by atrophy of all the receptors. From the examination of much more extensive material, and particularly with the successful application of activated protargol staining to complete serial sections of the entire nasal cavity after decalcification, we now know that this is not so. In fact, a considerable proportion of receptors persist (approximate counts of olfactory rods and nuclei on the operated and normal side indicate about 50 per cent), and these residual elements appear to be dis-
tributed more or less evenly, but with some local variations in density, over the whole extent of the olfactory epithelium (Fig. 8). A persistence of some of the receptors after bulbular ablation has been previously reported in the mouse by Nagahara, but we have not been able to confirm his claim that they are "resting" elements which by mitotic division provide the basis for regenerative processes. The significance of the residual receptors remains quite obscure at present. The possibility needs to be considered that they represent intrinsic elements whose axons terminate, not in the olfactory bulb, but in other parts of the epithelium. Or they might be elements whose main axons terminate in the bulb but also give rise to collaterals which effect connexions with neighbouring receptors in the epithelium. The difficulty with these "explanations" is that such intrinsic connexions have not so far been recorded in histological studies of the normal olfactory epithelium; nor have we been able to determine their existence in our experimental material. Hitherto we have only traced the axonal processes of the residual receptors into the remaining (relatively attenuated) fasciculi of olfactory nerve fibres, and it has yet to be determined how they end.

Whatever the significance of these observations may be, they are of some considerable interest in so far as they indicate that there are two major categories of olfactory receptor—those which disintegrate and disappear almost immediately after removal of the olfactory bulb, and those which persist. We do not know whether the residual elements retain any physiological activity, or whether in the normal epithelium they have differential functions. But it is difficult to suppose that the marked contrast which the two categories show in their reaction to bulbular lesions is not in some way correlated with a functional contrast.

Experiments carried out a few years ago showed that partial lesions of the olfactory bulb are followed by a secondary degeneration of receptors which has a localized regional distribution in the olfactory epithelium. This evidence was taken to indicate that there is some degree of spatial localization in the sense that different areas of the olfactory epithelium project to different regions of the bulb, a conclusion which is in general accord with Adrian's earlier observations based on the distribution of electrical potentials in the bulb following local stimulation of the olfactory epithelium. We have lately extended these experiments with confirmatory results. So far, however, the local lesions have in all cases involved the dorsal surface of the bulb, and a study of sections of normal material suggests that in this region the individual olfactory fasciculi pass more directly to individual glomeruli than may be the case in the more ventral regions. It has to be noted, also, that these local lesions must necessarily have involved the entering fasciculi of olfactory fibres as well as the bulb itself. It follows,
therefore, that the resulting degeneration in the olfactory epithelium may, at least in part, reflect the regional distribution of fibres within the involved fasciculi before the latter split up in a plexiform arrangement to reach their glomerular distribution within the bulb. In the ventral regions of the bulb the fasciculi are seen to break up into a highly complicated plexiform network so that the component fibres of each fasciculus appear ultimately to be distributed to widely separated glomerular formations. An enquiry is now being made into the distribution of regional degeneration in the olfactory epithelium following local lesions limited to the ventrally situated glomeruli, if possible without involving the olfactory nerve fasciculi as they enter the intracranial cavity.

SUMMARY

The essential structure of the olfactory receptors in the rabbit has been described on the basis of silver preparations. They have been shown to vary in the length and attenuation of the rod processes, the size of the terminal swellings, the number of olfactory hairs, and their affinity for silver stains. They also differ in their reactions to lesions of the olfactory bulb. In successful protargol preparations, the proximal processes of the receptors can be traced into olfactory nerve fasciculi; no evidence could be found of the confluence of several processes to form a single axon. Estimates based on the total cross-sectional area of fasciculi in the septum in relation to the known diameter of the olfactory nerve fibres do not conflict with the supposition that the axonal processes of all the receptors retain their individuality up to their termination in the olfactory bulb. Following bulbar lesions, a high proportion of receptors undergo necrosis and fragmentation within 48 hours. The possible significance of the residual receptors which persist after total ablation of the bulb is considered.

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