Organization of the Somatosensory Cortex in Elephant Shrews (*E. edwardii*)

CHRISTINE M. DENGLER-CRISH,[1] SAMUEL D. CRISH,[2] M. JUSTIN O'RIAIN,[3] AND KENNETH C. CATANIA[2]*

[1]Vanderbilt University Neuroscience Program, Vanderbilt University, Nashville, Tennessee
[2]Department of Biological Sciences, Vanderbilt University, Nashville, Tennessee
[3]Department of Zoology, University of Cape Town, Cape Town, South Africa

ABSTRACT

The superorder Afrotheria consists of a diverse group of mammals, including elephants, hyraxes, dugongs, sea cows, aardvarks, tenrecs, golden moles, and elephant shrews. Recent studies suggest this clade diverged from other placental mammals 100 million years ago and thus may represent the sister group to the remaining placental mammals. Despite this important taxonomic position, relatively few studies have investigated cortical organization in these species. Here we present results of an investigation of the somatosensory cortex in the Cape elephant shrew (*Elephantulus edwardii*). Using multiunit electrophysiological recording techniques, we identified a topographic map of the elephant shrew's body in a location and orientation consistent with the primary somatosensory cortex (S1). The elephant shrew's elongated snout, extensive facial vibrissae, and long tongue accounted for a large portion of the somatosensory representation, located in a relatively rostral area of cortex. Evidence for an additional somatosensory area, presumed to be secondary somatosensory cortex (S2), was found just lateral to S1. Visual and auditory responsive areas were also identified and the extent of visual cortex appeared to be quite large in these highly visual mammals. Despite the elephant shrew's exceptionally well-developed eyes, ears, and vibrissae, there were no anatomical correlates to sensory areas, or body part representations (e.g., barrels), that could be identified in the flatted cortex. Anat Rec Part 288A: 859–866, 2006.

Key words: Afrotherian; Macroscelidea; Cape sengi; neocortex; S1; brain; evolution

The recently defined superorder Afrotheria is an impressively diverse clade of mammals that diverged from other placentals over 100 million years ago (Murphy et al., 2001a, 2004). Afrotherians have African roots and include elephants, hyraxes, dugongs, sea cows, aardvarks, tenrecs, golden moles, and elephant shrews (Fig. 1). Its members have a wide range of brain sizes and sensory specializations and may provide important insights into mammalian brain evolution. Recently, tenrecs have been the focus of investigations because their small brains with little neocortex are thought to resemble the brains of ancestral mammals in a number of respects (Krubitzer et al., 1997; Kunzle, 2003). Manatees are of interest because of their unique ecological niche and unusual body form (Marshall and Reep, 1995; Reep et al., 2001, 2002). Closely related elephants have a complex social system and also represent an extreme in size that may provide insights into how brains scale with increasing body size (Hakeem et al., 2005). In addition, golden moles have remarkable specializations for digging through sand and detecting the slightest vibrations that may indicate the directions of prey items (Narins et al., 1997).

Given this diversity, Afrotheria seems to represent an untapped resource of information about mammalian sen-

*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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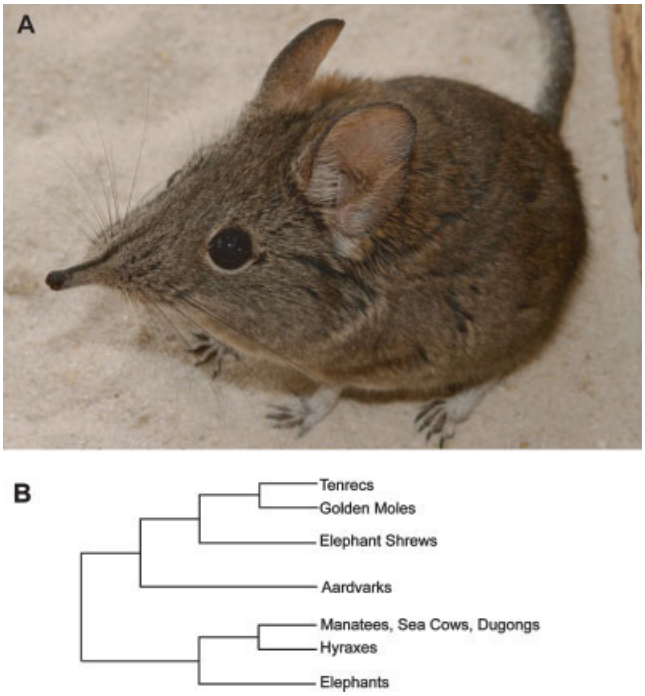

Fig. 1. A: The elephant shrew *Elephantulus edwardii*. Note the large eyes and pinna as well as the elongated snout covered with large vibrissae. B: Cladogram of relationships within the mammalian superorder Afrotheria.

sory systems and brain organization, yet relatively few studies have investigated cortical organization in these species. Here we present the results of an investigation of neocortex in the Cape elephant shrew (*Elephantulus edwardii*). This species is endemic to a limited region in the Cape Province of South Africa (Leon et al., 1983). These solitary animals are diurnal, live on rocky outcrops in a semiarid environment, and subsist mainly on termites and ants (Woodall and Currie, 1989). Very little is known about the neurobiology of their phylogenic order, Macroscelidea. We used electrophysiological recording techniques to identify somatosensory, visual, and auditory responsive areas in the neocortex. Although we were able to collect data from only three specimens, the results clearly indicate the location and topography of primary somatosensory cortex (S1), suggest the location for secondary somatosensory cortex (S2), and provide preliminary indications of the location and size of the auditory and visual areas. In addition, the results of examining histological sections of flattened cortex are discussed.

MATERIALS AND METHODS

Subjects

Three adult elephant shrews (*E. edwardii*; two male, one female) weighing between 51 and 67 g were used for this study. Elephant shrews were obtained from the University of Cape Town, Cape Town, South Africa, and were originally wild-caught from the Cape Province. All experimental procedures followed National Institutes of Health guidelines and were approved by the Vanderbilt University Animal Care and Use Committee.

Recordings from Cortex

A surgical plane of anesthesia was induced with injections (i.p.) of 15% urethane in distilled water (1 g/kg) and 10% ketamine in saline (50 mg/kg). Additional injections of one-fourth to one-half the initial dose of ketamine were given as needed. Body temperature was maintained with warm water bottles. A midline incision was made on the head to expose the skull and a craniotomy was performed. Animals were secured by a head post with dental cement and the cortex was exposed by craniotomy (the dura was left intact). The brain was protected with liquid silicon and a digital photograph of the cortical surface was taken. Tungsten microelectrodes (1.0 MΩ at 1 kHz) placed perpendicular to the cortical surface were used to make multiunit electrode recordings in the middle layers of cortex. Neuronal responses were amplified and delivered to an oscilloscope and speaker. Each electrode penetration was marked on the photograph of the brain surface. Electrolytic lesions (10 μA while withdrawing electrode at 50 μm/sec) were made at selected sites.

Receptive fields of neurons at each penetration site were mapped by manually stimulating the body surface, whiskers, and hair. Moving beams of light were used to identify visual responses, and auditory responses were probed with clicks and taps. Visual receptive fields and auditory frequencies were not defined.

After the recording procedure, elephant shrews were given an overdose of sodium pentobarbital (100 mg/kg) and perfused with heparinized saline (2,000 units/L in 0.01 M PBS) followed by fixative (4% paraformaldehyde in 0.01 M PBS). The brain was removed and the cortex was separated and flattened between glass slides in 30% sucrose/PBS. A freezing microtome was used to cut sections parallel to the cortical surface (60–90 μm). Tissue sections were processed for cytochrome oxidase (CO).

RESULTS

Figure 1 shows an elephant shrew with some of its obvious sensory specializations. The Cape elephant shrew has large eyes and ears as well as prominent sensory vibrissae. In addition, the elongated snout is in constant motion as they explore their environment and search for food. Our video recordings of elephant shrew behavior indicate the tip of the snout is seldom touched to the ground during this behavior [in contrast to moles; e.g., see Catania and Kaas (1997)]. Instead, the prominent snout and its constant motion appear to play a role in olfaction; however, details of this possibility remain to be explored.

Figure 2 is an illustration of the brain of *E. edwardii*. The elephant shrew has a large neocortex with well-developed olfactory bulbs and superior colliculi. Our recordings were concentrated in the somatosensory cortex; however, a number of auditory and visual responses were obtained in two cases.

Somatosensory Cortex

The results of our recording experiments are outlined in Figures 3–5. Case 03-02 provided the most detail (Fig. 3). However, the results from each of the three cases are consistent with one another and allowed us to identify confidently the location and orientation of pri-

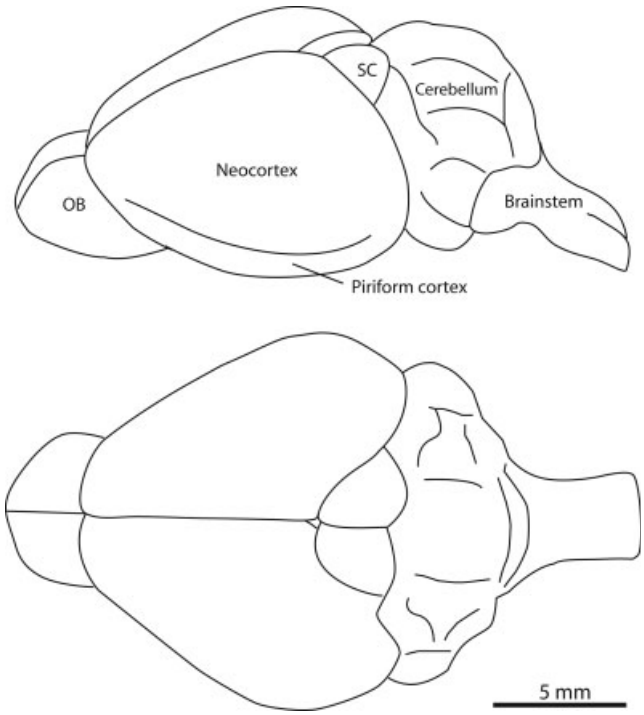

Fig. 2. Schematized illustration of an elephant shrew brain. OB, olfactory bulb; SC, superior colliculus.

mary somatosensory cortex (S1). In addition, the likely location of secondary somatosensory cortex (S2) was identified in case 03-02.

Primary somatosensory cortex (S1) was located in a relatively rostral strip of tissue with the representation of the hindlimb and caudal trunk (body) most medial in cortex (e.g., penetrations A and B, Fig. 3; penetrations H and I, Fig. 4) and with the face and snout represented more laterally in cortex (e.g., penetrations D–J, Fig. 3; penetrations E and D, Fig. 4; penetrations B–F, Fig. 5). Along the rostral-to-caudal axis in S1 cortex, the most distal body parts (e.g., forelimbs on the body, tongue on the head) were represented most rostrally in cortex. For example, the tongue representation was consistently found rostrally in S1 (penetration I, Fig. 3; penetration A, Fig. 4; and penetration A, Fig. 5), whereas the vibrissae were consistently represented more caudally. In the case of the head representation, penetrations A through F in Figure 5 provide an example of receptive fields that progressed caudally on the animal as the electrode was positioned successively more caudally in the cortex. There were fewer detailed receptive field progressions on the trunk of the body; however, case 03-02 provided evidence for the relative location of the trunk as compared to the limb representations (penetrations A, B, C, and surrounding areas, Fig. 3).

Within S1, the vibrissae representation dominated the responsive areas, but there was also a relatively prominent representation of the tongue and more distal snout. The trunk representation in S1 was only identified in the most extensive mapping case (Fig. 3) and this no doubt reflects its smaller representation and less prominent mechanoreceptor arrays compared to the face. The trunk representation was located caudal to the limb representations, as is reported for S1 in nearly all mammals [with rare exception: Calford et al. (1985)].

All of these results are consistent with the conclusion that S1 in the elephant shrew has an inverted representation of the body (i.e., foot representation medial, head representation lateral in cortex) and that within this representation distal body parts (limbs/rostral face and tongue) are represented most rostrally in cortex.

Lesions were placed in each of the highly responsive areas of tongue, forelimb, hindlimb, and vibrissae representations in somatosensory cortex (lesions were also made in visual and auditory cortex). Following the recording experiments, the cortex was flattened and sectioned parallel to the cortical surface in order to examine the relationship between body part representations and the chemoarchitecture of cortical fields. We were not able to identify any reflection of the representations of whiskers or other mechanoreceptor groups in the cortical architecture.

In case 03-02 (Fig. 3), we found evidence for an additional representation of the body just lateral to S1. For example, neurons at a number of electrode penetrations in far lateral cortex of case 03-02 responded to stimulation of the contralateral trunk and hindlimb (penetrations N and O, and see surrounding area in inset, Fig. 3). These representations are well separated from the more medial representations of the hindlimb and trunk. This area is likely the homologue to the commonly identified secondary somatosensory cortex (S2) that is located lateral to S1 in most mammals.

Visual and Auditory Cortex

Electrophysiological recordings revealed a relatively large region that responded to visual stimuli. Visual responses were found in cortical regions from the caudal border of S1 to within 1 mm of the caudal edge of the neocortex (Figs. 3 and 4). It is likely that visual cortex extended caudally, and perhaps medially, beyond the responsive areas delineated in this investigation. However, somatosensory cortex appears to form the rostral border of the visual areas and we can be fairly confident from our results that visual areas in elephant shrews extend far rostrally in cortex to include cortex just caudal to S1. Auditory responsive cortex was identified in two cases (Figs. 3 and 4) and was located caudal to S1 and lateral to visually responsive cortex.

DISCUSSION

The elephant shrew has a large well-developed cortex with several electrophysiologically distinct sensory areas. Figure 6 summarizes the results of this investigation and illustrates the relative position and orientation of primary somatosensory cortex (S1) in elephant shrews. The orientation of S1 is similar to that described for a range of other placental mammals that have a similar body plan (Fig. 6) (Kaas, 1983, 1993; Johnson, 1990; Krubitzer et al., 1993; Krubitzer, 1995). However, S1 is located in a relatively rostral location, supporting the suggestion from our recordings that a large amount of cortex is devoted to processing visual inputs. Elephant shrews appear to be highly visual diurnal mammals with large eyes and have been observed in our labora-

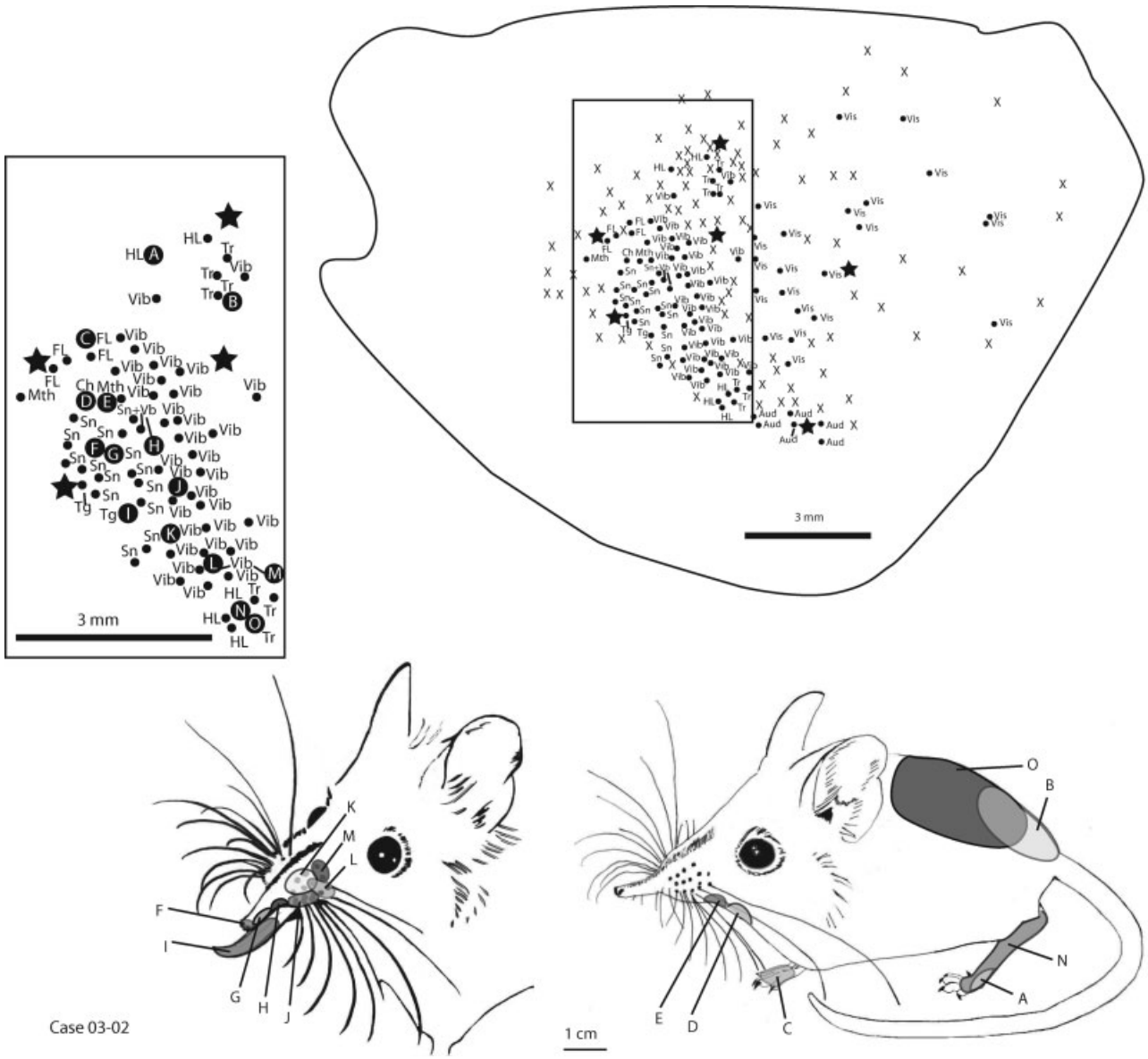

Fig. 3. Microelectrode recordings from the elephant shrew, case 03-02. The upper portion shows the flattened cortex with locations of electrode penetrations (dots) and lesions (stars) and abbreviations for the corresponding modality or body part represented. The inset is an enlargement of the somatosensory region. Receptive fields for penetrations A–O are shown in the illustrations of the elephant shrews at the bottom. Tg, tongue; Mth, mouth; Sn, snout, Vib, vibrissae; Ch, chin; Tr, trunk; FL, forelimb; HL, hindlimb; Vis, visual; Aud, auditory.

tory to rely on visual cues for detecting prey. They also use vision to detect predators and navigate quick escapes through their rocky environment. In the wild, they often act as sit-and-wait predators, spending most of their time in rock crevices and occasionally darting out to capture ants and termites (Stuart et al., 2003). This dependence on vision seems to be reflected in their brain organization. Note in this regard that visual cortex likely extends caudally and medially beyond the responsive areas we found in our limited recordings. Visual cortex in most small mammals extends to the caudal border of the cortex and relatively medially as well, and because we used only a limited range of stimuli to explore visual responses, it is likely that a number of unresponsive areas in our recordings are in fact parts of visual areas that would respond to more carefully controlled stimuli presented to specific parts of the visual field.

Although our evidence for the location of S2 comes from only one case, this area is historically difficult to explore because of its large receptive fields and lateral location in cortex. Nevertheless, we obtained a number

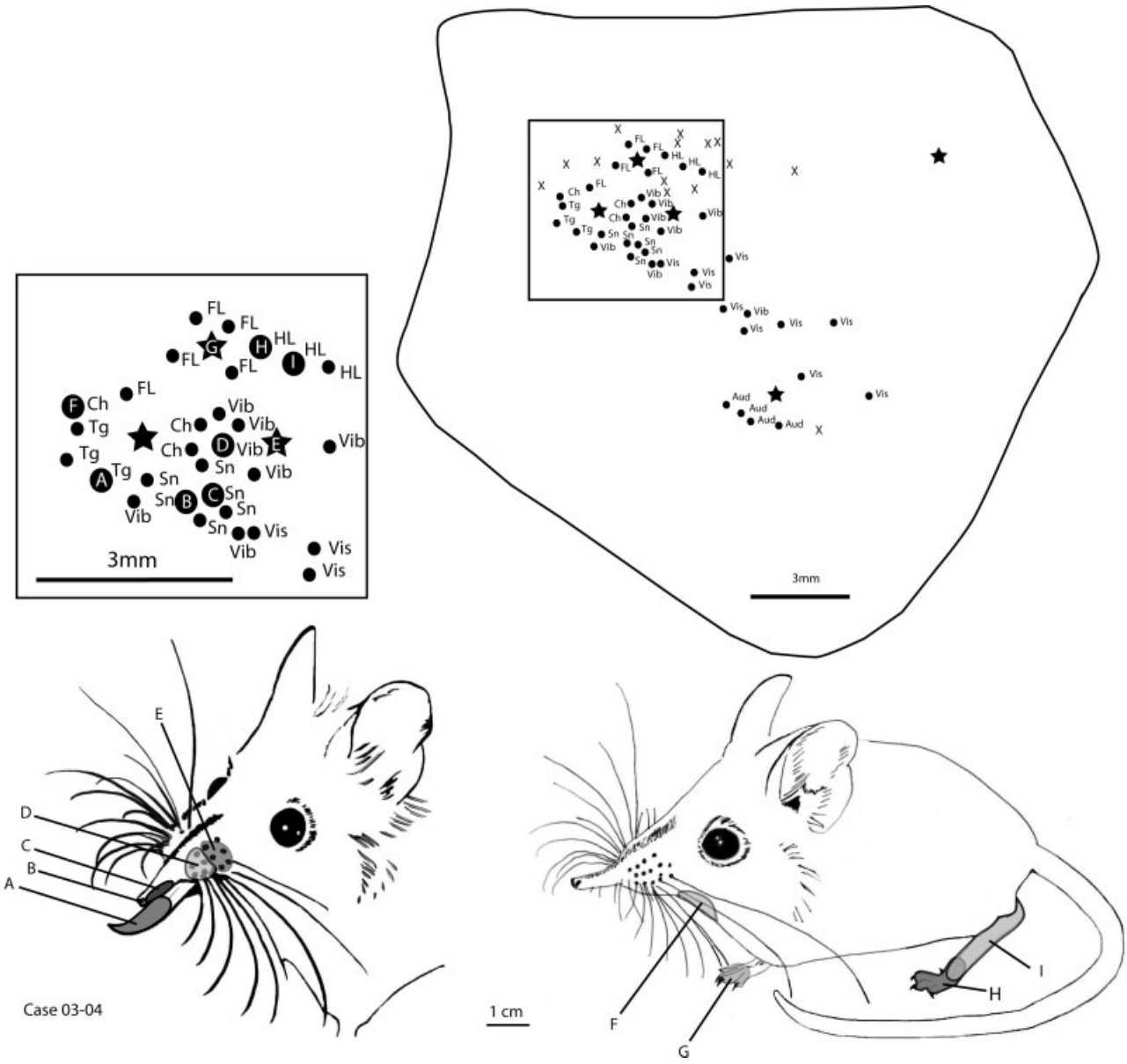

Fig. 4. Microelectrode recordings from the elephant shrew, case 03-04. The upper portion shows the flattened cortex with locations of electrode penetrations (dots) and lesions (stars) and abbreviations for the corresponding modality or body part represented. The inset is an enlargement of the somatosensory region. Receptive fields for penetrations A–I are shown in the illustrations of the elephant shrews at the bottom.

of responses from neurons with receptive fields on body parts that were also represented medially in S1. It is important to consider in this regard that S2 is generally a mirror image of S1, reflected along the midline of the face representation. Thus, a number of neurons responding to stimulation of the most lateral vibrissae and face in lateral cortex may be located in S2. Auditory cortex in elephant shrews was located in the expected location in lateral cortex caudal to S1 and closely adjacent to S2.

Many of these findings are consistent with similar studies in other small mammals, but details of elephant shrew brain organization and chemoarchitecture of their cortex (as shown by cytochrome oxidase histochemistry) set them apart from at least some placental mammals. Perhaps the most interesting comparison to make is between elephant shrews (order Macroscelidea) and the shrews and moles in the order Insectivora. This comparison seems important because elephant shrews were once considered to be members of the insectivore order (Kingdon, 1974) and thus closely affiliated with shrews (Soricidae) and moles (Talpidae). More recent investigation of these relationships based on molecular phyloge-

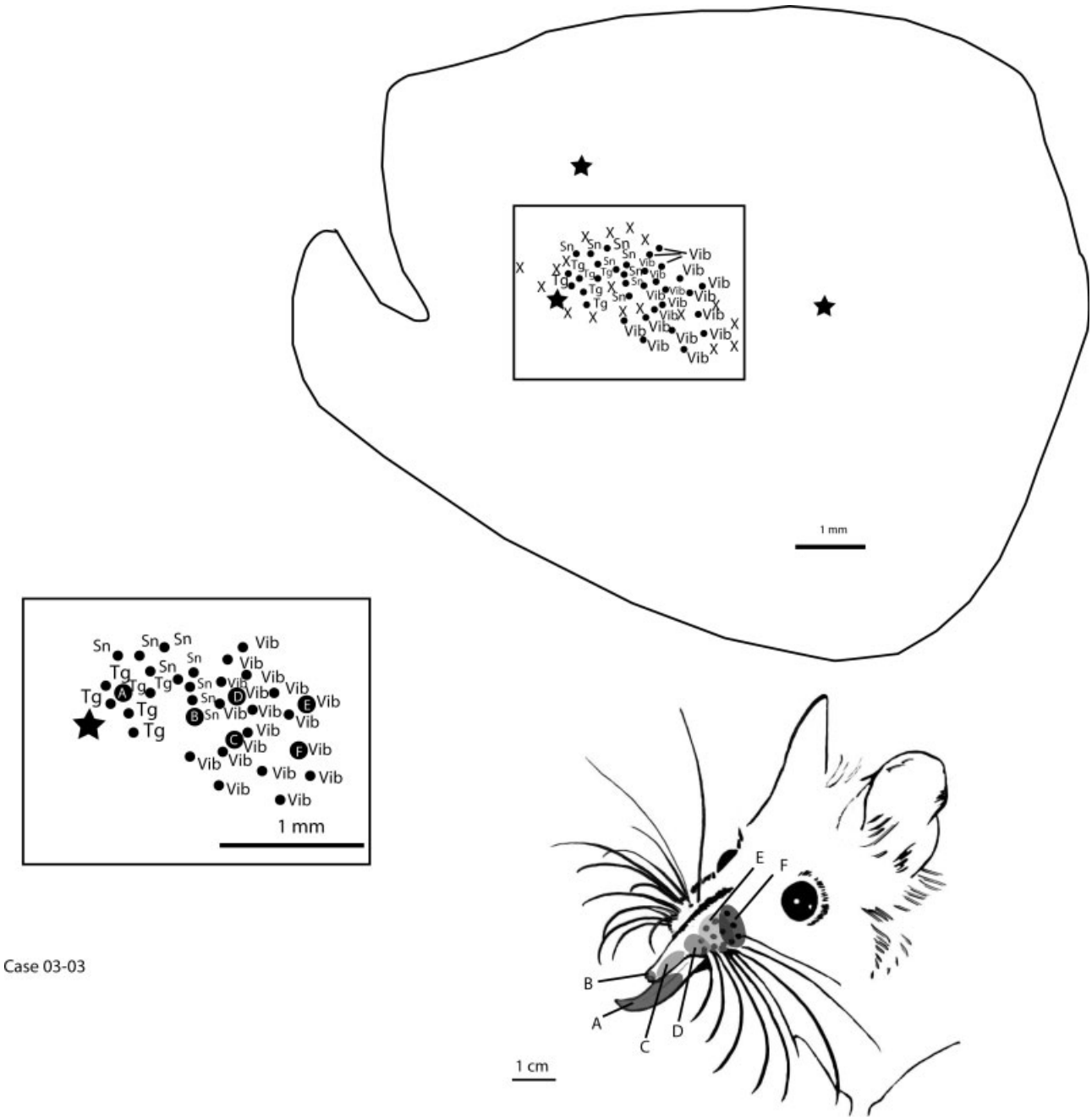

Fig. 5. Microelectrode recordings from the elephant shrew, case 03-03. The upper portion shows the flattened cortex with locations of electrode penetrations (dots) and lesions (stars) and abbreviations for the corresponding modality or body part represented. The middle is an enlargement of the somatosensory region. Receptive fields for penetrations A–F are shown in the illustration of the elephant shrew at the bottom.

netic evidence clearly separates elephant shrews from the order Insectivora (Murphy et al., 2001b) and some of our observations support this conclusion as well.

For example, sections of flattened cortex from insectivore shrews and moles contain a number of subdivisions that are visible based on chemoarchitecture of sections processed for cytochrome oxidase (Catania and Kaas, 1995, 1997; Catania et al., 1999). This includes visible representations of the nasal appendages in the star-nosed mole (as stripes in the cortex) and the whiskers in the eastern American mole (as barrels in the cortex). In addition, numerous additional subdivisions (e.g., auditory cortex and the representation of mouthparts and the forelimb in S1) are visible in the cortex of these spe-

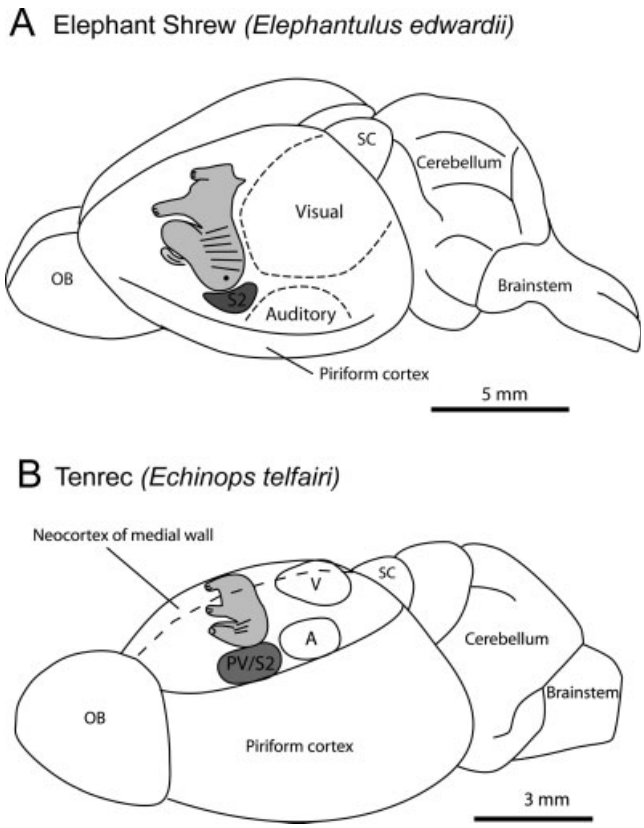

Fig. 6. Comparison of neocortex organization in two Afrotherian mammals. A: Summary of results from electrophysiological mapping experiments in elephant shrews. Relative location and size of primary (S1) and secondary (S2) somatosensory cortices. Dashed lines indicate encompassing areas that showed responses to visual and auditory stimuli. B: Summary of results from mapping experiments in the tenrec. Adapted from Krubitzer et al. (1997). Relative location and size of S1, S2/parietal ventral (PV), visual (V), and auditory (A) cortices. Cortex above the dashed line occupies the medial wall of the longitudinal fissure.

cies. Similarly, the extent of primary visual cortex, auditory cortex, and somatosensory cortex can be revealed in flattened sections of hedgehog (Erinaceidae) cortex (Catania et al., 2000). These findings are not surprising, given the relatively common reflections of sensory areas in cortical architecture. It was thus a strong expectation, based on the well-developed visual, somatosensory, and auditory senses in elephant shrews, that similar subdivisions would be apparent in their flattened cortex. However, no such subdivisions were found in the course of our study. This characteristic of cortex seems to set elephant shrews apart from the members of the order Insectivora, as has been indicated from molecular phylogenies.

In addition, the moles and shrews have a relatively small, crescent-shaped auditory cortex in far caudal cortex, whereas elephant shrews appear to have an auditory cortex much more typical in size and location than that found in insectivore shrews and moles. Finally, shrews and moles have a large S2 just lateral to S1, whereas elephant shrews appear to have a relatively small S2 typical of most other small mammals.

Within S1, the snout and vibrissa occupied the largest representation in the somatosensory cortex. This was expected, considering how prominent these features are in elephant shrews (Fig. 1). The unusual mobility and length of the elephant shrew snout, a defining characteristic for several Afrotherian mammals, suggest this structure is important to these species. However, the exact function of this mobile proboscis has yet to be determined for elephant shrews. In the course of our investigation, we filmed elephant shrews in their enclosures and these preliminary behavioral observations do not show the animal frequently using its snout for touch. However, in their natural habitat, elephant shrews may use their snout for probing crevices in search of prey.

We also found a pronounced tongue representation in elephant shrews. Considering their diet (ants and termites), it is not surprising that their large tongue is well represented in the somatosensory cortex, as we often have observed them using the tongue to obtain food items in narrow openings. Presumably, it is useful for this kind of behavior in their natural habitat in much the same way other species (e.g., aardvark and echidna) use their tongue to capture prey.

It is also interesting to compare the elephant shrew's cortex to that of tenrecs, both of which share a phylogenic superorder (Figs. 1 and 6). Tenrecs have been reported to have small brains with one of the smallest neocortices in mammals (Stephan et al., 1970, 1991; Krubitzer et al., 1997). Tenrec brains have been presumed to resemble brains in basal mammals. Yet closely related elephant shrews have a large well-developed brain, including sensory cortices that resemble cortex in other mammals in size and internal organization. Thus, our results suggest that brain organization in at least some of the Afrotherian species resembles brain organization in a wider range of other placental mammals.

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