

Merkel Nerve Endings Functioning as Mechanoreceptors in Vertebrates

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Summary

This study focused on those types of mammalian nerve endings originally described by Merkel in 1875. In all mammals, Merkel cells are found in the basal layer of the epithelium usually in close contact with nerve terminals. The Merkel cell is always positioned between the direction of the mechanical stimulus and the nerve terminal. Any similar cell without nerve contact may have neuroendocrine, but not mechanoreceptor functions. Thus, such cells should not be called Merkel cells, as there is no evidence for any relationship with those structures originally described by Merkel.

Introduction

In 1875, Friedrich S. Merkel first described "Tastzellen" (touch cells) and "Tastkörperchen" (touch corpuscles) in avian dermis and oral mucosa as well as in mammalian epidermis (Merkel 1875). In all cases, the Merkel cells were closely associated with nerve terminals. The name indicates that Merkel was convinced to look at mechanoreceptors.

Results and Discussion

Merkel Nerve Endings in the Mammalian Glabrous Skin

In contrast to the location of Merkel cells and Grandry corpuscles in the connective tissue below the epidermis in birds, Merkel cells in the mammalian gla-

brous skin are always found in the basal layer of the epidermis (Fig. 1). There are two types of glabrous skin in mammals. The first type (pegged skin) has solid epidermal pegs of different size anchoring the epidermis in the dermis. A typical example is found in the pig snout and planum nasale of mole and cat. The dermis contains blood sinus separating the epithelial pegs. In the basal layer of the epidermis at the base of these pegs are clusters of up to 40 Merkel cells. Smaller pegs may only have 6 Merkel cells. All Merkel cells are in contact with terminals of myelinated axons ($3\text{--}5\ \mu\text{m}$) losing their axon on entering the epidermis and branching into several discoid terminals with large numbers of mitochondria and electron microscopically empty vesicles. While in the nose of the mole only one axon innervates the Merkel cells of an epithelial peg, there are several axons supplying one epithelial peg in the pig snout.

Merkel cells are oval in shape with the longitudinal axis parallel to the basal lamina (Fig. 2). The nucleus is large and lobulated. The cytoplasm contains bundles of intermediary filaments and osmiophilic granules of about $60\ \text{nm}$ adjacent to the nerve terminal. Some regions of the membrane between Merkel cell and nerve terminal have synapse-like structures, while on the opposite site cytoplasmic processes extend into and between keratinocytes linked with desmosomes.

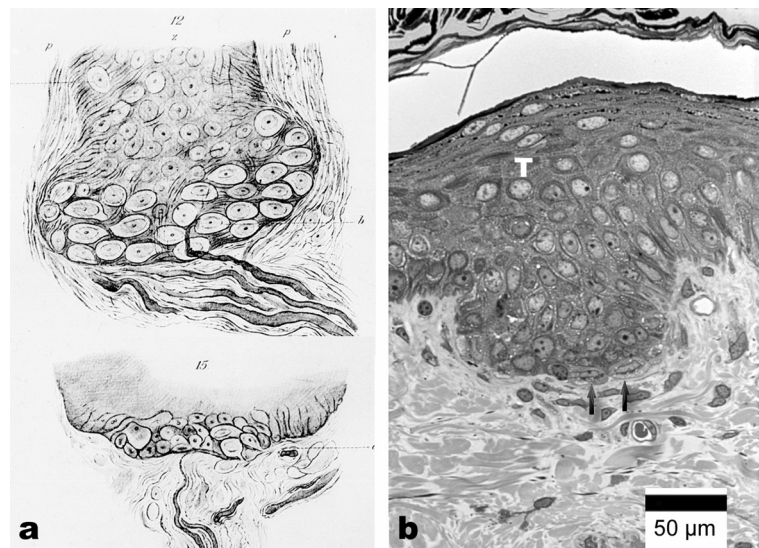


Fig. 1. **a** Original drawings from Merkel's publication (1875) illustrating "touch corpuscles" in mammalian glabrous skin. **b** Semithin section of a "Tastscheibe" (T) with Merkel nerve endings (arrows) in epidermal rete peg from the eyelid of a rhesus monkey

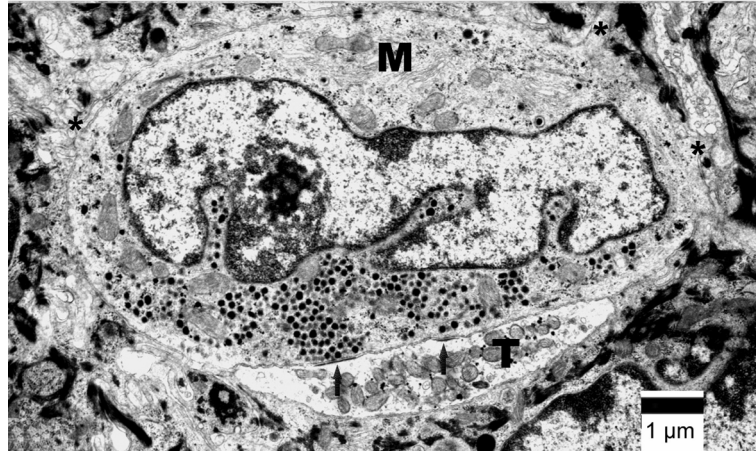


Fig. 2. High power electron microscopy of a Merkel cell (*M*) with nerve terminal (*T*) from the rete peg skin of the cat nose. Synapse-like contacts can be seen between Merkel cell and nerve terminal (*arrows*)

The second type of skin (ridged skin) is typically found in tips of fingers and toes of primates and marsupials. Clusters of up to ten Merkel nerve endings are found at the base of the epidermal ridges near the ducts of sweat glands. Moreover, in this location the long axis of the oval Merkel cells runs parallel to the surface with the nerve terminals below the Merkel cells towards the basal lamina.

Merkel Nerve Endings in Hairy Skin and Whiskers

Between hair follicles of the hairy skin, the epidermis forms epithelial pegs of different size and density, often referred to as touch disks ("Tastscheiben"). These are basically similar to the epithelial pegs in glabrous skin (see above), containing variable numbers of Merkel nerve endings, depending on the size of the touch dome. In addition, Merkel cells with a similar arrangement are found in the thickening of hair follicles below the sebaceous gland of guard and velus hairs. Whiskers are large hair follicles embedded in blood sinus with strong sturdy hairs. Merkel nerve endings in connection with whiskers are found in two locations. A small number can be seen at the transition between hair follicle and surrounding epidermis. Much larger numbers (up to 2,000) are located in the basal layer of the epithelium of the hair follicle in the thickened part below the sebaceous gland. This area is surrounded by the ring sinus. Merkel cells are arranged oblique to the basal lamina (glassy membrane) sending cytoplasmic processes of up to 15 μm through the glassy membrane (Fig. 3). All of them are in contact with discoid nerve terminals on the opposite side. The part of Merkel cells facing nerve terminals contains the typical dense core (osmiophilic) granules. After losing their myelin sheath and Schwann cells, the axons branch intensively supplying up to 50 Merkel cells. A more detailed review of morphology, development and physiology of Merkel cells is given in Halata et al. (2003).

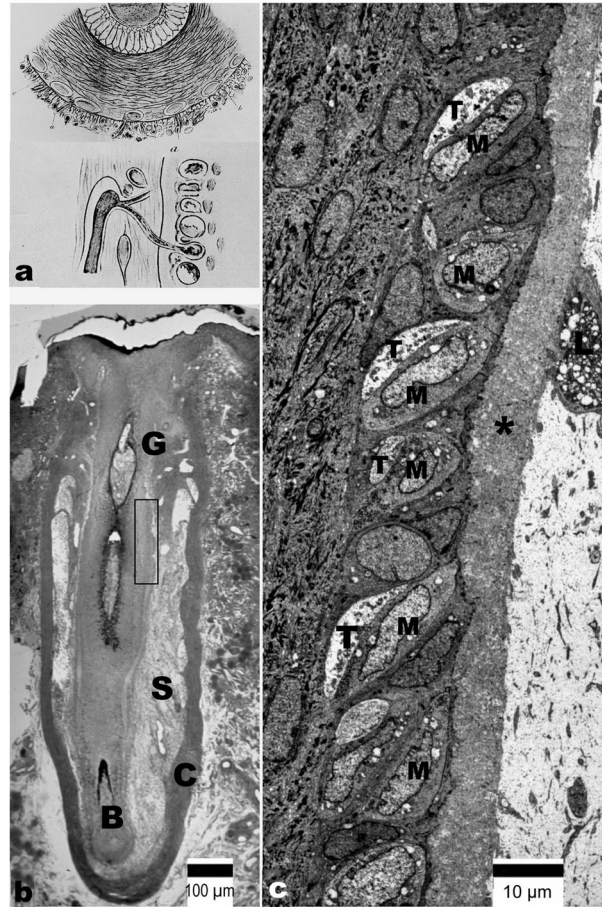


Fig. 3. **a** Original drawing from Merkel's publication (1875) illustrating "touch cells" in pig sinus hairs. **b** Semithin longitudinal section through a rhesus monkey sinus hair from the upper lip in low magnification showing a sebaceous gland (*G*), the cavernous blood sinus (*S*), the connective tissue capsule of the sinus (*C*) and the hair bulb (*B*). The *square* indicates the area shown enlarged in **c**. **c** Ultrathin longitudinal section through the thickened portion of the sinus hair follicle below the sebaceous gland. Merkel cells (*M*) and nerve terminals (*T*) are arranged obliquely to the glassy membrane (*) like the scales of a pine cone, with the Merkel cells always directed towards the glassy membrane. A lanceolate nerve terminal (*L*) in close contact with the glassy membrane (*) is seen on the outer side

References

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- Merkel F (1875) Tastzellen und Tastkörperchen bei den Hausthieren und beim Menschen. *Arch Mikr Anat* 11:636–652