

1 or 2 particularly broad and dark lamellae, which contained the nucleus, Golgi area and great amounts of rough ER (Figure 2). The individual lamellae were separated by a gap varying in width from 33 to 540 nm. These gaps were filled with scarce microfilaments, collagen fibrils and 2 basal laminae covering the surface of the cytoplasmic lamellae. As a rule, the intercellular gaps were seen to increase in size towards the periphery of the corpuscles. The innermost lamella was contiguous to the axon and attached to it by desmosomes.

The presence of baroreceptors in rabbit and cat adrenals has been postulated on the basis of electrophysiological experiments⁴. NIJIMA and WINTER⁴ found that changes in systemic blood pressure were accompanied by changes in the firing rates of decentralized adrenal nerves. The authors concluded that these receptors could be part of a reflex system involved in the regulation of regional blood flow.

It is well agreed that Pacinian corpuscles are rapidly adapting mechanoreceptors specialized for the reception of vibration stimuli⁷. Although the corpuscles described in the present study differ from classical Pacinian corpuscles in so far as they lack a clearly identifiable perineural sheath, they are most probably mechanoreceptors as well. Hence we suggest that they form the afferents of a system contributing to a local regulation of adrenal blood flow. Adrenergic nerves, which could be interpreted as the corresponding efferents, have been observed in the walls of blood vessels in both cortex and medulla of the guinea-pig adrenal⁸.

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The Central Tubuli in Distal Segments of Olfactory Cilia Lack Dynein Arms¹

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Summary. By means of the tannic acid-glutaraldehyde fixation method, the lack of dynein bridges between the central two tubuli in distal segments of mouse olfactory cilia is demonstrated. Consequently, these organelles are supposed to be unable to beat actively, in contrast to the proximal ciliary shafts.

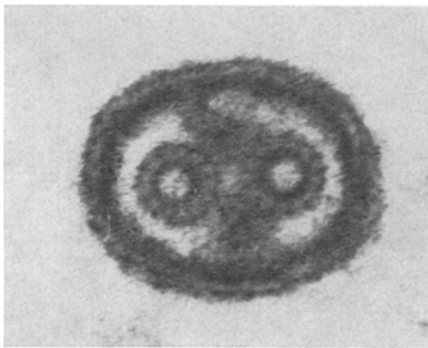
Olfactory cilia are the terminal processes of sensory neurons in the olfactory epithelium of many animals and of man. They are suspended in a superficial thick layer of mucus and exposed directly to stimulating molecules arriving from the inspired air. Besides the olfactory vesicles, cilia are candidates for the transduction of the stimulant-receptor interaction into an electrical event, either by the action of membrane associated proteins or membrane lipids^{3,4}.

Most commonly, olfactory cilia are built up by a proximal, thick shaft (diameter about 0.2 μm), and a distal, very long and thin segment, giving the cilium a total length of about 50 μm in rats⁵. With other centriole generated processes, the thick segments share the 9+2 pattern of tubuli. Towards the tip, the outer tubuli dis-

appear and finally the central pair extends to the distal segment of the cilium⁶.

The motility of olfactory sensory cilia is still an unsettled problem. According to the sliding filament hypothesis⁷, the presence of dynein arms on tubules is an essential requirement for active movement. The present study provides evidence that distal ciliary segments in the mouse olfactory mucosa lack dynein bridges and therefore are not able to beat actively.

Methods. Nasal septae of adult and newborn Swiss mice were excised as reported previously⁸, and fixed by immersion in 2.5% purified glutar aldehyde in 0.1 M cacodylate buffer pH 7.4. This fixative was supplemented with 4% tannic acid⁹, as a mordant for tubular protofilaments. After postfixation in veronal acetate buffered osmium solution¹⁰, and embedding in Epon 812 following routine techniques, thin sections were double stained in uranyl acetate and lead citrate solution¹¹, and examined in a Philips EM 200 electron microscope.



Transsection of a distal segment of mouse olfactory cilium. The unit membrane is covered both on its inner and outer side by an osmiophilic layer. Note the 2 branches of osmiophilic material, which insert into the inner submembranous layer and the tubuli respectively, where their arms span 4 of the 13 protofilaments. No dynein bridges are perceivable. $\times 500,000$.

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Results and discussion. Distal segments of olfactory vesicles display elliptic transsections, the diameters measuring 1400 Å and 900 Å, respectively. The double membrane is coated on its outside by a thin (60 Å), osmiophilic layer, and, more conspicuous, on its inner aspect by a relatively electron dense, homogenous 100 Å thick film. Exactly in the small axis of the ellipse from this interior coat originate dark staining branches (120 × 100 Å), which split in a fairly constant distance of 500 Å from their origin in 2 V-shaped arms, which in their turn insert into the central tubuli. This pattern was the only one to be observed in a few hundred transsections.

The tubuli are composed by 13 protofilaments, visible only in transsections. Tannic acid outlines the subunits and forms a cog wheel pattern (Figure). The V-shaped arms contact the tubuli in such a manner that 4 protofilaments lie between them in the center of the cilium, and the 9 left filaments remain outside. The interior border of the protofilaments is supported by a thin (30 Å) ring of highly osmiophilic substance. Lateral processes of tubuli that could correspond to dynein arms as seen in various cilia of the 9+2 pattern, were virtually absent in all preparations.

Active movement of olfactory cilia has been a matter of dispute in the past¹². Since olfactory cilia are likely to harbour receptor sites in their membrane, because of their particulate location in the upper storey of the olfactory surface, active motility was thought to facilitate both contact with stimulating molecules and cleaning of the cell surface after registration of odour substances on the membrane¹³.

Direct evidence for ciliary beating has been achieved by direct microscopical observation of the frog olfactory mucosa⁶. The proximal thick segments appeared to beat uncoordinated and very vigorously, especially after elimination of the distal segments. Distal segments seemed to be moved passively and to retard the movements of proximal parts.

The present study demonstrates that tubuli of distal segments lack dynein bridges, which have been convincingly demonstrated to be essential for active movement in human sperm¹⁴. Since the two tubules found in distal segments seem to be extensions of the central pair in the 9+2 pattern of proximal shafts, the lack of dynein bridges is actually not surprising, because they are devoid of these arms from their origin. According to the sliding filament hypothesis the central pair is the anchoring site of radial spokes of peripheral doublets. It mediates the conversion of the linear sliding of peripheral tubules into a bending of the whole cilium⁷. Thus, the possibility is excluded that the central pair of microtubuli acquires dynein bridges somewhere distal from the 9+2 portion.

As in many other instances, the tubuli are composed by 13 protofilaments, which are very prominent in transsections after tannic acid impregnation⁹. The osmiophilic submembranous coat in cilia may play an active role in the stabilization of intramembranous particles in olfactory cilia, as recently demonstrated in abundance by freeze etching⁸. The Y-shaped connections of this layer with the tubuli may provide an inner skeleton for distal ciliary segments, resembling the horizontal interconnecting filaments in microvilli of the intestinal brush border¹⁵.

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Failure of ³H-Serine to Induce Radioactivity in Presumed Glycinergic Retinal Neurons¹

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Summary. ³H-serine does not label retinal neurons selectively when injected intraocularly in rabbits, as would have been expected if it had been converted to neurotransmitter glycine. The reason is unknown, but one possibility is that the conversion was blocked during the conditions of the experiment.

Glycine has recently been advanced as a putative retinal transmitter in rabbits. It is present in the retina in freely extractable form in comparatively high concentration^{2,3}; it is actively and selectively accumulated by certain amacrine neurons with a high-affinity mechanism^{4,5}, and it is also stored in a comparatively protected pool⁶. Moreover, it has recently been demonstrated to be releasable by light stimulation both in vivo and in vitro^{7,8}. Glycine thus fulfills several of the main criteria of a transmitter substance.

Glycine is usually regarded as formed from serine by removing a hydroxyl group. It was thus of interest to see whether the neurons being labelled by ³H-glycine would also be labelled by ³H-serine. In a previous report, this was not the case⁶, but there the tritium label was in the hydroxyl group of serine, and any glycine formed would not necessarily have been radioactive.

Rabbits were therefore injected intravitreally with 25 µCi L-serine-³H (generally labelled), 4 or 24 h before processing the eyes for diffusion-free autoradiography as previously described⁶. The animals were kept in ambient

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