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The musculature of the mystacial vibrissae of the white mouse

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INTRODUCTION

Many anatomical (Woolsey & Van der Loos, 1970; White, 1976) and physiological (Waite, 1973; Shipley, 1974; Simons, 1978) studies have been carried out in recent years on the sensory relationship between the mystacial region and the central nervous system of the mouse and the rat in normal as well as in experimentally modified conditions. It has been established that the vibrissal follicles, each with its own set of receptors, project somatotopically to the parietal neocortex (see above references) and to the subcortical relays (thalamus: Van der Loos, 1976; brainstem: Belford & Killackey, 1979). Early postnatal destruction of vibrissal follicles has been shown to produce permanent alterations of the central projections (e.g. Van der Loos & Woolsey, 1973; Harris & Woolsey, 1979; Steffen & Van der Loos, 1980; Wong-Riley & Welt, 1980; Jeanmonod, Rice & Van der Loos, 1981).

Although the central representation of the follicular receptors is well described, little is known about the anatomy of the mystacial region itself. No data exist on the muscles moving the vibrissae nor on the topography of the sensory and motor innervation of the muzzle of the mouse, although one can extrapolate to some extent from descriptions of other species with vibrissae. Vincent (1913) described in the rat a flat muscle surrounding the follicle on three sides. Yohro (1977) studied the arrangement and the structure of sinus hair muscles in *Sorex unguiculatus*. According to his description, striated muscles originate from the base of the follicle and insert, usually divided into two bundles, in the superficial part of the adjoining caudal follicle. The association of the facial musculature to the vibrissal follicles, in particular m. levator labii superioris, was observed in Crocidura (Ärnback-Christie-Linde, 1907), in the hedgehog (Michelson, 1922), in some rodents (Schreiber, 1929), in marsupials and numerous placentals (Huber, 1930), and in the rat (Green, 1959), but a full, coherent description has not yet been given.

In the present study the muscles of mystacial vibrissae in a common albino mouse are described, not only for a better understanding of the topography involved in its own right, but also as an aid to experiments in this region, in general performed with the aim of modifying the structures of the corresponding centres in the brain.

MATERIAL AND METHODS

Sixty four adult albino mice of both sexes were examined (type ICR, Institut für Zuchthygiene, University of Zürich, CH-8057 Zürich). Forty were used for microdissection and 24 for histological examination. Mice were anaesthetized with Nembutal (60 mg/kg, i.p.) and perfused with 10 % neutralized formalin in 0·9 % NaCl. The region of the big mystacial vibrissae was studied. Their arrangement on

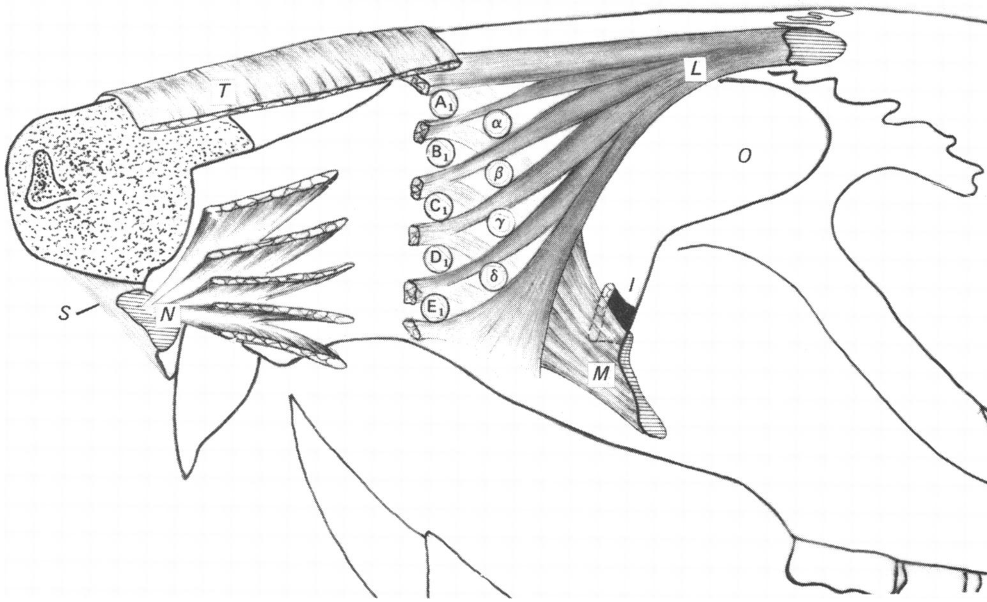


Fig. 1. Schematic drawing of the extrinsic musculature of the left whisker pad of a mouse. Origins of muscles are hatched; dotted area represents nasal cartilage. α–δ: the four follicles that 'straddle' the 5 follicle rows (A–E) of which only numbers 1 – the most caudal elements – are shown. *I*, infraorbital nerve; *L*, m. levator labii superioris; *M*, m. maxillolabialis; *N*, m. nasalis; *O*, orbit; *T*, m. transversus nasi; *S*, septum intermusculare.

the muzzle is shown in Figure 2; for more details see Van der Loos & Dörfl (1978). Fixed muzzles were cut partly in a cryostat at 40 μm and partly after paraffin embedding at 10–12 μm. The material was stained by the method of Mallory, resorcin-fuchsin and haematoxylin-eosin or, for nerve fibres, by modified methods of Lillie and Liesegang. The microdissection was done in ten mice on muzzles fixed with formalin. In 30 mice, formalin-fixed heads were placed for 36 hours in 20% nitric acid, neutralized for 24 hours in 5% Na_2SO_4, and washed in running tap water for 12 hours. After this treatment the skin and the connective tissue surrounding follicles became friable and easy to remove, whereas the muscles remained intact so that their topography, including their attachments, could be displayed in good detail. This technique was used particularly for the dissection of the intrinsic muscle group (Fig. 9).

RESULTS

Vibrissal follicles were surrounded by striated muscles that have been grouped in two categories: extrinsic and intrinsic muscles.

Extrinsic muscles (Fig. 1)

Extrinsic muscles belong to the group of facial muscles moving the upper lip and the wing of the nose. Some of these muscles are so closely linked to the mystacial region that the latter may be considered as their principal insertion zone. They are called extrinsic because of their origins on different regions of the skull outside the mystacial region.

M. levator labii superioris

Origin. Frontal bone, behind the nasofrontal suture. This flat muscle ran fan-shaped to the posterior margin of the mystacial region and penetrated between the five rows of mystacial vibrissae, also giving off two muscular bands, one lateral and one medial to the mystacial region. It was thus divided into six longitudinal bundles running superficially under the skin. They inserted into the corium between the vibrissal follicles. The most rostral part of these bundles attached to the corium of the wing of the nose lateral to the nostril and to the skin of the upper lip from the nostril nearly to the labial commissure.

M. maxillolabialis

Origin. From a tuberculum on the maxilla below the infraorbital fissure and from the lateral ridge of this fissure. Its fibres ran, covered by m. levator labii superioris, to the posterior border of the mystacial region, penetrated between the rows of mystacial follicles and blended with the longitudinal bundles of m. levator labii superioris.

M. transversus nasi

This was an unpaired, flat muscle on the dorsum of the muzzle where it extended from the posterior limit of the mystacial region to the tip of the nose. It was formed by transverse fibres crossing at right angles the medial longitudinal bundles of mm. levator labii superioris and maxillolabialis, which were partly covered and partly perforated by it. The transverse fibres could be followed laterally as far as row C.

M. nasalis

Origin. From the premaxillary bone just medial to the exit of the upper incisor and from a septum stretched in the median sagittal plane between the premaxillae and the nasal cartilages (see also Fig. 4). The muscle divided into fan-shaped muscular sheets running caudally in the spaces between the five rows of mystacial follicles. Terminal fibres crossed the three above mentioned muscles and inserted into the corium between the rows of follicles. Caudally the muscle reached the region of the biggest vibrissae (α, β, γ, δ).

Intrinsic muscles (Figs. 2, 3, 7, 8, 9)

Besides the four extrinsic muscles inserting in the corium between the follicles, there was another group of small muscles associated solely with vibrissal follicles without any bony attachment. Each one of these follicular muscles connected two adjacent follicles of the same row. The muscles had the form of a sling, surrounding the lower third of the rostral member of every pair of follicles and inserting by its extremities into the medial and lateral faces of the superior part of the caudal follicle; a small portion of the extremities inserted also to the adjoining corium (Fig. 3). In the case of the most caudal follicles (A_1, B_1, C_1, D_1, E_1 and α, β, γ, δ), these extremities blended with the fibres of m. levator labii superioris and m. maxillolabialis and appeared to insert partially in a condensation of connective tissue behind the mystacial region and partially in the adjoining corium. The size of the muscles increased with the size of the follicles, the biggest being those that were associated with follicles α, β, γ, δ. Follicular muscles were found around all follicles of rows A and B (normally four follicles per row) and the first six, or exceptionally

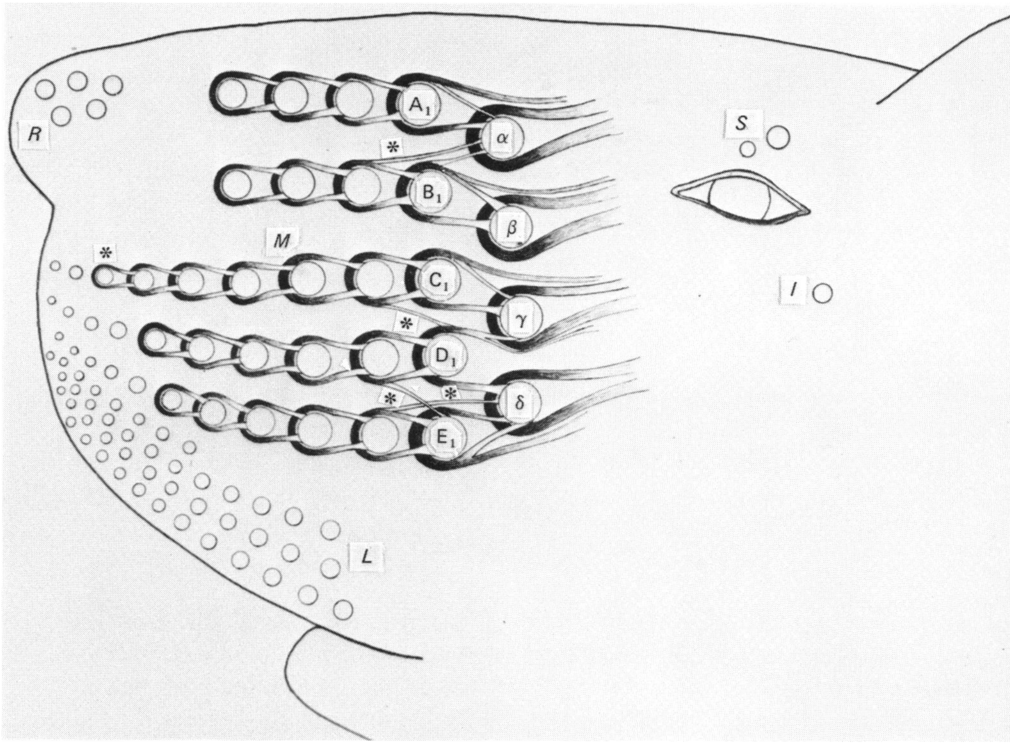


Fig. 2. Schematic drawing of the intrinsic musculature of the left mystacial region. Groups of sinus follicles are represented: *I*, infraorbital; *L*, labial; *M*, mystacial; *R*, rhinal; *S*, supraorbital. Each mystacial follicle is rostrally embraced by a muscle sling. These arciform part of the slings are represented in black, the ends of the slings, directed posteriorly, in shades of grey. Asterisks indicate rare muscle bundles. Note that the rostral follicles of rows C, D and E have no intrinsic muscles.

seven, follicles of rows C, D, E (Fig. 2). The more rostral follicles of rows C, D, E were closely spaced and richly surrounded by the fibres of extrinsic muscles; intrinsic muscles associated with them were not found.

The follicles with their muscle slings were placed in adipose tissue allowing the free movement of follicles. In this adipose tissue were condensations of connective fibres in the form of bands parallel to the skin surface, connecting the lower parts of the follicles of the same row. Follicles seemed to perforate this band, giving it the aspect of a fenestrated ribbon. The condensation of fibres was especially marked between the rostral and caudal faces of two neighbouring follicles where they took on a plate-like form. These plates fixed caudally to the deep border of the follicular muscle sling and to the adjacent part of the caudal follicle; rostrally they were attached to the posterior face of the rostral follicle below the penetration of the vibrissal nerve (branch of the infraorbital nerve penetrating from the medial side between the two extremities of each follicular muscle and perforating the posterior face of the follicle (Figs. 3, 7, 8, 9). Rostrally the bands could be followed to the anterior part of the lip where they terminated in the loose connective tissue filling the space between the sheets of m. nasalis and around the most rostral follicles.

Intrinsic muscles were innervated by the facial nerve whose branches reached the region between the two extremities of the follicular muscle. At that point each branch bifurcated into medial and lateral rami which innervated the corresponding

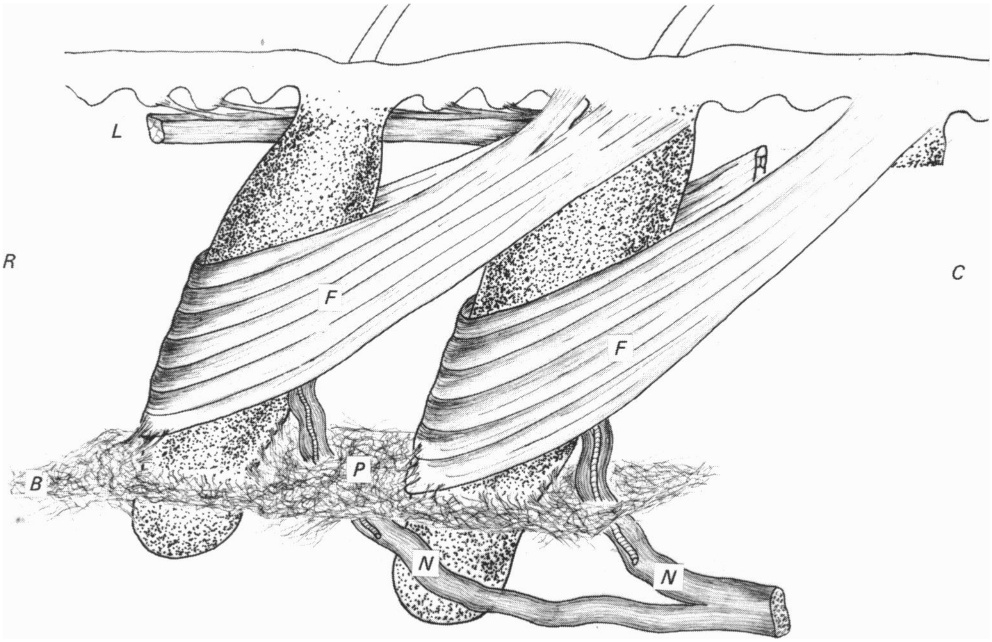


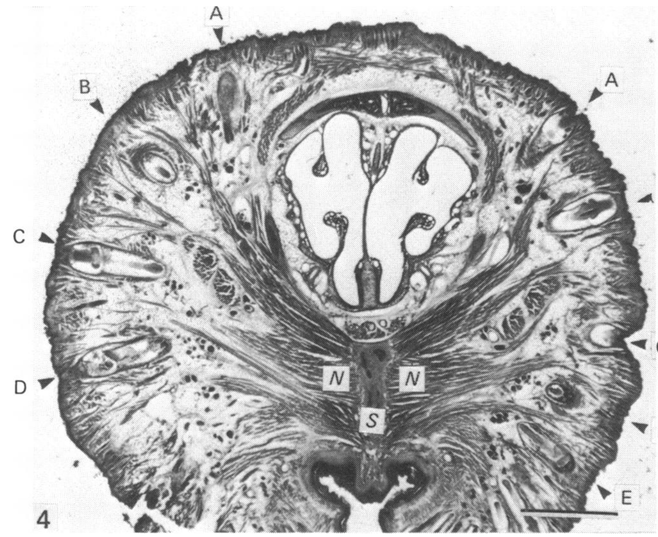
Fig. 3. Schematic drawing of two neighbouring mystacial follicles in the same row. Medial view. *R*, rostral; *C*, caudal. *B*, fibrous band connecting the lower parts of the follicles; the part of the band between the rostral and caudal faces of two adjacent follicles is called plate (*P*). *F*, follicular (intrinsic) muscle; *L*, longitudinal muscular band formed by fibres of m. levator labii sup. and m. maxillolabialis; *N*, follicular nerve accompanied by an artery.

extremity of the follicular muscle. Nerves were never observed in the rostral, arciform portion of the muscle sling, i.e. where it looped around the rostral aspect of the follicle. Detailed descriptions of the sensory and motor innervation of the mystacial region will be published separately.

DISCUSSION

Our present understanding of the functions of the extrinsic and intrinsic muscles is based largely on observation of their topography; their functions have not been studied by stimulation of the nerve or by electromyography. Welker's (1963) description and analysis of the sniffing behaviour of the rat has led, however, to some interesting conclusions about the function of these muscles. According to Welker (1963) the sniffing cycle is composed of two phases: approach and withdrawal. The approach phase, i.e. that time when the nose makes contact with a surface, is characterized by the retraction of the tip of the nose and the maximal protraction of the vibrissae. Simultaneously, the head approaches the object in question and the rat inspires. In the withdrawal phase, which follows immediately and is about twice as fast as the approach phase, the tip of the nose protracts, the vibrissae retract, the head goes back, and the animal exhales.

Casual observation of the sniffing mouse shows clearly that not only the tip of the nose but also the whole mystacial region is displaced in various directions. It is suggested that this is due to the action of the extrinsic muscles: the m. levator labii superioris pulling the mystacial region backwards and medially, the m. maxillolabialis pulling backwards and laterally, the m. transversus nasi moving both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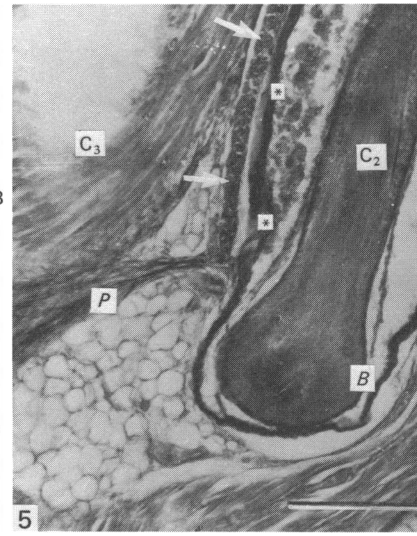
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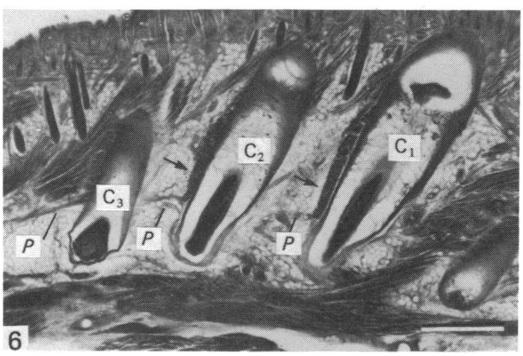
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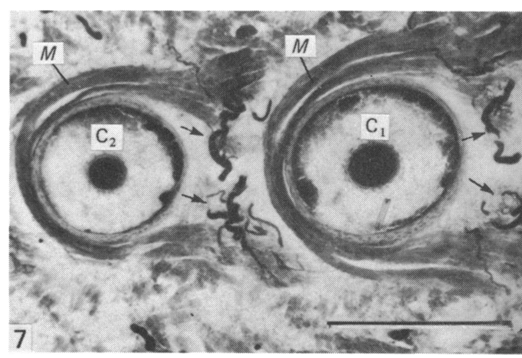
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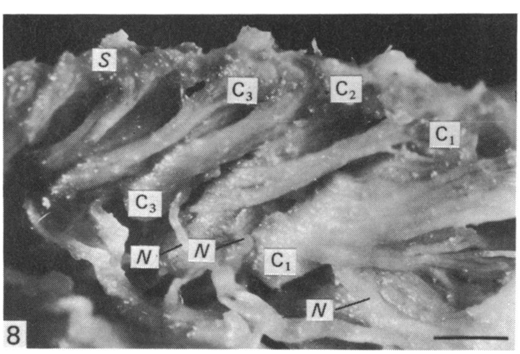
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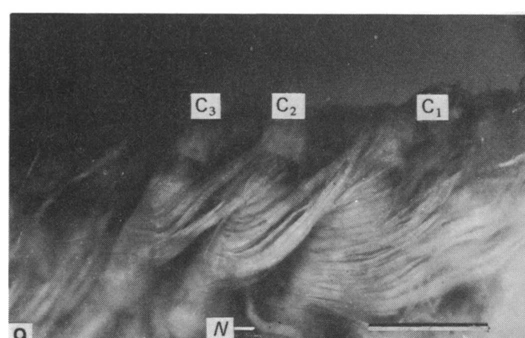
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mystacial regions medially while the m. nasalis is responsible for the protraction of the mystacial region. The tip of the nose is moved by other, deeper muscles which do not insert into the skin of the mystacial region or into the mystacial follicles.

The movement of an individual vibrissa results from the movement of its follicle. The follicle is fixed to the dermis of the skin by the uppermost broadened part of its fibrous capsule, the conical body. The region of the conical body may be considered a fulcrum, the bulb of the follicle being the region of greatest excursion during the movement of the follicle. One may deduce from the topography and insertions of the intrinsic muscles that their contraction causes the follicle base to be displaced backwards, a movement expressed on the surface of the muzzle as a protraction of the vibrissa. In sleeping mice, the vibrissae are retracted, which seems to be their resting position. This corresponds to the fact that, in anaesthetized or perfused mice, the bases of the follicles are directed forwards. There is no muscle producing an active retraction of vibrissae. The fast return of a protracted vibrissa to its resting position appears to be caused by the elasticity of the connective tissue that surrounds the follicles. It is proposed that the fibrous bands, connecting the bases of the follicles of one row with each other and with the front end of the muzzle, become stretched during the protraction of vibrissae; they would contract immediately after the termination of the shortening of the muscle slings: an economical way of executing a stereotyped, fast to-and-fro movement.

SUMMARY

Striated muscles of the mystacial region of the common albino mouse have been described. They were divided into two categories: extrinsic and intrinsic.

The four extrinsic muscles (m. levator labii superioris, m. maxillolabialis, m. transversus nasi, m. nasalis) belong to the facial muscles. They originate on the skull and insert into the corium between the mystacial vibrissae. Their contraction moves the whole mystacial region in directions dependent on their origins.

Fig. 4. Transverse section through the cartilaginous portion of the muzzle. Arrowheads point to vibrissal follicles defined by row. 40 μm thick section. Mallory stain. *N*, m. nasalis; *S*, septum intermusculare (see also Fig. 1). Scale = 1 mm.

Fig. 5. Rostrocaudal section, perpendicular to the skin, through the deeper half of follicle C_2. Anterior is to the left. Note the fibrous plate (*P*) that is attached to the deep limit of the follicular ('intrinsic') muscle sling; its arciform portion (arrows), applied to the anterior aspect of the follicle (asterisks), is cut transversely. *B*, base of the follicle; C_3, para-axial cut through follicle C3. 12 μm thick section. Mallory stain. Scale = 0·2 mm.

Fig. 6. Rostrocaudal section, perpendicular to the skin, through follicles 1–3 of row C. Anterior is to the left. Arrows point to the transversely cut arciform portions of the follicular muscles. *P*, fibrous plates, as shown in detail in Fig. 5. 12 μm thick section. Mallory stain. Scale = 0·5 mm.

Fig. 7. Section, parallel to the skin, through follicles 1 and 2 of row C. 40 μm thick section. Lillie stain. *M*, follicular muscle cut longitudinally; arrows point to branches of facial nerve which innervate the follicular muscles. They are here shown to penetrate the extremities of muscle slings. Scale = 0·5 mm.

Fig. 8. Microdissection of formalin-fixed preparation of the right mystacial region. C row of follicles with their muscle slings was dissected from the medial side (cf. Fig. 3). For both of the two adjacent follicles, the follicular muscles are slung around the rostral aspect of the rostral follicle's deep portion, while their ends, directed obliquely towards the skin, insert into the medial and lateral aspects of the caudal follicle's superficial portion and into the neighbouring dermis. *S*, skin; *N*, follicular nerve coming from below to penetrate the dorsal aspect of the follicle after a short journey between the ends of the muscle sling. Scale = 0·5 mm.

Fig. 9. Microdissection of preparation similar to that of Fig. 8. The difference is in the post-fixation treatment of the tissue with nitric acid. *N*, follicular nerve to C_2. Scale = 0·5 mm.

Intrinsic (follicular) muscles are associated solely with the vibrissal follicles and have no bony attachment. They were found around follicles α, β, γ, δ, around all follicles of rows A and B, and around the first six follicles of rows C, D and E. The form of the follicular muscle is a sling connecting two adjacent follicles of the same row. The arc of the sling surrounds the inferior part of the rostral follicle and the two extremities insert to the conical body of the caudal follicle and to the neighbouring corium. They are the protractors of the vibrissae.

The inferior parts of the vibrissal follicles of a given row are fixed in a fibrous band which inserts in the anterior part of the muzzle. It is proposed that these bands become stretched during the protraction of vibrissae and contract, by their elasticity, immediately upon the end of the follicular muscles' contraction, executing the fast return of vibrissae to their resting, retracted position.

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REFERENCES

Ärnback-Christie-Linde, A. (1907). Der Bau der Soriciden und ihre Beziehung zu anderen Säugetieren. I. *Morphologisches Jahrbuch* **36**, 463–513.

Belford, G. R. & Killackey, H. P. (1979). Vibrissae representation in subcortical trigeminal centers of the neonatal rat. *Journal of Comparative Neurology* **183**, 305–321.

Green, E. Ch. (1959). *The Anatomy of the Rat*. New York: Hafner.

Harris, R. M. & Woolsey, T. A. (1979). Morphology of Golgi-impregnated neurones in mouse cortical barrels following vibrissae damage at different postnatal ages. *Brain Research* **161**, 143–149.

Huber, E. (1930). Evolution of facial musculature and cutaneous field of trigeminus. *Quarterly Review of Biology* **5**, 133–188.

Jeanmonod, D., Rice, F. L. & Van der Loos, H. (1981). Mouse somatosensory cortex: alterations in the barrelfield following receptor injury at different early postnatal ages. *Neuroscience* **6**, 1503–1535.

Michelson, G. (1922). Die Hautmuskulatur des Igels (*Erinaceus europaeus*). *Morphologisches Jahrbuch* **51**, 147–230.

Schreiber, H. (1929). Untersuchungen über die Facialismuskulatur einiger Nager. *Morphologisches Jahrbuch* **62**, 243–318.

Shipley, M. T. (1974). Response characteristics of single units in the rat's trigeminal nuclei to vibrissa displacements. *Journal of Neurophysiology* **37**, 73–90.

Simons, D. J. (1978). Response properties of vibrissa units in rat SI somatosensory neocortex. *Journal of Neurophysiology* **41**, 798–820.

Steffen, H. & Van der Loos, H. (1980). Early lesions of mouse vibrissal follicle: Their influence on dendrite orientation in the cortical barrelfield. *Experimental Brain Research* **40**, 419–431.

Van der Loos, H. (1976). Barreloids in mouse somatosensory thalamus. *Neuroscience Letters* **2**, 1–6.

Van der Loos, H. & Dörfl, J. (1978). Does the skin tell the somatosensory cortex how to construct a map of the periphery? *Neuroscience Letters* **7**, 23–30.

Van der Loos, H. & Woolsey, T. A. (1973). Somatosensory cortex: structural alterations following early injury to sense organs. *Science* **179**, 395–398.

Vincent, S. B. (1913). The tactile hair of the white rat. *Journal of Comparative Neurology* **23**, 1–36.

Waite, P. M. E. (1973). The response of cells in the rat thalamus to mechanical movements of the whiskers. *Journal of Physiology* **228**, 541–561.

Welker, W. I. (1963). Analysis of sniffing of the albino rat. *Behaviour* **12**, 223–244.

White, E. L. (1976). Ultrastructure and synaptic contact in barrels of mouse SI cortex. *Brain Research* **105**, 229–251.

Wong-Riley, M. T. T. & Welt, C. (1980). Histochemical changes in cytochrome oxidase of cortical barrels after vibrissal removal in neonatal and adult mice. *Proceedings of the National Academy of Science of the U.S.A. Neurobiology* **77**, 2333–2337.

Woolsey, T. A. & Van der Loos, H. (1970). The structural organisation of layer IV in the somatosensory region (SI) of mouse cerebral cortex. The description of a cortical field composed of discrete cytoarchitectonic units. *Brain Research* **17**, 205–242.

Yohro, T. (1977). Arrangement and structure of sinus hair muscles in the big-clawed shrew, *Sorex unguiculatus*. *Journal of Morphology* **153**, 317–332.