The sense of touch in the star-nosed mole: from mechanoreceptors to the brain

Kenneth C. Catania*
Department of Biological Sciences, Vanderbilt University, Nashville, TN, USA

Star-nosed moles are somatosensory specialists that explore their environment with 22 appendages that ring their nostrils. The appendages are covered with sensory domes called Eimer’s organs. Each organ is associated with a Merkel cell–neurite complex, a lamellated corpuscle, and a series of 5–10 free nerve endings that form a circle of terminal swellings. Anatomy and electrophysiological recordings suggest that Eimer’s organs detect small shapes and textures. There are parallels between the organization of the mole’s somatosensory system and visual systems of other mammals. The centre of the star is a tactile fovea used for detailed exploration of objects and prey items. The tactile fovea is over-represented in the neocortex, and this is evident in the modular, anatomically visible representation of the star. Multiple maps of the star are visible in flattened cortical preparations processed for cytochrome oxidase or NADPH-diaphorase. Star-nosed moles are the fastest known foragers among mammals, able to identify and consume a small prey item in 120 ms. Together these behavioural and nervous system specializations have made star-nosed moles an intriguing model system for examining general and specialized aspects of mammalian touch.

Keywords: somatosensory; tactile; skin; neocortex; evolution

1. INTRODUCTION
Important advances in our understanding of nervous system function and organization have often come from studies of specialized species. Perhaps, the best-known example is the use of the squid giant axon by Hodgkin & Huxley [1] to determine the ionic basis of action potential conduction. Other well-known examples include studies of barn owls for determining the neural substrate of auditory localization [2], investigations of the bird song system for exploring the interaction between environmental stimuli and brain development [3,4], and use of electric fish for determining the computational rules that underlie motor responses [5–7]. In the case of mammalian touch, the landmark study by Woolsey & Van der Loos [8] identifying cortical barrels in the mouse somatosensory system led to the development of rats and mice as important model systems for understanding mechanosensation and brain organization in mammals. This system, in particular, continues to provide new insights spanning the fields of molecular biology, neurosciences and robotics [9–14]. Each of the species listed above is particularly good at some behaviour—rapidly escaping from a host of predators (squid), detecting prey based on sound (owls) or exploring and navigating dark surroundings through touch (rodents).

A glance at the astonishing face of a star-nosed mole suggests that it too may be an expert at some task (figure 1a). The nose of this species is ringed by 22 fleshy appendages that are in constant motion as the mole explores its environment. But the function of the star is not immediately obvious and it is natural to wonder what this structure is for, how and why it evolved, and what it might tell us about mammalian sensory systems. These questions are addressed by drawing on evidence ranging from the mole’s habitat and behaviour to single unit neuronal recordings. The picture that emerges suggests that star-nosed moles are an extreme in mammalian evolution, with perhaps the most sensitive mechanosensory system to be found among mammals. As might be expected, the star projects to greatly expanded areas of the somatosensory neocortex and these areas are organized into modules that correspond to the sensory appendages in the periphery, much like the barrel system in rodents. But unlike the rodent somatosensory system, details of the mole’s brain maps are more typical of a visual system than a somatosensory system, and this in turn can be explained by star-nosed mole behaviour. Comparative studies across species reveal intermediate forms that link the star to other mammalian skin surfaces, suggesting how this structure evolved from the more common configurations of mammalian skin.

2. STRUCTURE AND EVOLUTION OF THE STAR
Star-nosed moles are relatively small mammals, weighing 40–50 g. The star itself is roughly a centimetre across (figure 1), and thus has a diameter slightly smaller than a typical human fingertip. Examination of the star under the scanning electron microscope (SEM), or in tissue sections, reveals a remarkably specialized epidermis consisting entirely of small raised domes.
approximately 30–50 μm in diameter (figure 1c). These domes are Eimer’s organs, a sensory structure found in nearly all of the approximately 30 species of mole [15]. Each organ appears as a dome or papilla containing a central column of epidermal cells. Under the SEM, the top of the cell column is often visible on the outer surface of each organ as a small circle. There are approximately 25 000 Eimer’s organs on a typical star, and each organ is associated with a Merkel cell–neurite complex at the base of the cell column, a lamellated corpuscle in the dermis just below the column, and a series of free nerve endings that originate from myelinated fibres in the dermis and run through the central column, ending in a ring of terminal swellings just below the outer keratinized skin surface (figure 1g, left side). In addition, a ring of thinner free nerve endings is usually found at the margins of each Eimer’s organ.

From these observations some important conclusions can be drawn. For example, the star is devoted entirely
to Eimer’s organs and no other receptor organs (e.g. taste buds, ampullary organs, hair cell, etc.) are present. Thus, although the star is unique in its shape and size, the epidermis that comprises the structure is similar to that found in a wide range of other moles (figure 1d,e). The star is therefore a variation on a more common theme—the existence of sensitive epidermal sensory organs (Eimer’s organs) on the tip of the snout. A further comparison to shrews (the closely related sister group to moles) suggests the major overall difference between moles and other small mammals that led to the evolution of the star [15]. Shrews and rodents (and many other small mammals) rely primarily on facial whiskers to gather tactile information, whereas moles use direct contact of the glabrous skin to explore their environment (in addition to using whiskers). Once the ‘tactile shift’ from whiskers to glabrous skin began in ancestral moles, selection could act on the nose to produce more and more elaborate skin surfaces and ultimately the star. This scenario is supported by the examination of the diversity of epidermal sensory organs in moles, including the existence of one species with a ‘protostar’ configuration (figure 1d,e). Adults of the latter species (genus Scapanus) have a snout that resembles the star during embryonic development [16].

In a sense, the star may be to glabrous skin what whiskers are to hair—an extension and expansion of an already sensitive structure. If so, why do not more species of mammals—moles in particular—have elaborate sensory appendages? It is difficult to identify the many selective pressures and tradeoffs that might lead to such a structure. But one factor is obvious—thin skin is delicate. The two most obvious functions of skin are to act as a sensory surface and to protect the underlying tissues from desiccation and abrasion. These two functions are at odds with one another in the case of Eimer’s organs. In wild caught moles of many species, the Eimer’s organs show obvious signs of wear and abrasion [15]. The constant and repeated contact with the soil apparently takes a toll on the sensory organs, which have a thin keratinized epidermis. Star-nosed moles are the only species that live in the moist, muddy soil of wetlands. The high humidity and soft mud in this particular niche may have lessened a major constraint on how elaborate the skin surface could become. These issues are less of a constraint on whiskers, which consist of long, keratinized extensions with the mechanoreceptors embedded in the skin at the base, well protected from the environment. In the case of star-nosed moles, another factor that probably led to elaboration of the snout was the small prey that can be found in wetlands [17]. Exploiting this resource requires a higher resolution sensory surface than is typical of other moles. Thus, a shift to the woodland environment may have provided both a selective advantage for a more elaborate sensory structure, and the release of a constraint (less abrasive soil) that allowed this structure to evolve.

3. FUNCTION OF EIMER’S ORGANS

Evidence for the mechanosensory function of Eimer’s organs comes from a number of sources. Mole behaviour suggests that Eimer’s organs are mechanosensory organs. But more direct evidence comes from electrophysiological recordings and from anatomical investigations of the central and peripheral nervous systems. In the case of star-nosed moles, recordings from somatosensory cortex [18] show that each appendage is sensitive to very light tactile stimulation, and neurons have tiny receptive fields that must be defined under microscopic examination (figure 2). Unit recordings from 145 spontaneously active neurons in primary somatosensory cortex (S1) revealed that 97 per cent responded to tactile stimulation of the star with a mean latency of 11.6 ms. A fairly large proportion of these neurons (41%) were inhibited by stimulation of nearby Eimer’s organs outside of their excitatory receptive field. The small receptive fields and inhibitory surrounds for cortical neurons with short latency responses are consistent with a role for the star in rapidly determining the location and identity of objects in the environment.

Additional evidence of Eimer’s organ function comes from recordings of primary afferents innervating Eimer’s organ in the coast mole (Scapanus...
This study made use of a dedicated ‘Chub-buck’ mechanosensory stimulator [20] and revealed three main classes of receptor [19]. These included one slowly adapting type and two apparently different rapidly adapting types. The slowly adapting responses were similar to the typical response profile of a Merkel cell–neurite complex and are consistent with the large number of this receptor class evident from the anatomy of Eimer’s organ (figure 1g). The rapidly adapting responses included a Pacinian-like response profile with maximum sensitivity to sinusoidally compressive stimuli at a frequency of 250 Hz. These responses are also consistent with anatomical findings, as each Eimer’s organ is associated with one or more lamellated corpuscles in the dermis just under the central cell column. These receptors appear much like small Pacinian corpuscles and are probably rapidly adapting receptors. A second class of rapidly adapting responses required greater compression amplitude and was maximal at lower frequencies of simulation. These may correspond to the free nerve endings that terminate in swellings just below the keratinized epidermis at the apex of the cell column (see Marasco & Catania [19] for discussion). In addition to these findings, neuroanatomical details suggest a mechanosensory role for some, but not all, components of Eimer’s organ. Marasco et al. [21] found that the nerve endings associated with the central cell column in coal moles are immunoreactive for neurofilament 200, consistent with a mechanosensory role. In contrast, a ring of thinner fibres on the margins of each Eimer’s organ (figure 1g) was immunoreactive for substance P, indicating a role in nociception.

An additional important finding from afferent responses was directional sensitivity for many isolated units. This was explored using a computer-controlled piezo bending element [19], and significant directional sensitivity was found for 15 of 17 isolated units. Previous investigators have speculated that the conspicuous ring of free nerve endings at the apex of each Eimer’s organ—also found in the apparently independently derived push-rod in monotremes [22]—may transduce directional information [23]. The data from afferent responses support this possibility; however, it is important to keep in mind that moles do not slide Eimer’s organs over objects when exploring them. Rather the unit of behaviour is repeated brief touches that compress the organs against objects or the substrate. In the course of natural behaviours, the directional sensitivity may be an important component of Eimer’s organ function. Indeed, incorporating this component of the response into a relatively simple model suggests one way in which Eimer’s organs may function to allow rapid discrimination of objects in the mole’s environment. Figure 3 provides a basic outline of how these responses, integrated across an array of Eimer’s organs, could code for different shapes and textures. The main feature of this proposal is the differential deflection of the terminal neurites (figure 3a) at the apex of each cell column. In this model, an important variable is the number of terminal neurites deflected in opposition to one-another relative to the number of neurites deflected in the same direction (figure 3b,c). Presumably, rough surfaces would predominantly elicit the former response, whereas smooth surfaces would elicit the latter. But are the Eimer’s organs deflected as suggested in this model?

One way to address this question is to compress the star against an object (post-mortem) and fix the skin surface, so that the positions of organs can be directly observed under the SEM. This was done using a fine wire with a diameter of 120 μm (figure 4). The results reveal how the Eimer’s organs were mechanically deformed by the stimulus and suggest that the central cell columns containing the array of terminal neurite swellings would indeed be compressed as suggested in figure 3. This is emphasized by illustrating the top of each cell column independently (the circular disc at the apex of each organ is a single epidermal cell that can be traced). Figure 4c shows this, carefully drawn from a high-resolution image of figure 4b, with the resulting surfaces individually scaled by 200 per cent to aid visualization. The tops of the cell columns are clearly deflected by the cylindrical shape such that contacted areas change their position and angle relative to one another (centre of figure 4b), whereas un-contacted cell columns (left and right of figure 4b) remain more uniform with surfaces roughly tangential to the skin surface.

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4. ORGANIZATION OF SOMATOSENSORY CORTEX

Investigation of the star and the very dense innervation of associated sensory organs immediately suggested that interesting correlates of this sensory surface might be found in the mole’s somatosensory cortex. This possibility followed from the landmark findings of Woolsey & Van der Loos [8] showing that each whisker on the face of a mouse is represented by a histologically visible cortical barrel. To explore this possibility in moles, maps of the star and other sensory surfaces (figure 5) were determined with microelectrode recordings and later correlated with flattened sections of the neocortex processed for the metabolic enzyme cytochrome oxidase (CO). The results revealed a remarkable pattern of stripes and modules in layer 4 that correspond to the star and other sensory surfaces on the mole [24]. We have since found that a number of histological stains of the cortex reveal such modules in mole cortex. For example, figure 5b shows the modular organization of the mole’s layer 4 cortex as revealed by NADPH-diaphorase histochemistry.

A number of striking specializations were apparent from both the electrophysiological recordings and the anatomical sections of flattened cortex. Most obviously, the star representation in primary somatosensory cortex is patently visible as a series of dark stripes, each stripe representing an appendage from the nose. A second obvious and apparently unique feature of star-nosed mole somatosensory cortex is the presence of additional, visible maps. Just lateral to S1, in secondary somatosensory cortex (S2), a second, large visible map of the star is evident. Electrophysiological mapping shows that this representation, like that in S1, processes inputs from only the contralateral side of the star. This map is distinct from S1 in its cyto and chemo architecture (figure 5). Finally, a third, smaller map of the star is visible caudal to the S2 representation (S3 in figure 5). Thus unlike rodents, which have a series of barrels visible only in S1, star-nosed mole neocortex contains three visible maps of the star. The most medial and rostral map of the star clearly corresponds to S1. This conclusion is based on many features, including its location relative to the other areas, its prominent architecture and size, its continuity with the body representation found more medially in the typical position of S1 in most mammals and its ‘handedness’. The latter refers to the topographic relationships of the star appendages in the representation, which are appropriate for S1 [25]. In contrast, the S2 star representation is a mirror image of the S1 pattern, and cannot be superimposed on the S1 pattern by translation or rotation. Thus S2’s star topography is inconsistent with S1 ‘handedness’ as found in other mammals. The third star representation has been termed S3 (star 3) as it is apparently not homologous to any area in other moles nor to areas in the sister group of shrews, which appear to have only S1 and S2 representing the face and body parts. Therefore, the most parsimonious conclusion is that the third star-map has evolved independently in the star-nosed mole, perhaps as a result of the need to process high volumes of complex sensory information from the star.
Figure 5. Anatomical modules and septa in layer 4 cortex of the star-nosed mole as revealed by processing sections for NADPH-diaphorase and cytochrome oxidase (CO) histochemistry. (a) Summary of cortical organization in the star-nosed mole based on multi-unit electrophysiological mapping. Two relatively large somatosensory areas (primary, S1, and secondary, S2) contain complete maps of the contralateral body and large representations of the star. A third, apparently new representation of the star (S3) is found in lateral cortex. (b) A series of modules and stripes correspond to different body parts in flattened sections processed for NADPH-diaphorase histochemistry. The most obvious part of the pattern corresponds to the S1 star representation [1–11]. (c) A different case processed for CO also reveals the three different, visible representations of the contralateral star.
of neuroanatomical tracers into the S1 representation of
the star have shown that all three representations are
topographically interconnected, forming a processing
network for somatosensory inputs from the star [26].
The specific role of these different star maps has yet
to be elucidated; however all three areas are responsive
to tactile stimulation of the contralateral star.

An additional intriguing finding is evident from even
casual inspection of the flattened cortical sections. The
11th, central appendage of the star is greatly over-
represented, taking up approximately 25 per cent of the
S1 star map, despite its relatively small size on the snout
and comparatively few sensory organs (figure 1b). A simi-
lar expansion of the 11th is evident in S2 (figure 5c). The
representation of the 11th appendage is so greatly
enlarged relative to its proportions on the star that the
first views of the flattened cortex were hard to interpret.
It did not seem possible that such a large anatomical
module could correspond to such a small appendage.
Yet, electrophysiological recording clearly showed that
this was the case. The reason for this mismatch was
suggested by observing mole behaviour.

5. A TACTILE FOVEA IN THE STAR-NOSED MOLE

When star-nosed moles explore their environment or
search for food, the star is constantly touched to differ-
ent objects or prey items. This behaviour is extremely
fast such that moles may touch between 10 and
15 different places every second. High-speed video of
this behaviour reveals that the 11th appendage acts as
a tactile fovea and is used to repeatedly explore objects
of interest—particularly potential prey. When foraging,
moles search in what appears to be a random pattern
of touches until contact is made to a potential prey
item with any part of the star. Each touch is a discrete
unit of behaviour lasting 20–30 ms. Once contact is
made—usually with some part of the large appendages
1 through 9—the star is quickly shifted, so that one
or more touches are made with appendage 11 before
prey is eaten. In the case of small prey, this entire
sequence is remarkably fast. A mole can detect poten-
tial prey with the peripheral appendages, foveate to
the central 11th appendage for an additional contact,
take the food into its mouth, and begin to search for
more prey in as little as 120 ms, although the average
time is 227 ms [17]. The sequence just described con-
stitutes ‘handling time’ as defined in foraging theory
paradigms [27]. In all of hundreds of trials analysed
with high-speed video, the mole always foveated to the
11th appendage when exploring a food item [28].
In a number of trials, moles foveated to rubber dis-
tractors before rejecting them. The use of the 11th
appendage as the tactile fovea was surprisingly similar
to the manner in which eyes are used to explore details
of a visual scene [29]. For example, the rapid foveation
movements of the star have a time-course and form
similar to foveating eye movements (saccades). It is
quite appropriate to refer to these star movements as
saccades, given the analogous ‘foveating’ function of
the behaviour in moles and the meaning of saccade—a
jerky movement [30].

With these behavioural observations in mind, the
expanded representation of the 11th, foveal appendage
is less surprising, and might be predicted. However,
these findings raise additional fundamental questions
about how central representations of sensory surfaces are
organized. For example, previous studies in mouse
somatosensory cortex have convincingly shown that the
size of a cortical barrel in S1 is directly proportional to
the number of primary afferents innervating the corre-
ponding whisker on the face [31,32]. This suggests the
possibility that afferent number determines cortical rep-
resentational size generally, and (if so) that cortical
magnification is perhaps more appropriately referred to
as a ‘peripheral scaling factor’—as suggested by Lee &
Woolsey [33] for the barrel system. But in the case of
the primate visual system, the same question was asked
with varying results coming from different laboratories.
Some investigators concluded that the representation
of the retinal fovea was proportional to the number of
ganglion cells in the retina [34–36], whereas others
reported a preferential expansion of the fovea [37–40].
These different results from different studies are a testa-
mament to the difficulty of making such measurements in
the visual system of primates. Azzopardi & Cowey [41]
ultimately resolved this issue by making injections of a
retrograde transneuronal tracer into the visual cortex,
and reported a preferential expansion of the foveal rep-
resentation. They found that ganglion cells from the
retinal foveal were allocated an average of three to six
times more cortical territory in V1 than ganglion cells
at more peripheral locations in the retina.

Star-nosed moles are a particularly convenient and
interesting case for similar investigations because
measurements of afferent number and cortical area
can be made with comparative ease. A single large
branch of the trigeminal nerve innervates each append-
age, and the corresponding representation of the
appendage is visible in the cortical anatomy (as is the
case for mouse whiskers). In addition, the number of
sensory organs on each star appendage can be counted
to provide another dimension of analysis—revealing
how the sensory periphery is differentially specialized
across the star [42].

As expected from its size, the 11th appendage
has comparatively few Eimer’s organs on its surface
(figure 6). Most of the appendages have over 1000
organs, whereas appendage 11 has an average of 870
on its surface (only appendage 10 has fewer). When
these counts of Eimer’s organs are compared with the
numbers of primary afferents innervating each append-
age, a clear trend is evident. The two values covary
almost precisely for appendages 1–9—with an average
of four afferents per organ (figure 6d). But appendages
10 and 11 stand out with higher ratios of afferents
per organ with an average of 5.5 and 7, respectively. Thus,
appendage 11 has almost twice the innervation density
of most other appendages. This shows that the tactile
fovea is specialized in the periphery in a manner that
can be compared with a retinal fovea.

From these data, it might be guessed that the higher
innervation density accounts for the larger representa-
tion of no. 11 in the cortex. But closer consideration
of the numbers shows this is not possible. Although
appendage 11 has a higher innervation density per sen-
sory organ, this is largely explained by its having a fairly
typical number of afferents (11% of the afferents

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innervating the star), but comparatively few total sensory organs owing to its small size. Yet, the representation of the 11th appendage takes up 25 per cent of the S1 star representation. When the number of afferents from each appendage is compared directly with the size of each central representation, it is clear that the somatosensory fovea is preferentially over-represented in the cortex (figure 6c). There is a general trend that the appendages nearest the fovea have larger cortical areas per afferent than the more peripheral appendages. The 11th appendage has the greatest over-representation, and the degree of this expansion (three to four times greater than the most peripheral appendages) is similar to that reported for the retinal fovea in primates [41]. The overall organization of the mole’s somatosensory system and behaviour, therefore, shares a number of surprising similarities with visual systems in other mammals.

6. CONCLUSIONS AND FUTURE DIRECTIONS
Star-nosed moles provide many interesting new insights into the organization, function and evolution of somatosensory systems and corresponding brain areas. The existence of a tactile fovea in the star-nosed mole can be compared with the well-known retinal fovea in other mammals, and also with the acoustic fovea of bats. Moustached bats have a well-characterized acoustic fovea evident from the level of the cochlea [43] to the auditory cortex [44], and Doppler shift compensation behaviour [45] can be considered functionally equivalent to a foveation movement. The existence of a fovea-periphery division of sensory surfaces in the visual, auditory and somatosensory systems of different mammals suggests that this organizational scheme is an efficient general solution to producing a very high-resolution sensory system. An obvious benefit is that only a small portion of the sensory surface need be high-resolution, and only its corresponding representation in the central nervous system need have a large representation for enhanced processing. A cost of this organizational scheme is the requirement of constant reorientation of the fovea to explore the environment (or movement of the outgoing frequency of echolocation calls in the case of bats [45]). But this is apparently a small cost relative to the alternative of investing in larger areas of high-resolution sensory surfaces in both the periphery and corresponding central nervous system representations.

In addition to extending evidence for this common theme of sensory system organization to touch, star-nosed moles provide potential insights into a number of other areas of mammalian brain organization and behaviour. For example, it is clear in data from star-nosed moles that cortical representational space is not always directly proportional to peripheral innervation density. Rather, as is true in visual systems, behaviourally important inputs may be allocated more territory. On a larger scale, it appears that star-nosed moles have added a somatosensory processing area to the cortical network (compared with other moles and shrews). As in the case of sensory foveas, this may also reflect a general organizing principle for efficient processing of sensory information. Animals with particularly well-developed senses often have many corresponding cortical areas, and this is thought to underlie computational ability and behavioural complexity. The subdivision of primate visual cortex into many different areas provides a well-known example [46–49]. In terms of auditory cortex,
echorolating moustached bats have many auditory areas, but appear to have few visual areas. A number of similar examples could be suggested, but the significance of cortical areas may be difficult to interpret across species with drastically different brain sizes or having distant phylogenetic relationships. In the case of the star-nosed mole, the apparently new somatosensory area (S3, figure 6) not found in close relatives [50] allows us to suggest more confidently that the modification was related to the expansion of the star and corresponding search behaviours. This in turn supports the proposal that adding cortical areas, in general, may enhance sensory processing.

As a final example, the shapes of the modules in star-nosed mole cortical maps indicate that not all sensory surfaces are represented in the form of a traditional cortical column [51]. Numerous investigators have suggested that the fundamental unit of the cortex is a cylindrical cortical column, sometimes called a macrocolumn, 300–600 μm in diameter with discrete borders. The circular barrels described by Woolsey & Van der Loos [8] have often been cited as anatomical reflections of this general principle. But an alternative explanation (also pointed out by Woolsey & Van der Loos [8]) is that barrels simply reflect the somatotopic mapping of mechanoreceptors that are organized into a circular array around the whisker [52,53]. If so, one would predict that mechanoreceptors organized into different, non-circular arrangements would not appear as columns. This is the case for star-nosed moles, where the appendage representations appear as a series of bands or stripes reflecting the anatomy of the star. A similar, non-circular series of modules has also been identified corresponding to the primate hand [54], suggesting that a topographic, rather than strictly columnar, reflection of mechanoreceptor arrays is a widespread phenomenon.

These examples indicate some ways that very specialized star-nosed moles may provide new information about how mammalian sensory systems are organized. These studies are still in their early stages, and many questions remain to be explored. Some obvious future questions include: (i) how the star is represented in the trigeminal nuclei and thalamus, (ii) what functional roles the different cortical maps may play in processing tactile information, (iii) how the Eimer’s organs quickly transduce information about shape and texture, (iv) what role behaviour might play in shaping the developing cortical maps, and, (v) what transduction channels may be expressed in mechanoreceptors of the star [55]. There is little doubt that future studies of star-nosed moles will provide a wealth of information about touch.

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