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RESEARCH ARTICLE

THE SENSONEURAL ORGANIZATION OF THE SNOUT SKIN OF THE COW (*BOS INDICUS*) IN LIGHT OF THE SOMATOSENSORY ADAPTATIONS OF MAMMALS

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ABSTRACT

Background: In bovines, snout is used as a tactile organ while foraging for food and in social interaction. The snout has the surface that is comparable to the glabrous skin of most non-hooved mammals.
Aim of study: To study the structure, pattern of innervation and nerve terminations in the snout of the cow, so as to understand somatosensory adaptation of mammals.
Material and Methods: Skin samples from fifteen animals (cow/ox) were taken, sections prepared and stained with a cytological (Haematoxylin – Eosin and Von Gieson's stains) and a neural stain (Silver Impregnation).
Results: With cytological stain, the bovine snout consisted of glabrous skin having well defined dermal ridges. Three types of cells were seen in the epidermis- keratinocytes, melonocytes and Merkel's cells. After silver impregnation, nerve plexuses were observed in the dermis, from which myelinated nerve fibers ascended up towards epidermis. Four types of nerve fibers were observed in the snout: free nerve endings, Merkel's nerve endings, papillary nerves and bovine corpuscles. Free nerve endings were sparse due to their loss to tactile friction i. e. grazing. Merkel's cells were grouped at the dermal pegs. The bovine corpuscular nerve endings, present in the dermal papillae, were two types: one was elongated or cylindrical and the other oval or globular, formed high up in the dermal papilla, close to stratum granulosum. Both types consisted of capsule formed of collagen fibers and capsular cell; surrounding inner core formed by ramifying afferent nerve fibers, Schwann/lamellar cells and collagen fibers. The terminal nerve fibers of the bovine corpuscles formed modifications like neurofibrillar networks, closed end bulbs and neuro fibrillar varicosities.
Conclusion: Snout of the cow possess the tripartite array of nerve end organs associated with Eimer's organ of mammals, consisting of free nerve endings, Merkel's discs and corpuscular end organs, which indicates that the snout is a highly specialized somatosensory organ of bovine animals.

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INTRODUCTION

Skin serves many functions, including to house and protect the organs and internal body parts, and to act as the body's largest sensory organ sensitive to tactile, thermal, and chemical stimuli. (Chuong *et al*., 2002) Mammalian skin has evolved from the integument of earlier vertebrates via a complex path that is still only partially understood. (Maderson, 2003) Evolutionally, hair had a largely tactile function and their subsequent proliferation allowed hair to gain a secondary role as an insulator. The primary sensory role of hair is retained in the tactile hair, or vibrissae, found on all therian mammals (marsupials and placentals) except humans. (Mitchinson *et al*., 2011) The sense of touch develops early in phylogeny and is one of the most important senses for the survival of the animal. Many mammals have evolved areas of non-hairy, glabrous skin. In humans, these include the skin areas on the lips, hands and fingertips and the soles of the feet. In other mammals, it includes snout and prehensile tail. (Organ *et al*., 2011) These are the parts of the body that are most important when physically interacting with the world and where accurate tactile discrimination is most critical; unsurprisingly, then, glabrous skin in mammals has a high density of mechanosensory receptors including Meissner's corpuscles, Pacinian corpuscles, Merkel-cell neurite complexes and Ruffini endings. (Moayedi *et al*., 2015) These fibers are particularly sensitive to light stroking touch and thus are thought to underlie an affective, or

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social, touch capacity that may be unique to mammals. (McGlone *et al*., 2014) Long facial whiskers, or macrovibrissae, are found in many mammalian species, projecting outwards and forwards from the snout of the animal to form a tactile sensory array that surrounds the head. (Mitchinson *et al*., 2011)

In mammals the tip of the snout has a role in tactile sensitivity similar to the one played by the finger tips in anthropoids and bears certain resemblance to the human finger tip. (Wood Jones, 1920; Macintosh, 1974) Snout is used as a tactile organ while foraging for food and in social interaction. The snout has the only surface that is comparable to the friction areas of most non-hooved mammals (palms and soles). The sense of touch detects forces that bombard the body's surface. In metazoans, an assortment of morphologically and functionally distinct mechanosensory cell types is tuned to selectively respond to diverse mechanical stimuli, such as vibration, stretch, and pressure. A comparative evolutionary approach across mechanosensory cell types and genetically tractable species is beginning to uncover the cellular logic of touch reception. (Ellen *et al*., 2010)

Aim of the study

Relatively little data is available on the distribution and comparative morphology of mammalian sensory nerve endings. This lack of comparative data is problematic when modeling the origins and evolutionary ecology of mammalian somatosensory adaptation. It was in this context that study of "The sensoneural organization of the snout skin of the cow (*Bos indicus*) in light of the somatosensory adaptations of mammals" was undertaken to correlate with the similar nerve endings of other studied animals, so as to understand the comparative somatosensory adaptations of mammals.

MATERIALS AND METHODS

The material was obtained as biopsy from the snout of 15 cattle (cow/ox, age 2-11 years), immediately after their accidental death, euthanasia or slaughter. The specimens thus obtained were cut into 1x1 cm pieces and fixed in 10% buffered formal saline for seven days. Five µm thick sections were prepared and stained with cytological stains like Haematoxylin- eosin and Von Gieson stain. To study the nerve endings and pattern of innervation, the sections were impregnated with silver by modified Winkelman technique. (Winkelman and Schmidt, 1957) The sections were cleared of wax by treating with xylene for 1-2 minutes, flooded with absolute alcohol for 30 seconds and rinsed in distilled water for two changes. Then the sections were treated with 20 per cent silver nitrate at 37 ºC for 25-30 minutes and rinsed in distilled water, then flooded twice, 10 second each time, with 10 per cent formalin in tap water, impregnated with ammoniacal silver for 30 seconds, drained off silver solution and flooded slide with two changes of 10 per cent formalin for 1 minute each and rinsed in distilled water, fixed in 5 per cent sodium thiosulphate for 5 minutes to remove precipitated silver and washed in tap water, dehydrated through 70 per cent , 95 per cent and absolute alcohol (30 seconds in each), cleared in xylene for 1 minute and mounted in synthetic resin and observed under compound light microscope, fitted with a measuring scale in the eye piece for measuring various dimensions. The morphological aspects of nerve endings and corpuscles, like number of nerve fibers entering, ramification and tortuosity etc. were studied, while observing at x400 magnification. Some horizontal sections were also used to study the nerve fibers.

Observations

Cattle have dense pelage over whole body, except snout which is conspicuous by absence of hair. Bovine animals have a protruding but blunt rhinorium or muzzle consisting of two nostrils, between which is a large hairless area, which continues downwards as the upper lip. The snout has the only surface that is comparable to the friction areas of most non-hooved mammals (palms and soles). The skin covering the hairless area has pattern of surface ridges similar to ridges on the finger tips of humans. The skin is grooved by intersecting lines which form characteristic geometric patterns. When the sections were stained with cytological stains, it was observed that hairless area of snout is covered with stratified squamous keratinized epithelium. The stratum corneum is deep and compact, and somewhat resembles that of the friction surfaces of the skin of other mammals. The stratum basale is composed of columnar cells with lot of keratohyaline granules. The basal lamina is seen to be undulant, getting pushed towards the epidermis, producing abundant dermal papillae. Some demal papillae showed cupping pattern. The dermal papillae filled up to 4/5th of the epidermis and some papillae reached up to stratum corneum, where the papilla expanded into an oval or globular structure (figure 1). The dermal papillae of snout were tall and narrow; while those of upper lip were short and broad. In transverse section dermal papilla or corpuscle looked like round cellular structure, with Schwann cell nuclei embedded in fine collagen matrix. The dermis consisted of loose areolar tissue with irregularly arranged collagen bundles, fibroblasts, blood vessels, Schwann cell nuclei and sweat glands.

Silver Impregnation

When sections were impregnated with silver, the glabrous skin of snout was covered by keratinized squamous epithelium with broad epidermal ridges. The epidermis consisted of the usual layers with rounded keratinocytes. Melonocytes were seen in the basal and prickle cell layer and contained melanin granules in the pale cytoplasm. Merkel's cells were seen in the basal layer of epidermis, having larger size than keratinocytes and indented nucleus. The dermis consisted of papillary and reticular layers, with dermal nerve plexus between them. The nerve plexus consisted of horizontally running nerve bundles. Some of the nerves moved up and entered into the dermal papillae and epidermis. As a result of frequent divisions and change of course of nerve fibers, axonal areas overlap and it was difficult to suggest how many axons took part in the supply each dermal papilla.

Epidermal nerve endings

Two types of nerve endings were observed in the epidermis- Free nerve endings and nerve fibers associated with Merkel's discs.

(i) ***Free nerve endings:*** These originated from the myelinated fibers of dermal nerve plexus, entered the basal layer of epidermis, moved upwards and ended in the upper layers of stratum spinosum or the stratum granulosum. The epidermal nerves formed network of nerve fibers, branching and rebranching in different directions (Figure 1). These nerve fibers moved in different directions and in different depths, so while following them continuity was lost.

(ii) ***Nerve fibers associated with Merkel's cells*:** These were located in the basal layer of epidermis. The afferent nerve fibers originated from nerve plexus in the papillary layer of the dermis. The axon branched in the papillary layer of dermis so that one axon innervated several Merkel' cells. On its way the nerve fiber swells to form a knob like termination close to the Merkel's cells -the disc. The Merkel's cells were clustered at the base of papillary ridges, interdigitating with the keratinocytes (Figure 3). Due to plane of section, the nerve fibers associated with the Merkel's cells were not easily seen.

Dermal Nerve endings

Three types of nerve endings were observed in the dermis of snout- free nerve endings, papillary nerves and bovine corpuscular end organs:

(i) ***Free dermal nerve endings*:** These nerve endings were derived from the deep myelinated nerve plexus in the dermis. Two dermal plexuses were observed in the dermis- one plexus in the reticular layer and other in the papillary layer. The reticular plexus consisted of medullated nerve trunks, usually running parallel to the skin surface. The papillary plexus consisted of interconnected thick nerve fibers which branched repeatedly and sometimes formed mesh like structure. The nerve fibers were 1 to 4 µm in diameter, and the length of nerve bundle reached up to 120 µm. As the axons ramify, their areas of supply overlapped so that every spot of the skin seemed to be supplied by several axons. The papillary plexus gave origin to the nerves supplying to the dermal papillae and to epidermis. Some free nerve endings ended blindly in the dermis; while others ramified into many branches.

(ii) ***Papillary nerve endings:*** These nerve fibers originated from the papillary nerve plexus of dermis and innervated the dermal papillae without forming any recognizable structure or corpuscle. They entered the bases of the papilla and ascended to the copular portion where they terminated. Some nerves were thick and others thin. The course of nerves within the papilla was sometimes straight and sometimes wavy. 1-5 dermal nerves entered each papilla, ascended up usually, giving terminating branches to the sides of the papilla (Figure 3). In some the papillae dermal nerves formed well defined structures/corpuscles; while in other papillae the nerve fibers ascended up to stratum granulosum or even to stratum corneum and expanded into an oval structure.

(iii) ***Bovine corpuscular end organs:*** These were located within the dermal papillae going into the epidermis. These were of two types:

a) In the first type, the nerve terminals associated with these corpuscles originated from myelinated axons of dermal plexus with average diameter of 5-7 µm, entered the dermal pole of the corpuscle and formed an intertwining elongated, cylindrical neural structure (Figure 4). These corpuscles were covered with thin capsule consisting of fine collagen fibers in which were interspersed capsular cells. The capsular cells were flattened with branching processes compared to the more rounded keratinocytes (Figure 5) The capsular cells contained large flattened nuclei having deeply stained chromatin material. It was noted that the capsule splits at the basal end of the corpuscle to allow the passage of 2-6 nerves and becomes continuous with the dermal connective tissue. The capsule surrounded the core of bovine corpuscle which consisted of branching and tortuous nerve fibers, covered by flattened Schwann cells (lamellar cells). Under high magnification of vertical and horizontal sections three types of nerve endings were observed in each corpuscle: Neurofibrillar networks, closed end bulbs and Neuro fibrillar varicosities. In neurofibrillar networks, the nerve fibers ramified and formed a mesh like structure; in closed end bulbs the nerve fibers terminally expand into a bulb or knob like structure; while as in neurofibrillar varicosities, the nerve fibers expanded into a bead like structure or thickening which again tapered into the nerve fiber. In between the nerve fibers of the core fine collagen fibers were observed (Figure 5)

b) In the second type of bovine corpuscle, the nerves from the papillary plexus entered the papilla, moved up to the upper layers of stratum spinosum and expanded into globular or oval receptor. This type of bovine corpuscle also consisted of outer capsule and inner core. The capsule was well defined consisting of collagen fibers oriented perpendicular to the skin surface and interspersed with flattened capsular cells. The nerve terminals inside the core originated from the dermal nerves and were covered by few transversely placed lamellar cells (Figure 6).

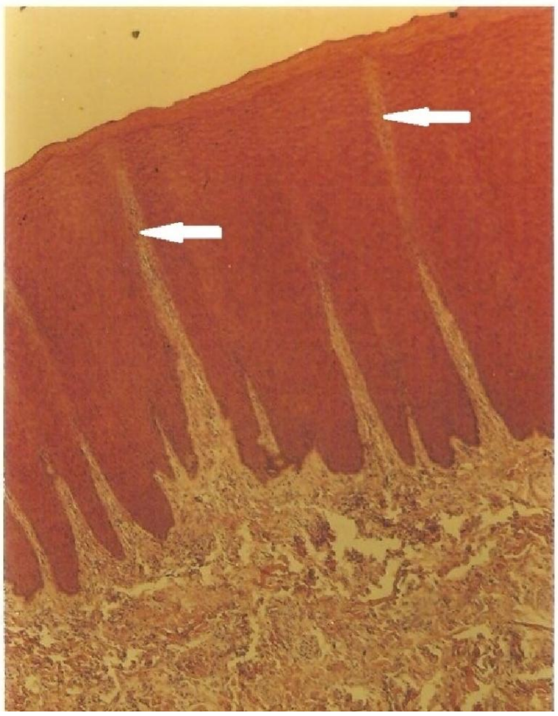

Figure 1. Microphotograph of longitudinal section of skin from snout of cow, showing elongated dermal papillae (arrows) going up to stratum corneum (Haematoxylin Eosin stain, x40)

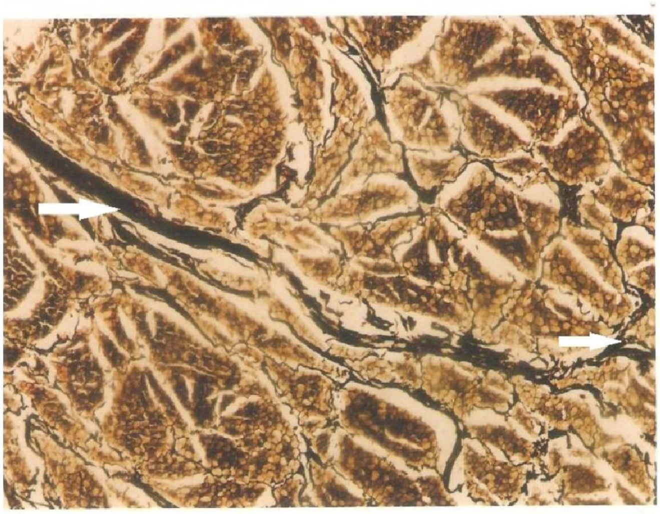

Figure 2. Microphotograph of snout skin of cow showing thick epidermal nerve bundles (arrows) branching into smaller fibers (silver stain x400)

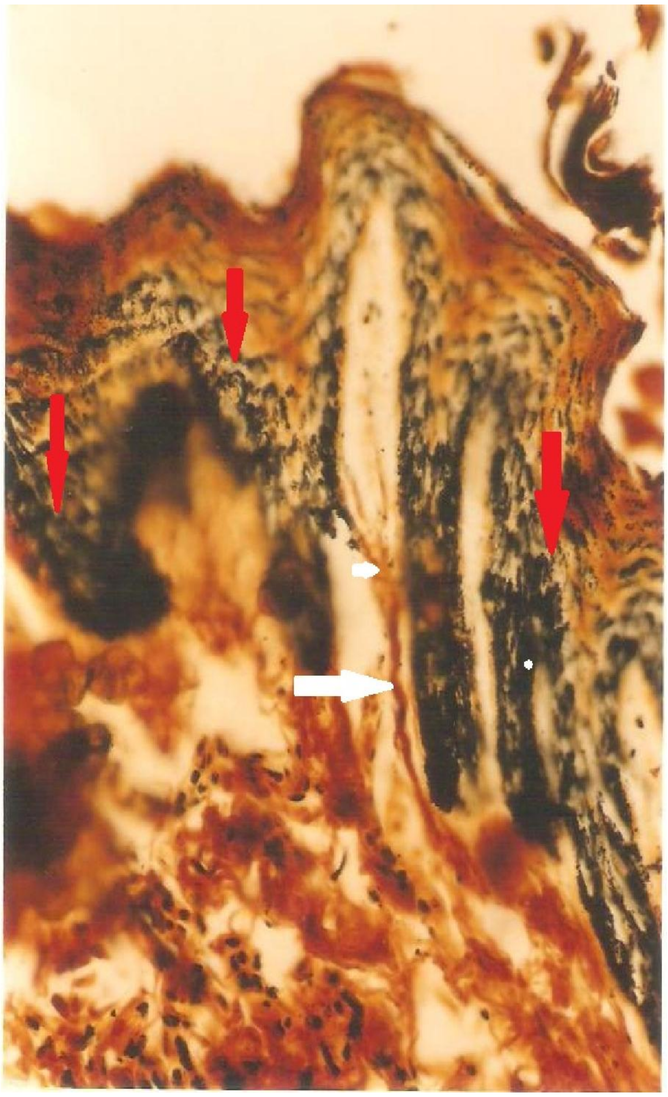

Figure 3. Microphotograph of longitudinal section of skin from snout of cow, showing papillary nerve (white arrow) and its branches (arrow head) innervating a dermal papilla and Merkel's cells (red arrows) (Silver stain, x200)

Figure 4.Microphotograph of longitudinal section of skin from snout of cow, showing four bovine corpuscles (arrows) (silver x100)

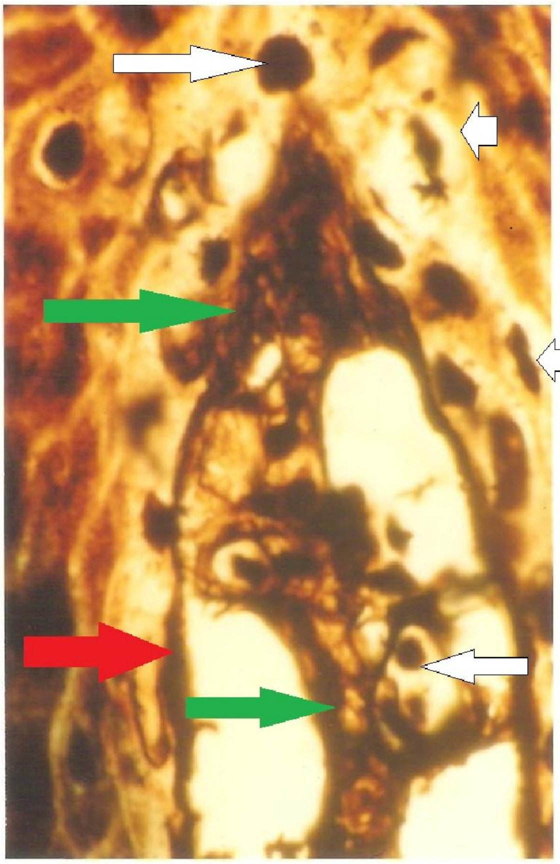

Figure 5. Microphotograph of longitudinal section of skin from snout of cow, showing capsular cells (arrow heads) and nerve terminals of bovine corpuscle- bulbous endings (white arrows), varicosities (red arrow) and neurofibrillar networks(green arrows) (silver stain x1000)

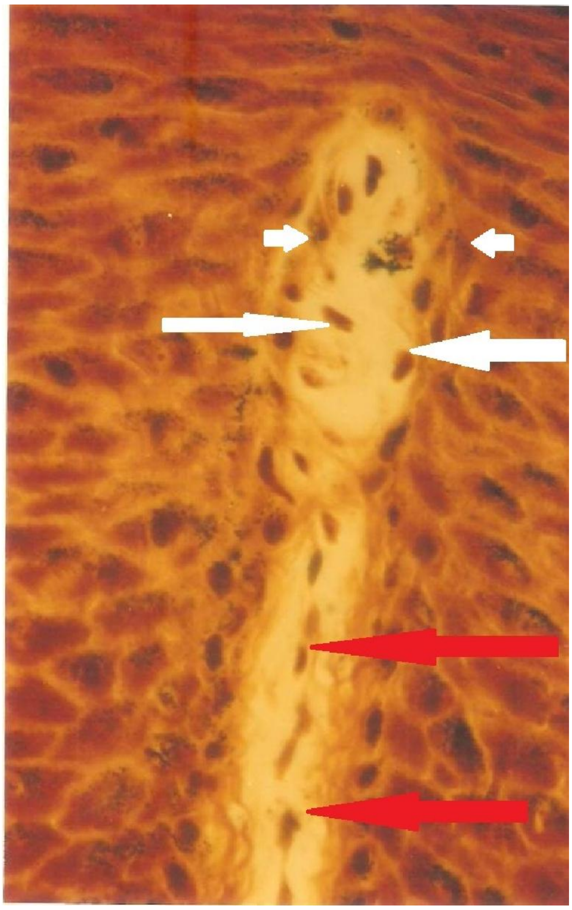

Figure 6. Microphotograph of longitudinal section of skin from snout of cow, showing lightly stained oval bovine corpuscle with capsular cells (arrow heads), transversely placed lamellar cells (white arrows) and Schwann cell nuclei (red arrows) (silver stain x400)

DISCUSSION

In mammals the tip of the snout has a role in tactile sensitivity similar to the one played by the finger tips in anthropoids and bears certain resemblance to the human finger tip, (Wood Jones, 1920; Macintosh, 1974). Snout is used as a tactile organ while foraging for food and in social interaction. The snout has the only surface that is comparable to the friction areas of most non-hooved mammals (palms and soles). The sense of touch detects forces that bombard the body's surface. In metazoans, an assortment of morphologically and functionally distinct mechanosensory cell types is tuned to selectively respond to diverse mechanical stimuli, such as vibration, stretch, and pressure. A comparative evolutionary approach across mechanosensory cell types and genetically tractable species is beginning to uncover the cellular logic of touch reception. (Ellen *et al*., 2010) Innervation of snout has been studied in number of animals including: rat, (Macintosh, 1974) mole, (Armstrong and Quilliam, 1961; Quilliam, 1966b) opossum, (Munger, 1965; Loo and Halata, 1995) pig, (Fitzgerald, 1962; Nafstad, 1971) tree shrew, (Loo, 1972) slow loris, (Loo and Kanagasuntheram, 1973) water mole, (Buisseret *et al*., 1976) European hedgehog (Abrahám, 1982) and short nosed bandicoot (Loo and Halata, 1995) The surface of cow snout is ridged with dermatoglyphic pattern similar to digital skin of anthropoids, Cauna (1959), who reported the importance of the epidermal and dermal ridges in sensory discrimination in human digital skin. In the cow snout the ridges almost play a similar role.

The present study lends support to the unifying concept of sensory endings advocated by Miller *et al*., 1958, who described basic triad of nerve endings consisting of free, expanded tip and encapsulated types. This triad of intraepidermal endings, Merkel's cells and corpuscular end organs constitutes Eimer's organ, originally described by Eimer in 1871 (Eimer, 1871), as consisting of epidermal pegs penetrated by profusion of intraepidermal nerves with a thick central fiber. Later description of Eimer's organ included Merkel's discs and corpuscular end organs. (Quilliam, 1966b) The thick central fiber seen in the Eimer's organ was not observed in present study

(i) Intraepidermal nerve endings: In the present study few intraepidermal nerve endings were observed originating from dermal nerve plexus. Cauna (1959) and Fitzgerald (1962) has put forward evidence to suggest that in the snout constant shedding of epidermal cells results in loss of superficial portion of intra-epidermal fibers. Winkelman and Schmidt (1957) and Bourland (1962) reported that silver impregnation is not ideal stain for demonstration of intraepidermal nerves, while as other stains like methylene blue (Miller *et al*., 1958) and cholinesterase technique (Dickens *et al*., 1963) are better alternatives to identify intraepidermal nerve endings.

(ii) Merkel's neurite complex: In the present study Merkel's discs were seen as flattened noncapsulated nerve endings adjacent to specialized tactile Merkel's cells as has been observed in slow loris (Loo and Kanagasuntheram, 1972) and opossum. (Loo and Halata, 1995) Merkel cells were clustered in groups, interdigitating with the keratinocytes in the epidermal pegs or intermediate ridges. Merkel cells are derived from epithelial precursors, rather than neural crest, and are positioned in the basal layer of the epidermis. (Morrison *et al*., 2009) In the present study, nerve endings close to the Merkel's cells formed disc like thickening; others reported leaf like structure. (Ridley, 1969) Merkel's cell complex are slowly adapting receptors which innervate both hairy and glabrous skin of mammals and respond to mechanical forces on the skin with a sustained and graded dynamic response followed by bursting at irregular intervals. (Coleman *et al*., 2001) These receptors are also present in hairy skin though at lower density. In rodents, large collection of Merkel's cells are associated with whiskers follicles, but they are also found in glabrous skin of the paws and associated with guard hairs in hairy skin, the noses of moles, the wings of bats, whisker pads, mucosae of the mouth and lips. (Halata *et al*., 2003) These complexes are infrequent or absent in skin regions in which special acuity is not paramount, such as genitalia. (Halata and Munger, 1986) Functionally, studies mainly performed in humans and other primates indicate that the glabrous-skin Merkel cell complex conveys information about texture, curvature, and object shape with high spatial acuity. (Maricich *et al*., 2009)

(iii) Corpuscular nerve ending: The anatomical structure associated with rapidly adaptive receptor in glabrous skin of mammals is a corpuscle with varied nomenclatures in different orders; in the order primate, these associated corpuscles are referred to as Meissner corpuscles. Regardless of slight interspecies variations, all corpuscles of mammals are thought to be evolutionarily derived from a common ending known to serve the same function in glabrous skin. (Abraira and Ginty, 2013) The Meissner corpuscle of primates is the best characterized anatomically and it is made up of flattened lamellar cells arranged as horizontal lamellae, like a helix, embedded in connective tissue. Each individual corpuscle can be supplied by up to six large myelinated fibers that are interwoven within the capsular cells of the corpuscle. (Bhat *et al*., 2008; Castano *et al*., 1995)

In the present study, the most conspicuous and elaborate nerve ending of the snout in the cow was the corpuscular nerve ending, which resembled on one hand with the innominate corpuscles described by Quilliam, (1966) and on the other hand to the primate Meissner's corpuscles described by Bhat *et al.* (2008); Hashimoto, (1973) and Organ *et al*. (2011). This supports the view that these bovine corpuscles are rapidly adapting nerve endings, functionally similar to the Meissner's corpuscle. The bovine corpuscles consisted of two types. The first type consisted of cylindrical or elongated structure having a of capsule of collagen fibers, interspersed with fibrocyte variety of capsular cells and core comprising of ramifying nonmyelinated nerve fibers, Schwann cell (lamellar cell) nuclei and collagen matrix. Similar end organs have also been described in raccoon's forepaw (Munger and Pubols, (1972) and in human digital glabrous skin (Bhat *et al*., 2008; Cauna, 1969). The other type of corpuscle was rounded or oval structure formed high up in the upper layers of stratum spinosum and stratum granulosum. Such types of corpuscle formed high up close to stratum granulosum (type second) have not been described in any other mammal and is hence called as bovine corpuscle. The basic components of the bovine corpuscles are same as the Meissner's corpuscles of primates or murine corpuscles of rodents, with some minor differences- the bovine corpuscles are less complex in structure- the capsule being less distinct and core consisting of nerve fibers ramifying but not forming typical helix or spiral of typical Meissner's corpuscle. The arrangement of lamellar cells and nerve terminals within the Meissner corpuscle is thought to play a critical role in shaping the physiological properties of rapidly adaptive Meissner's corpuscle. (Abraira and Ginty, 2013) Upon indentation of glabrous skin, collagen fibers that connect the basal epidermis to lamellar cells of the corpuscle provide the mechanical force that deforms the corpuscle and triggers action potential volleys that quickly ease as a result of the rapidly adapting nature of the receptor. When the stimulus is removed, the corpuscle regains its shape, and in doing so it induces another volley of action potentials, generating the distinctive on-off responses. One rapidly adaptive afferent nerve can branch repeatedly to innervate several corpuscles. (Pare *et al*., 2002) The nerve endings within the bovine corpuscles being simpler, the somatic sensory acuity will be less in bovine glabrous skin. To compensate for this reduced sensory acuity, the bovine corpuscles tend to become elongated or form corpuscular structure in the superficial layers of epidermis. The terminal nerve endings in the bovine corpuscles like end bulbs, varicosities and neurofibrillar networks are the similar to those seen in Meissner's corpuscle.

From the above we can conclude that snout of the cow possess the tripartite array of nerve end organs associate with Eimer's organs, consisting of free nerve endings, Merkel's discs and corpuscular end organs, which are also found in other mammals. The richly innervated snout could be said to supplement the visual sense in mammals and indicates that the snout is a highly specialized somatosensory of bovine animals.

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