

Evolution of Sensory Specializations in Insectivores

KENNETH C. CATANIA *

Department of Biological Sciences, Vanderbilt University, Nashville, Tennessee

ABSTRACT

Although insectivores have traditionally been thought of as primitive mammals with few specializations, recent studies have revealed great diversity in the sensory systems and brain organization of members of this mammalian order. The present article reviews some of these findings in three insectivore families that are thought to form a monophyletic group. These include hedgehogs (Erinaceidae), moles (Talpidae), and shrews (Soricidae). Members of each group live in unique ecological niches, have differently specialized senses, and exhibit different behaviors. Hedgehogs have well-developed visual, auditory, and somatosensory systems. Shrews make use of visual and auditory cues, but appear to depend most heavily on touch, particularly through prominent vibrissae. Moles are somatosensory specialists with small eyes and ears and unique epidermal mechanoreceptors called Eimer's organs used to identify prey and investigate their environment. In contrast to historical views of the insectivore order, members of this group have discrete and well-organized cortical sensory areas with sharp borders as determined from both electrophysiological mapping and analysis of cortical histology. Comparison of cortical organization across species reveals a number of specializations, including expansion of cortical representations of important sensory surfaces, the addition of cortical areas to some processing networks, and the subdivision of areas into separate cortical modules. In the case of the star-nosed mole, the somatosensory system has a tactile fovea and shares a number of features in common with the visual systems of sighted mammals. © 2005 Wiley-Liss, Inc.

Key words: brain; cortex; neocortex; somatosensory; tactile; Eimer's organ

The mammalian order Insectivora has historically been viewed as a group of small-brained primitive mammals that have not changed much in the course of mammalian evolution. As a result, they have often been used as stand-ins for the ancestral mammalian condition and have been the focus of a number of studies aimed at understanding how the earliest mammalian brains were organized (Ebner, 1969; Lende, 1969; Kaas et al., 1970a,b; Valverde and Facal-Valverde, 1986; Glezer et al., 1988; Michaloudi et al., 1988; Stephan et al., 1991; Regidor and Divac, 1992). Early electrophysiological studies of neocortex in hedgehogs and moles seemed to confirm this viewpoint, as maps of sensory areas were found to be overlapping with little internal topography (Lende and Sadler, 1967; Allison and Van Twyver, 1970).

A number of more recent investigations have revised this view of insectivores. Although it is true that most of these species have relatively small brains (particularly the shrews), it is not the case that few sensory specializa-

tions exist in insectivores. For example, a number of shrews (e.g., the water shrew) have exceptionally well-developed sensory vibrissae. Similar specializations in rodents (Woolsey and Van der Loos, 1970) have made them the model system of choice for exploring many aspects of mammalian brain organization related to mechanosensa-

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*Correspondence to: Kenneth C. Catania, Department of Biological Sciences, Vanderbilt University, VU Station B, Box 35-1634, Nashville, TN 37235. Fax: 615-343-6707. E-mail: ken.catania@vanderbilt.edu

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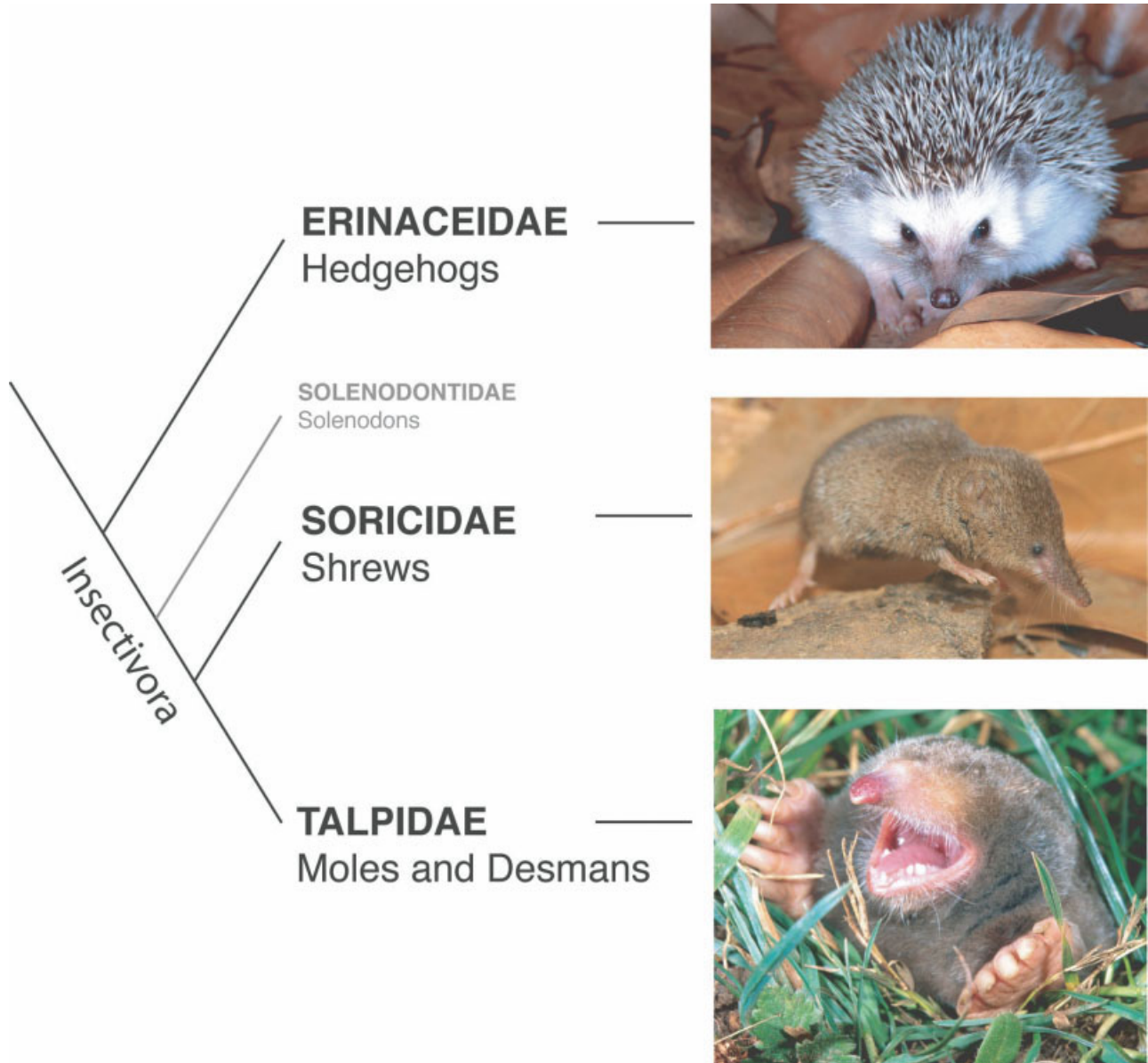


Fig. 1. Phylogenetic relationships of four families of insectivores that are considered to comprise a single clade. The panels on the right illustrate the basic anatomical features of the three families of mammals discussed in this review. Moles and shrews are sister taxa, and this close

relationship is reflected in their brain organization. Solenodons are rare shrew-like species from Cuba and little is known about their brain organization.

tion. A more obvious example of sensory specialization can be found in the star-nosed mole. This species has perhaps the most acute sense of touch among mammals and is able to discriminate prey items with remarkable speed (Cattania and Remple, 2005).

It is also not evident that insectivores generally have primitive or simple behaviors. Anyone who has attempted to handle or photograph some of the smaller Soricidae (e.g., Fig. 1) can attest to their incredible dexterity and speed as well as their uncanny ability to locate escape routes. Of course, such basic observations are not tests of behavioral complexity, but the assumptions often made about shrews (e.g., they are nocturnal) are frequently not

borne out by observations (e.g., we trap shrews throughout the day). Clearly, much remains to be learned about behavior in these species. However, for the purposes of this review, I will concentrate on the more tractable investigations of sensory specializations and brain organization.

The task of reviewing sensory specializations in the order Insectivora has been simplified in recent years by revisions of mammalian phylogenies that indicate a number of traditional families from the group are more closely affiliated with other mammalian orders. For example, elephant shrews (Macroscelididae), tenrecs (Tenrecidae), and golden moles (Chrysochloridae) are now considered to



Fig. 2. An east African hedgehog (*Erinaceus albiventris*) covered with spines embedded in a subcutaneous muscular sheath. The muscle forms a bag into which the body can be withdrawn, while the most heavily muscled margins contract like a draw-string to enclose the body



completely (right). Note the large eyes, prominent vibrissae, extensive glabrous rhinarium, and the protruding pinnae. Reproduced with permission from Catania et al. (2000).

be part of a separate endemic African clade (the super-order Afrotheria) (Springer et al., 1997; Stanhope et al., 1998). It therefore seems reasonable to limit the discussion of insectivores to a monophyletic grouping of four families: hedgehogs (Erinaceidae), solenodons (Solenodontidae), moles (Talpidae), and shrews (Soricidae; Fig. 1). Of these four families, the solenodons consist of two rare species that cannot be practically investigated beyond the examination of museum collections. This leaves three remaining families of insectivores (shrews, moles, and hedgehogs) and members of each of these groups have been the subject of extensive recent investigations. The results of these studies of the sensory periphery and brain organization will be reviewed and discussed.

HEDGEHOGS (FAMILY ERINACEIDAE)

Of the three insectivore families included in this review, the moles and shrews are sister groups that share a number of features in common. The hedgehogs differ substantially from the former in both body size and form. The most obvious specialization in many hedgehog species is the dense coat of spines covering much of the body surface (Fig. 2). These spines are embedded in a thick muscle sheath unique to hedgehogs (Kingdon, 1974). The muscle essentially forms a bag into which the entire body can be withdrawn (Fig. 2) and also causes erection of the spines at opposing angles to form a dense network of barbs. Although this defensive armor is a sensorimotor specialization (e.g., there is local control of spine erection in response to tactile stimuli), the spiny surface and related muscles clearly do not require high-resolution sensory processing or fine motor control. Thus, it is not surprising that the spines have only a small representation in somatosensory cortex.

Hedgehogs have relatively large eyes and ears as well as prominent whiskers on the lateral surface of their snout. In addition, a dense array of fine hairs or microvibrissae

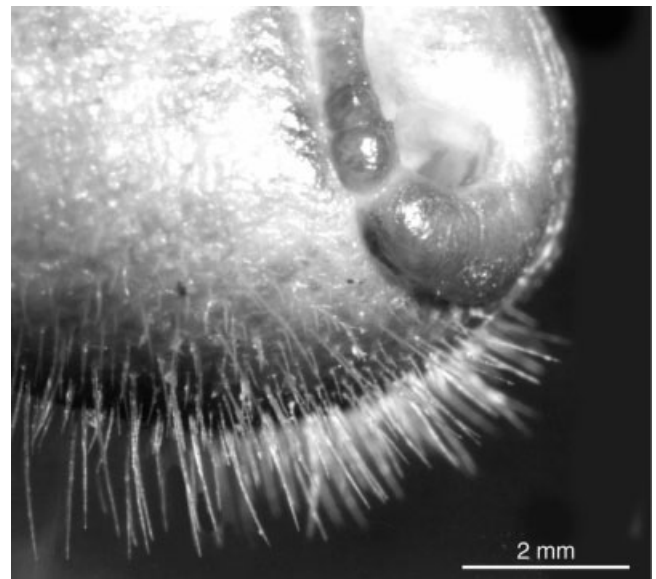


Fig. 3. A side view of the ventral snout of the hedgehog showing the large number of fine microvibrissae. The microvibrissae have a large representation in the somatosensory cortex. Reproduced with permission from Catania et al. (2000).

(Brecht et al., 1997) is located just below the glabrous skin surface at the tip of the snout (Fig. 3). From these observations, hedgehogs appear to have well-developed senses generally, as opposed to moles, which are clearly somatosensory specialists with small eyes and ears.

Hedgehog cortical organization is of particular interest because early studies using surface electrodes suggested that cortical areas were poorly organized, with little to-

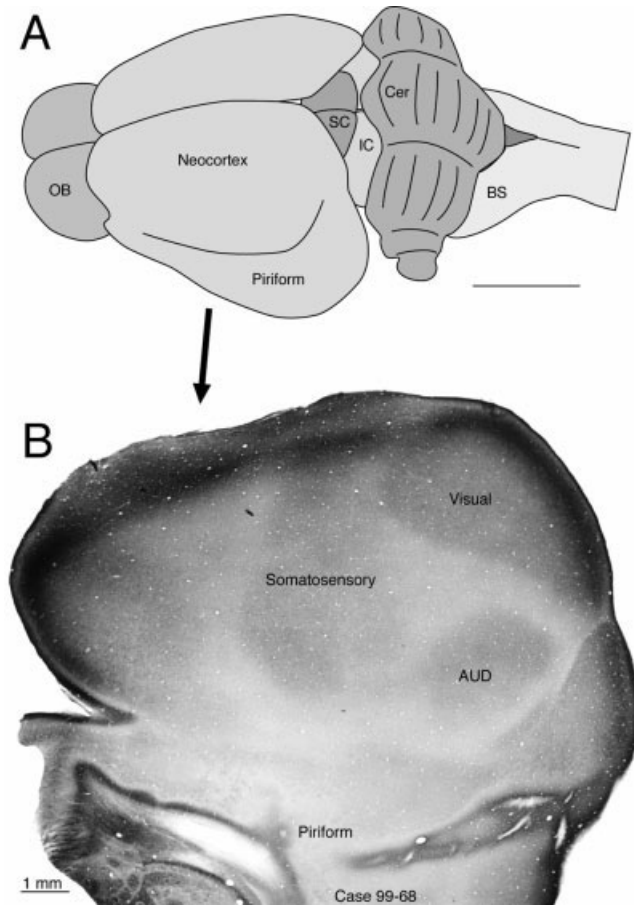


Fig. 4. The brain and neocortex of the African hedgehog. **A:** A view of the brain showing the relative size of the olfactory bulbs (OB), neocortex, and cerebellum (Cer). Scale bar = 5 mm. SC, superior colliculus; IC, inferior colliculus; BS, brain stem. **B:** A single section from middle layers of flattened cortex cut parallel to the surface and processed for cytochrome oxidase histochemistry. A number of distinct subdivisions are apparent, corresponding to the locations of auditory (AUD) somatosensory and visual cortex. Reproduced with permission from Catania et al. (2000).

pography and extensive overlap of visual, somatosensory, and auditory cortex (Lende and Sadler, 1967). Our more recent investigations using microelectrodes and the technique of flattening and sectioning cortex to visualize area boundaries have revealed a very different view of the hedgehog brain. The results of microelectrode recordings might be anticipated by examining layer 4 cortex processed for the metabolic enzyme cytochrome oxidase (Fig. 4). This procedure reveals a number of separate areas with relatively sharp boundaries, in the expected locations for primary somatosensory (S1), visual (V1), and auditory (A1) cortex. Our recordings from these areas revealed neurons that were exceptionally responsive to sensory stimuli (Catania et al., 2000). For example, any faint noises in the room tended to elicit responses in auditory cortex, small movements of objects around the dimly lit room often elicited visual responses in V1, and the slightest deflection of quills or hairs (within the appropriate receptive field) elicited strong responses in somatosensory

cortex. We investigated somatosensory cortex in detail and identified three separate representations of the contralateral body surface corresponding to S1, secondary somatosensory cortex (S2), and the parietal ventral areas (PV). Within S1, the topographic arrangement of body parts is typical for mammals (e.g., an inverted representation with limbs and ventral body parts represented most rostrally in cortex). Interestingly, the microvibrissae have the largest representation in S2, whereas the larger whiskers on the face take up only a small proportion of cortex. As might be expected, the quills had only a small representation in sensory cortex. PV and S2 encircle auditory cortex and in both areas the limb representations are located most laterally in cortex, although it was difficult to determine the detailed internal topography of the face and head representations in S2 and PV due to the large receptive fields of neurons in these areas.

We recorded visual responses between V1 and somatosensory cortex, suggesting an additional visual area (V2) is located in this region. In addition, previous investigations of receptive fields in the European hedgehog (Kaas et al., 1970a,b) and corticocortical connections in the Pakistani hedgehog (Gould and Ebner, 1978) suggest that hedgehogs in general have a single secondary visual area located in this region corresponding to the expected location of V2 (area 18) as found in a range of other mammals (Kaas, 1980, 1987, 1989; Rosa and Krubitzer, 1999).

Auditory cortex in the east African hedgehog corresponds to the location of the CO-dense region in caudolateral cortex (Fig. 4). Investigations in the long-eared hedgehog (Batzri-Izraeli et al., 1990; Batzri-Izraeli and Wollberg, 1992) revealed two separate tonotopic representations in this region, suggesting that hedgehogs have at least two auditory areas in this part of cortex.

Thus, in contrast to many historical ideas about hedgehog brain organization, the cortex in this species contains numerous sensory areas with sharp boundaries and well-organized internal topographies (Fig. 5). These features of hedgehog cortical organization are apparent in electrophysiological recording experiments and in the histology of layer 4 cortex processed for cytochrome oxidase (e.g., Fig. 4).

SHREWS (FAMILY SORICIDAE)

Shrews are anatomically similar in many respects to rodents, but they are only distant relatives. Like rodents, shrews have prominent sensory vibrissae and these are their most important tactile sensory organs. Their eyes are often small relative to their heads, and given their small absolute head size, visual capabilities are probably limited in many species. The most obvious feature of shrews is their diminutive size. Figure 6 shows an adult masked shrew weighing approximately 3 g. Its brain is correspondingly small as shown on a penny for scale. Because fossil endocasts from a number of early ancestral mammals indicate they had small brains with little neocortex (Kielan-Jaworowska, 1983, 1984, 1986; Jerison, 1990), shrews have been of particular interest for theories of mammalian brain evolution.

Despite this long-standing interest in insectivore brain organization, the neocortex of shrews has only recently been investigated in detail. Perhaps the most interesting question in this species is how many areas exist in such a small neocortex. Even in rodents, there is still some disagreement regarding how many cortical areas exist and

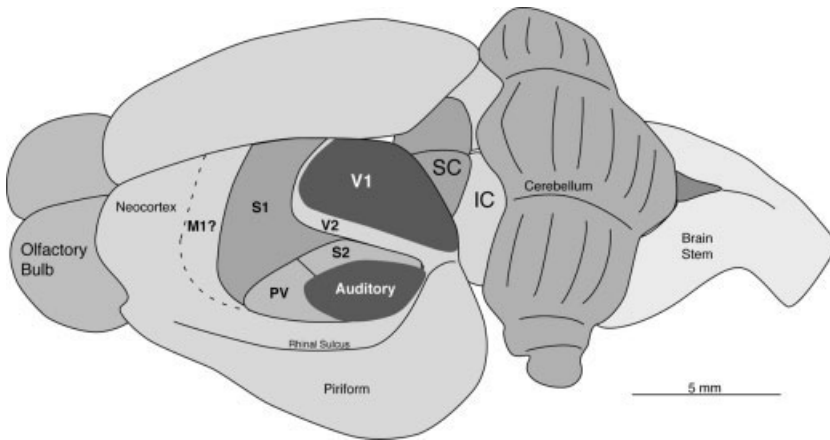


Fig. 5. A. A schematic of the hedgehog brain showing the relative size and location of the major subdivisions of the neocortex and sensory areas. Reproduced with permission from Catania et al. (2000).

how they may be homologized across species. For example, it has been suggested that rodents have as many as 10 visual areas forming a complex processing network (Montero, 1993) and that many of these areas are homologous to primate visual areas. Yet more recent analysis of visual areas across mammalian species indicates that most small mammals have a relatively simple visual system with V1 and V2 (e.g., hedgehogs; Fig. 5) and few other visual areas (Rosa and Krubitzer, 1999). The masked shrew's cortex is particularly valuable for such comparisons because this species is approaching the lower size limit for mammals (Schmidt-Nielsen, 1984) and therefore may provide the clearest example of how neocortical organization differs between large and small brained mammals. By extension, this may also inform us about the likely differences between small-brained ancestral mammals and many of the modern lineages that have undergone extensive expansion of the neocortical sheet.

As in hedgehogs, we examined the organization of shrew cortex using both microelectrode mapping and the analysis of flattened sections of cortex processed for cytochrome oxidase (Catania et al., 1999a). We investigated five species of shrew, but were unable to record from the neocortex of masked shrews because of their sensitivity to anesthesia. Nevertheless, its neocortex contained a number of distinctive subdivisions visible in flattened cortical sections. An analysis of the results from the five shrew species indicates how different cortical subdivisions in the masked shrew relate to different body parts and also allow us to identify visual and auditory cortex across species. Figure 7 shows a section of cortex from the masked shrew with the subdivisions labeled.

Several important conclusions can be drawn from these investigations. First, the neocortex of shrews contains discrete subdivisions with sharp borders (e.g., Fig. 7A), as has been found in other mammalian species (Kaas, 1987). Second, microelectrode recordings from shrew cortex (Catania et al., 1999a) reveal well-organized topographic representations of the contralateral body surface in both S1 and S2. The organization of S1 in shrews is consistent with the somatotopic organization of this area across mammalian species (Johnson, 1990) in that the face and mouth are represented most laterally in cortex, whereas the limbs and body are represented more medially. As in other mammals, secondary somatosensory cortex (S2) forms a mirror image of S1 in lateral cortex. However, S2

is much larger in its relative proportions than is typical of S2 in other species (Krubitzer et al., 1986). Finally, and most importantly, it is clear that shrews have only a very few cortical areas that are closely adjacent to one another with no room for additional intervening processing areas. For example, V1 is directly adjacent to the lateral border of S1, leaving no room for a secondary visual cortex or additional higher-level processing areas. Similarly, S2 is directly adjacent to the relatively small crescent-shaped auditory cortex (Fig. 7), leaving no room for additional somatosensory or auditory areas.

In shrews, the solution to having small brains is to have a few well-organized areas that take up the majority of the neocortex, rather than having many tiny interconnected areas. This suggests that V1 in shrews is involved in all cortical processing of visual information. Presumably the many cortical subdivisions found in larger-brained species (e.g., the 30 or more visual areas of primates) (Kaas, 1997) allow for specialization of function within each area and parallel processing of different facets of visual information. The addition of cortical areas to the network is likely an important mechanism by which greater sophistication of visual behaviors can be achieved in primates and other mammals. Yet there are also some potential processing advantages to having only one area. The single visual area in shrews may allow for high levels of connectivity between all neurons involved in visual processing, in contrast to the less interconnected groups of neurons spread widely across the networks in primate visual systems (Kaas, 2000). In addition, conduction times are likely to be exceptionally short in the small neocortex of shrews, allowing for small diameter axons and dendrites (Ringo, 1991; Ringo et al., 1994) and small supporting cell bodies. Therefore, more neurons may be able to fit in the small local networks of shrew cortex.

In the case of the somatosensory system, there are presumably far fewer primary afferents from the masked shrew's tiny body relatively to larger mammals, potentially allowing only two somatosensory areas to function with high efficiency. There is evidence for a separate motor area rostral to S1 in shrews (Nudo and Masterton, 1990; Catania et al., 1999a) and this region is also likely to have fewer demands than motor cortex in larger-bodied mammals with many more muscles to control and therefore more efferent output. Interestingly, the somatosensory system of shrews is the only component of cortex that

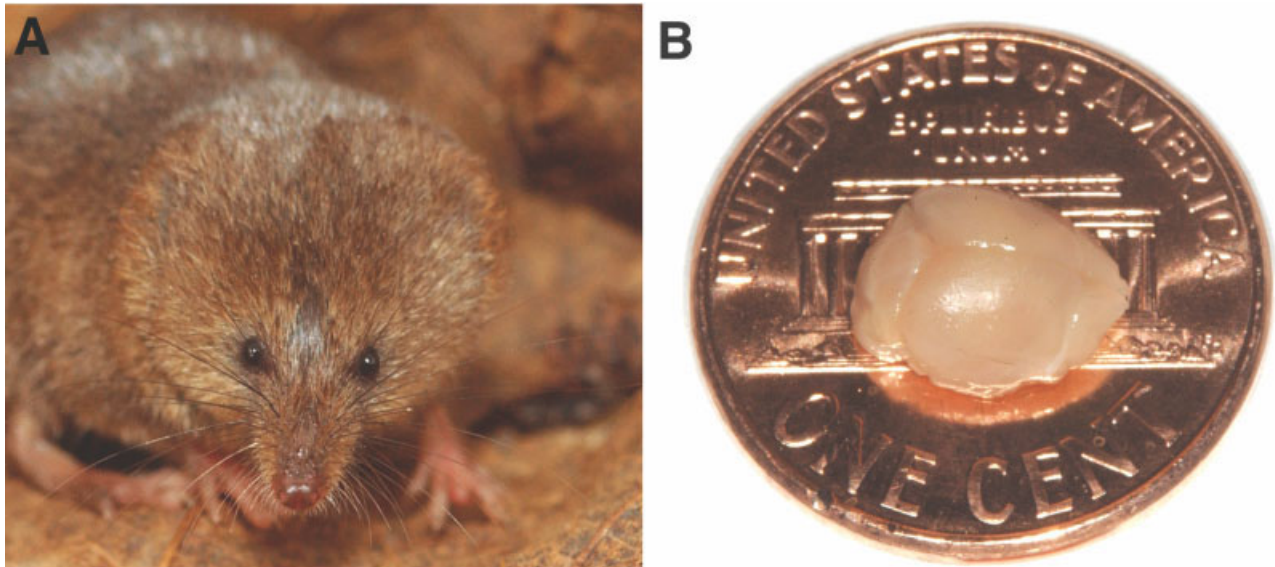


Fig. 6. **A:** A tiny masked shrew (*Sorex cinereus*) weighing only 3 g. Note the prominent whiskers on the snout and forward facing eyes. **B:** The brain of a masked shrew is shown on a penny for scale.

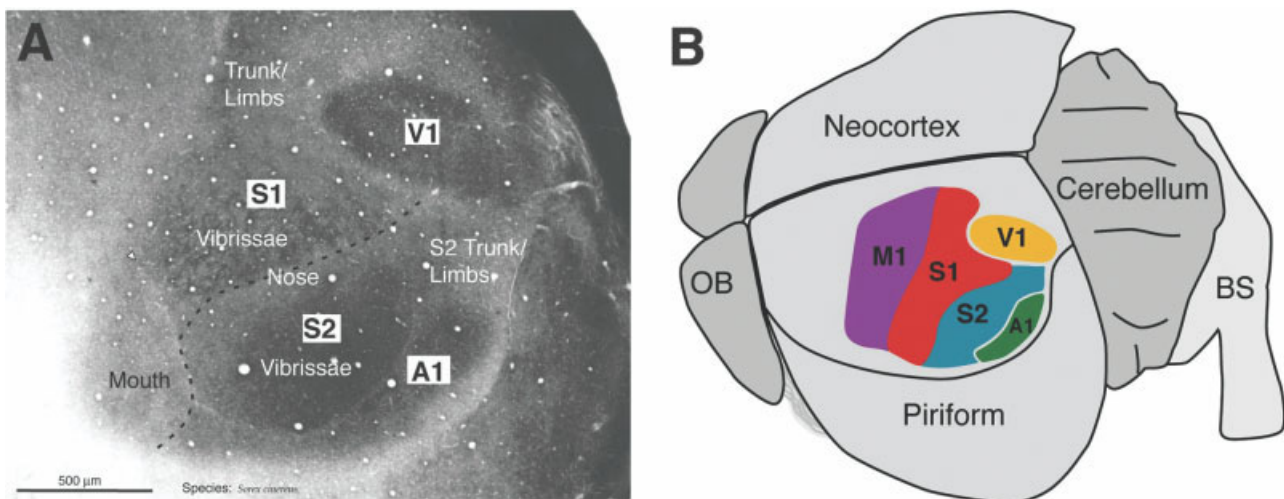


Fig. 7. **A:** A section of cortex from *S. cinereus* demonstrating the direct adjacency of cortical areas in a single section processed for cytochrome oxidase. Note for example the close proximity of the S1 vibrissae representation to the primary visual cortex medially and the direct adjacency of A1 to S2. Each cortical area has a distinctive appearance, while subareas (such as mouth, vibrissae, and trunk) within S1 and S2 are also distinct. **B:** Summary of cortical organization in shrews. The sensory areas are located in caudal, lateral cortex. Two representations of the contralateral body surface were found, one corresponding in location and organization to S1, the primary somatosensory area, and

the other more lateral area corresponding in location and organization to S2, the secondary somatosensory area. Auditory cortex was found at the extreme caudolateral end of neocortex, partially surrounded by S2. A striking feature of cortical organization in these small-brained mammals is the adjacency of sensory areas. This condition seems to exclude the possibility of intervening higher level or association areas typical of other larger-brained mammals. OB, olfactory bulb; BS, brain stem; V1, primary visual cortex; A1, auditory cortex; S1, primary somatosensory cortex; S2, secondary somatosensory cortex; M1, motor cortex.

clearly contains more than one processing area. This is perhaps not surprising given that shrews appear to be somatosensory specialists. In the masked shrew, roughly 25% of the entire neocortex is devoted to somatosensation (S1 + S2). Approximately 70% of S1 and S2 combined is devoted to the representation of the vibrissae, testifying to the importance of these sensory structures for shrews. The

rhinarium, or tip of the snout, has only a small representation in cortex, and this can be contrasted with the somatosensory system of moles. The neocortex of the masked shrew does not contain obvious barrels; however, the area representing the whiskers has a distinctive patchy chemoarchitecture that distinguishes this region from surrounding cortex and may reflect the representa-

tion of individual whiskers. In addition, the representation of the mouth and oral structures is evident as a cytochrome oxidase-dense area of rostralateral cortex separated from the S1 and S2 vibrissae representations by a cytochrome oxidase-light septum (Fig. 7). S1 and S2 are chemoarchitecturally distinct from one another and also separated by a CO-light septum (Fig. 7).

To summarize, shrews appear to have only six obvious cortical areas, including S1, S2, A1, V1, and a motor area (M1). Evidence for M1 comes from the location of corticospinal projecting neurons relative to S1 (Nudo and Masterton, 1990; Catania et al., 1999a). There is little room for additional sensory areas in caudal cortex. The relative sizes of the different sensory areas suggest that shrews are somatosensory specialists with more limited dependence on vision or audition. For example, auditory and visual cortex take up only about 3% and 5%, respectively, of total neocortex, compared to the 25% taken up by S1 and S2. It is interesting to note that S2 in shrews is unusually large compared to S2 in virtually all other mammalian species that have been investigated (with the exception of moles). The significance of this specialization is not clear.

MOLES AND DESMANS (FAMILY TALPIDAE)

Moles are a particularly interesting group of insectivores because they are generally specialized for life underground (with some notable exceptions, e.g., the semiaquatic desmans) and thus have elaborate somatosensory systems and generally reduced visual and auditory abilities. Moles are the sister taxon to shrews, and there is some overlap in the specializations of the two families. For example, there are mole-shrews (shrews specialized for life underground) and shrew-moles (moles specialized for life aboveground). Yet there are some distinctive differences between moles and shrews, particularly in regard to their somatosensory systems. Because of the close affinity of these two groups and the range of variation exhibited, it is informative to see these specializations compared (Fig. 8).

The most obvious difference between mole and shrew somatosensory systems, reflected in both their anatomy and behavior, is a shift from the use of vibrissae as the major sensory organs for touch in shrews (and most other small mammals) to the use of the hairless (glabrous) tip of the snout in moles. Although moles retain whiskers along their snout, these are generally reduced in size compared to other mammals. Moles instead probe their environment with the tip of their noses. For this purpose, the snout of nearly every Talpid species is covered with complex mechanosensory organs called Eimer's organs (Fig. 8). An Eimer's organ is an epidermal specialization consisting of a swelling or papillae containing free nerve endings, merkel cell-neurite complexes, and lamellated (or paciniform) corpuscles in the underlying dermis. Using these touch receptors, moles are able to make rapid and accurate tactile discriminations as they forage for prey and navigate their environments (Catania and Remple, 2005).

Although the Eimer's organ is the basic receptor unit found in the epidermis of moles, the number of these organs, their form, and the anatomy of the snout containing these touch receptors vary considerably across species. The middle panels of Figure 8 show scanning electron micrographs of the snout of a shrew and three species of mole. No species of shrew has been found to possess Ei-

mer's organs, and this is reflected in the smooth skin surface of the rhinarium. The eastern American mole is one of the few mole species that does not possess fully developed Eimer's organs, probably because it lives in a relatively dry and harsh soil environment and therefore must have a thick keratinized layer of epidermis on the rhinarium (Fig. 8, bottom panel). Nearly all of the remaining mole species have Eimer's organs covering their snouts in various numbers (Catania, 2000a).

The most extreme nasal specialization can be found in the elaborate nose of the star-nosed mole (Fig. 8, right side). The entire star is essentially composed of Eimer's organs arrayed along the 22 appendages that ring the nostrils. This structure is one of the most elaborate touch specializations to be found among mammals. The central lower pair of appendages acts as the tactile fovea of the star and is used for detailed investigations of objects, whereas the other peripheral appendages are used to scan the tactile environment for objects of interest. The star-nosed mole's behavior includes frequent nasal saccades that bring the touch fovea into contact with objects or prey items that have been detected by the larger array of peripheral appendages (Catania and Remple, 2004). The parallels with the visual system are striking and are also reflected in the organization of neocortex.

The comparisons in Figure 8 are particularly informative in an evolutionary context. By itself, the star-nosed mole's nose with its unique appendages covered with 25,000 Eimer's organs is a bit of an enigma. Yet comparisons across the different mole species reveal that Eimer's organs are a common specialization among moles. In addition, the modules of Eimer's organs found at the caudal end of the rhinarium of the coast mole have a distinctive "proto-star" appearance and strongly suggest the kind of ancestral state that may have given rise to the star (for more details, see Catania et al., 1999b). Finally, the less developed components of the Eimer's organ found in the eastern American mole are similar to the arrays of mechanoreceptors found in a range of mammalian skin and suggest the precursors that gave rise to the more organized arrays found in the Eimer's organs of most moles. In this context, it is perhaps not surprising that at least one other lineage of mammals has developed a similar sensory structure based on the same sensory building blocks. Both the duck-billed platypus and the echidna (monotremes) have push-rods in the snout that are essentially the same as Eimer's organ (Manger and Pettigrew, 1996).

Although little is known about their brain organization, the desmans have unique peripheral sensory specializations of the snout that warrant some discussion. The two desman species are semiaquatic members of the talpid family that spend much of their time diving and swimming in search of prey (Gorman and Stone, 1990). They have a fringe of hairs around their rear feet that provides additional surface area for efficient paddling and they do not have the large clawed forelimbs characteristic of fossorial moles. Yet they are clearly talpids and are more closely related to fossorial moles than to shrews. Their rhinarium reflects this association, as it is covered with Eimer's organs. But in addition to Eimer's organs, desmans have a remarkable arrangement of nearly microscopic short hairs covering the distal snout (Fig. 9). These hairs are surrounded by Eimer's organs, resulting in one of the more elaborate configurations of receptors to be found among mammals. These hairs are obviously not

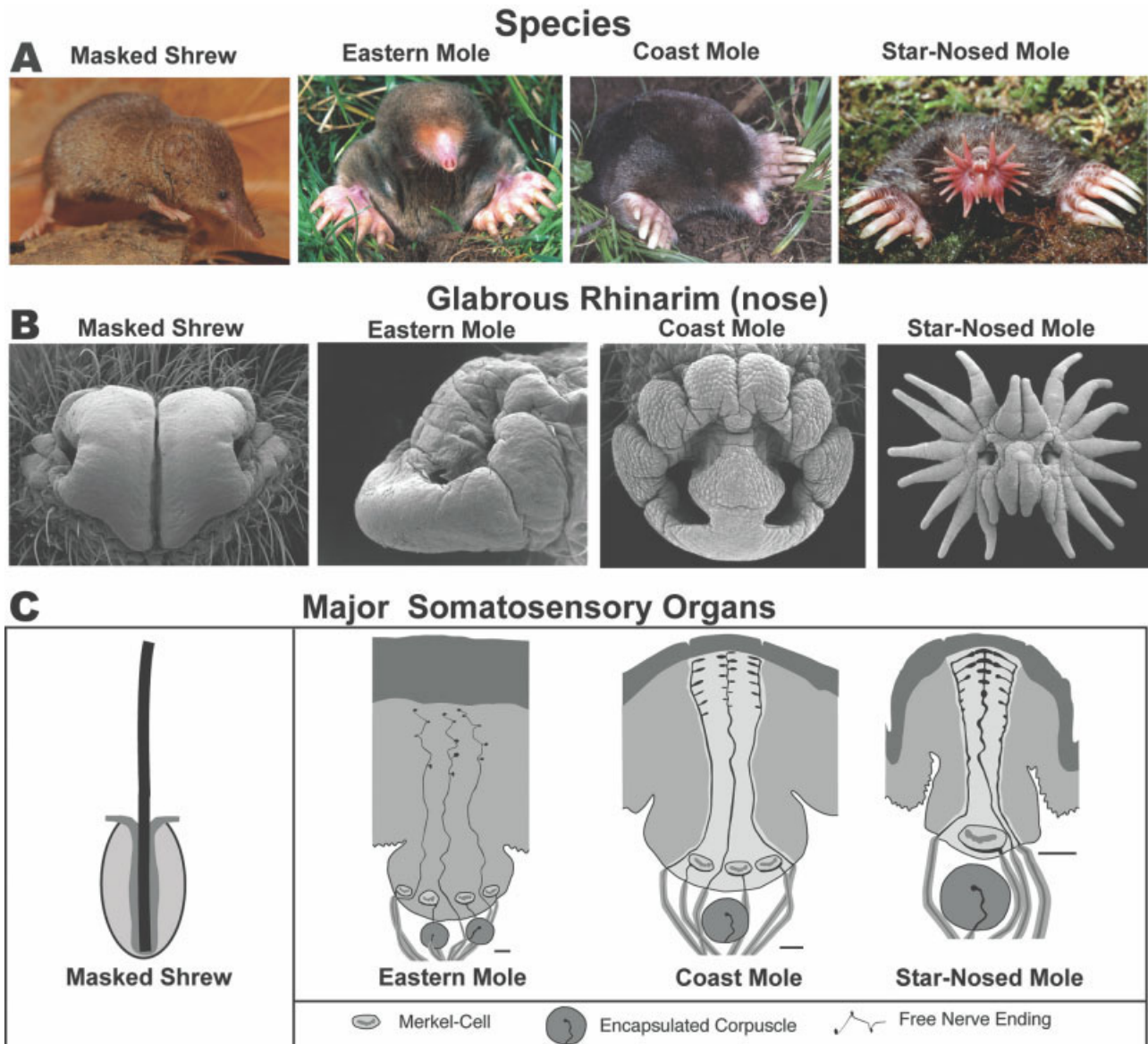


Fig. 8. A comparison of body types and sensory specializations between a shrew and three moles with different degrees of elaboration of the mechanosensory snout. **A:** A small-bodied masked shrew, an eastern American mole, a coast mole, and a star-nosed mole. **B:** The tip of the nose of each species. The masked shrew has the least specialized snout and uses sensory vibrissae for the majority of tactile explorations. Moles have made a shift in this sensory priority and instead use the tip of their nose to explore their environment through touch. There is pro-

gressive enlargement of the skin surface and evidence of mechanosensory organs (Eimer's organs) covering the outer skin surface in the form of epidermal papillae (most obviously the coast mole example). **C:** The sensory organs of the skin surface in each respective species. The masked shrew depends on vibrissae, whereas the Eimer's organs of the moles are progressively more organized and smaller in the graded series of sensory specializations illustrated from left to right. Scale bar in lower panel = 10 μ m.

useful for detecting distant objects through touch, as is the case for many longer vibrissae. What might be their function? A number of recent investigations have shown that the relatively large whiskers of semiaquatic mammals, such as seals and manatees, are used to detect water movements (Dehnhart et al., 1998a, b; Reep et al., 1999). The tiny hairs on the desman snout may be the ultimate expression of this ability in mammals through receptors that are convergent with the neuromasts found in the

lateral line system of fish. Neuromasts consist of hair cells with an apical extension, a cupula, that is deflected by water movements. The tiny (100–200 μ m) hairs on the desman snout are similar in size and form to the cupula of a neuromast (Blaxter and Fuiman, 1989). Unfortunately, the desmans are threatened species and little is known about their brain organization.

However, a number of recent studies have revealed details of brain organization in moles related to their sen-

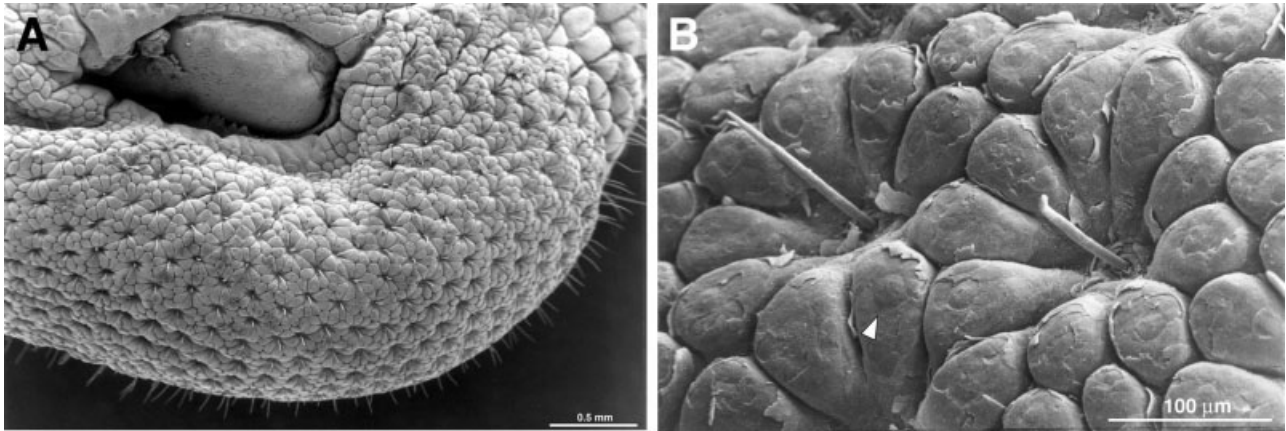


Fig. 9. The rhinarium of the Pyrenean desman, *Galemys pyrenaicus*. **A:** Scanning electron micrograph of the snout. This species forages for prey primarily in water and has a complex configuration of the epidermis, covered with both microvibrissae and Eimer's organs. Note that the nostril can be closed. **B:** Higher magnification of an area of epidermis

reveals evenly spaced microvibrissae surrounded by Eimer's organs. The sensory hairs are exceptionally short, similar to the cupulae of neuromasts, and they could play a role in detecting water movements similar to the neuromasts of fish and amphibians. Reproduced with permission from Catania (2000a).

sory specializations. Some of the most striking findings can be seen (literally) in the cortex of the star-nosed mole (Fig. 10). As is the case for shrews, the cortex of the star-nosed mole contains a number of distinctive subdivisions visible in flattened sections of cortex processed for cytochrome oxidase. In a particularly dramatic example of how sensory surfaces may be represented in modular configurations of cortex, the S1 cortical representation of the star is visible as 11 distinctive modules of cytochrome oxidase-dense tissue (for more details, see Catania and Kaas, 1995). Within this representation, the module representing the 11th appendage (the tactile fovea) is greatly enlarged relative to the proportion of the star taken up by this sensory surface [Fig. 10A and B and see Catania and Kaas (1997)]. This finding illustrates another parallel between the mole's somatosensory system and the visual systems of other mammals in which the representation of the retinal fovea is greatly enlarged in primary visual cortex.

In addition to the modules in S1, two additional cortical areas (S2 and S3) in more lateral cortex contain modular reflections of the representation of the star (Fig. 10C). Therefore, star-nosed moles have arguably the most distinctive cortical cytoarchitecture in relationship to the representation of sensory surfaces to be found among mammals. For example, although rodents have barrels in S1 that reflect the representation of each mystacial vibrissae on the snout (Woolsey and Van der Loos, 1970; Welker and Woolsey, 1974), the S2 and the parietal ventral (PV) cortical areas do not contain large representations of the vibrissae with corresponding modules.

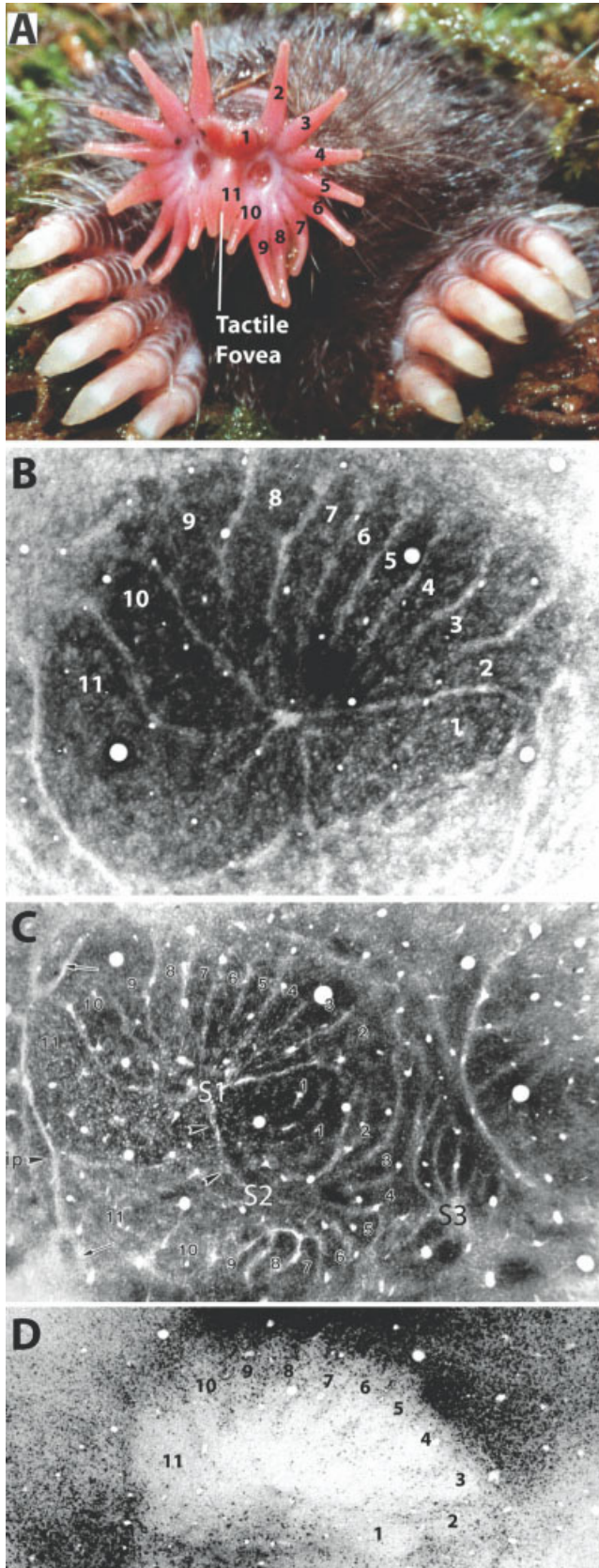
The reasons for such modules in the cortex are not entirely clear; however, different components of the cortical modules in star-nosed moles are connected in different ways to other brain areas. For example, the septa that separate the representations of the different appendages in star-nosed mole S1 and the areas directly surrounding the star representation are densely connected to neurons on the opposite hemisphere through the corpus callosum

(Fig. 10C). In contrast, the central part of each module is interconnected to the homologous appendage representations in S2 and S3 (Catania and Kaas, 2001).

CONCLUSION

Clearly, star-nosed moles have an elaborate somatosensory system with specializations of the sensory periphery reflected in the central nervous system. Because the star-nosed mole represents an extreme in the elaboration of the tactile receptors of the snout, it is interesting to consider and compare how the brains of less specialized moles are organized, and how this compares to brains in shrews and hedgehogs. Figure 11 shows a comparison of cortical organization across these species. A number of interesting conclusions can be drawn from this comparison. First, hedgehog cortex is organized in a manner similar to that found in many other small mammals. Three somatosensory areas occupy much of the central cortical area, flanked caudally and laterally by visual and auditory cortex, respectively. Note S1 is relatively much larger than either S2 or PV in hedgehogs and auditory cortex has a relatively large representation in lateral cortex coextensive with a cytochrome oxidase-dark region visible in flattened sections of cortex (Fig. 4). In contrast, the neocortex of shrews contains only two somatosensory areas (S1 and S2) of similar size. The unusually large size of S2 in shrews was evident during the mapping of the vibrissae, which usually have a much smaller representation in S2 of other mammals (Remple et al., 2003). In addition to this specialization, auditory cortex consists of an unusual crescent of cortex caudal to S2. Finally, in shrews, there was no evidence for a secondary visual area (V2).

The eastern American mole cortex reflects the general organization of areas in moles (Catania, 2000b). The representation of the rhinarium is relatively large compared to shrews and corresponds to the cortical processing area for information from the Eimer's organs. Note that both the star-nosed mole and the eastern American mole have a large S2 compared to most mammal species. In addition,



the auditory cortex of moles (which is particularly sensitive to low frequencies and vibrations) consists of a crescent of tissue caudal to S2. These specializations are unusual, and similar to the unusual configuration of cortex in shrews. This is an important shared derived character of brain organization that reflects the close affinity of the Talpidae and Soricidae families.

A comparison of the eastern American mole to the star-nosed mole is particularly relevant because these two species are very closely related and have a similar brain and body size. They also share a common body plan with the exception of the sensory organs of the nose. Clearly, the star-nosed mole brain must process large volumes of complex information coming from the star, whereas the eastern mole snout is much less specialized. In a sense, this is nature's own experiment in which primarily only one dimension of the animal's body plan has changed between the two species. We may then ask how brain organization differs between these two species and confidently attribute the differences to the requirements of sensory processing.

An obvious difference in cortical organization between the two species is the size of the nose representation. Eastern moles have a larger representation of the whiskers and a comparatively small representation of the rhinarium. In contrast, the representation of the rhinarium in star-nosed moles is huge and takes up much of lateral cortex. More importantly, however, star-nosed moles have an extra cortical processing area in this lateral network of somatosensory areas. Other moles and shrews have only S1 and S2 (Catania et al., 1999a; Catania, 2000b). This strongly suggests the ancestral condition for the star-nosed mole consisted of only two cortical areas, and as the demands for sensory processing from the nose increased, an extra area was added to the cortex of star-nosed moles. This supports the general conclusion that the addition of cortical sensory areas is one important way in which behavioral complexity is produced in mammals. Although this is not a new idea, conclusions based on comparisons between large-brained and small-brained mammals are confounded by the drastically different sizes of the cortical sheets being compared, and thus the significance of different numbers of cortical areas found in comparisons across distantly related species of different brain size is not always obvious.

To summarize, modern investigations of brain organization in insectivores are in striking contrast to his-

Fig. 10. The unusual mechanosensory star and its corresponding cortical representation in the star-nosed mole (*Condylura cristata*). **A:** A star-nosed mole showing its large forelimbs and the 22 fleshy, tactile appendages surrounding each nostril. The 11th appendages on each side act as the somatosensory fovea and are used for detailed tactile investigations. **B:** The pattern of cortical modules in S1 visible in flattened cortical sections processed for the metabolic enzyme cytochrome oxidase. Note the expanded representation of the somatosensory fovea (appendage 11). **C:** A section of flattened cortex revealing all three cortical representations of the star visible as a series of modules, each representing an appendage from the contralateral star. **D:** An example of the specificity of callosal connections around the S1 star representation. Cells and terminals are concentrated in the septa between appendage representations and surrounding the star representation but are absent from the centers of each cortical stripe. Reproduced with permission from Catania (2002).

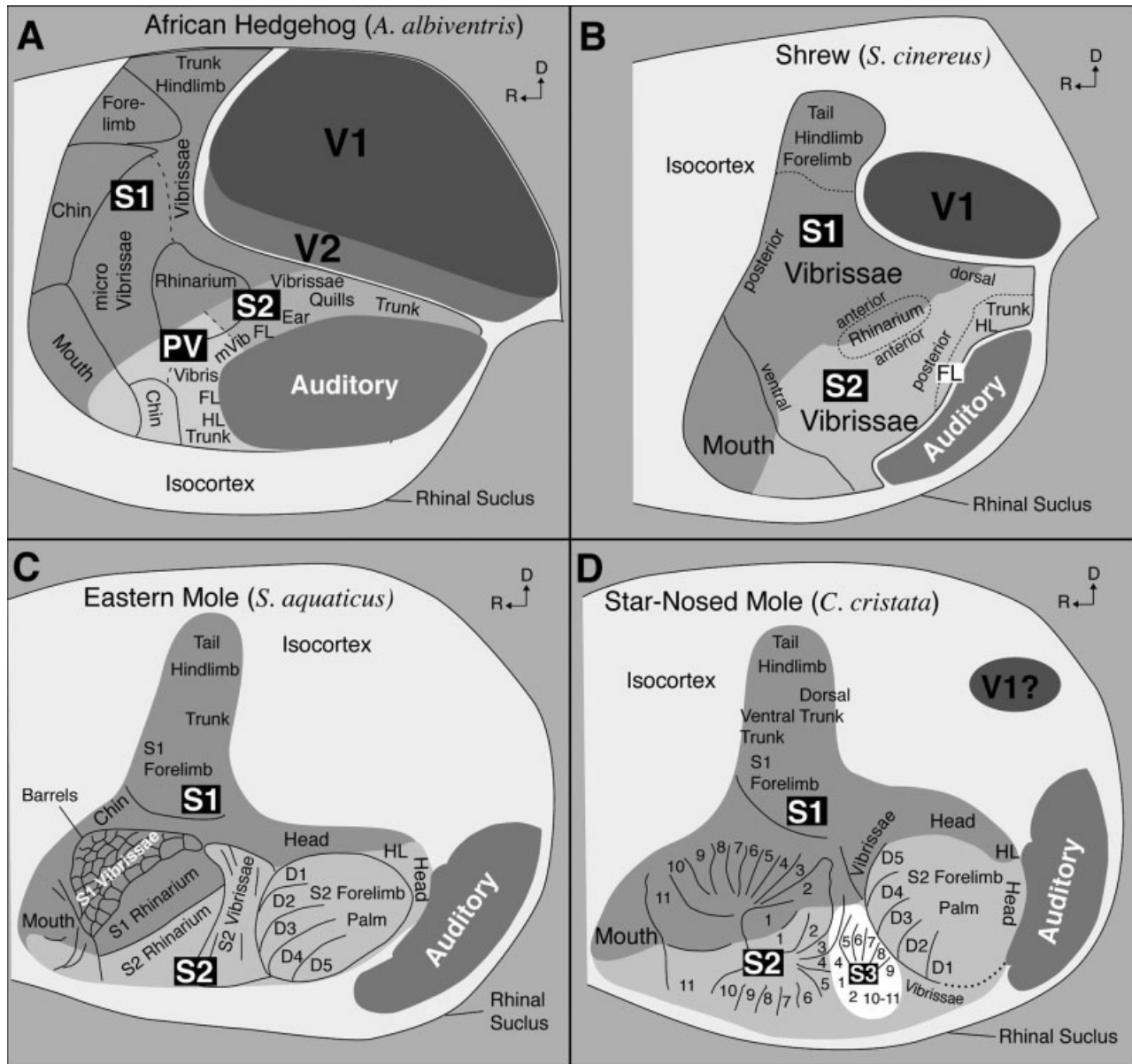


Fig. 11. The organization of sensory areas in the isocortex of four insectivores. **A:** In the east African hedgehog, three somatosensory areas contain topographic representations of the body surface. The primary somatosensory area (S1) is located medially while the smaller parietal ventral (PV) and second somatosensory (S2) areas are located in lateral cortex. Primary and secondary visual areas (V1 and V2) are located in caudomedial cortex. Auditory cortex forms a broad oval in lateral and caudal cortex. **B:** Sensory areas in the masked shrew. Shrews have two relatively large somatosensory areas (S1 and S2) dominated by the representations of the large mystacial vibrissae and containing only a very small representation of the rhinarium. Auditory cortex is found in an unusually small caudal crescent. **C:** The organization of sensory areas in the eastern mole. Eastern moles have S1 and S2 containing large

representations of both the vibrissae and the rhinarium. A large representation of the forelimb is located in S2. Both the S2 forelimb and S1 vibrissae representations contain modules visible in flattened sections of cortex (see Figs. 6 and 7). The auditory region is located in a caudal crescent of cortex. **D:** The organization of sensory areas in the star-nosed mole. The representation of the star dominates much of somatosensory cortex, containing three topographic representations of the rhinarium (compared to two in the eastern mole). Each of the three representations of the star contains modules or stripes corresponding to the nasal appendages as numbered above. Moles and shrews share an unusual auditory cortex. FL, forelimb; HL, hindlimb; mVib, microvibrissae. Reproduced with permission from Catania (2000c).

torical views of these species. Every member of this order appears to have a series of discrete and well-organized sensory areas that are reflected in both electrophysiological mapping procedures and anatomical analysis of the cortex. There is diversity in brain orga-

nization across the species, with hedgehogs resembling most other small mammals, and shrews and moles sharing a derived and unusual configuration of cortex. Small-brained shrews are at the lower size limit for mammalian brains and this is reflected in a cortex that

contains only a few sensory subdivisions. Moles also have few cortical subdivisions, but their reduced visual and auditory systems make generalizations across sensory systems difficult. However, moles are clearly somatosensory specialists and the star-nosed mole has one of the most well-developed tactile sensory organs among mammals. This is reflected in a modular somatosensory cortex that is equally well-developed and parallels features of visual cortical areas in other mammals.

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