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Organization of Sensory Neocortex in Prairie Voles (*Microtus ochrogaster*)

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ABSTRACT

In the current investigation, the functional organization of visual, auditory, and somatosensory cortex was examined in prairie voles (*Microtus ochrogaster*) by using electrophysiological recording techniques. Functional boundaries of cortical fields were directly related to myeloarchitectonic boundaries. Our results demonstrated that most of the neocortex is occupied by the visual, auditory, and somatosensory areas. Specifically, a small area 17, or primary visual area (V1), was located on the caudomedial pole of the neocortex; a large auditory cortex (AC), which contains the primary auditory area (A1) and other auditory fields, encompassed almost the entire temporal pole; and a large area 3b, or primary somatosensory area (S1), contained a complete representation of the contralateral body surface. Furthermore, these areas were coextensive with distinct myeloarchitectonic appearances. We also observed that the AC appeared to be disproportionately large in the prairie vole compared with other rodents. In addition, we found that both primary and nonprimary areas contained neurons that responded to auditory stimulation. Finally, we observed within S1 a disproportionate amount of cortex that was devoted to representing the perioral hairs and the snout and also that neurons within this representation had very small receptive fields. We discuss the expanded auditory domain and the enlarged representation of perioral hairs as they relate to the specialized life style of the prairie vole. J. Comp. Neurol. 502:414–426, 2007.

Indexing terms: primary somatosensory cortex; primary auditory cortex; cortical magnification; evolution

Rodents are a diverse group of mammals that occupy many niches, ranging from the arboreal squirrel to the subterranean naked mole rat. Behavioral adaptations associated with these different life styles have coevolved with alterations in peripheral morphology, sensory receptors, and central nervous system structures and have allowed different species to perform optimally in their given environment. Examining species that have evolved unique behaviors within this broad group of mammals can provide important insights into the relationship between neocortical organization and behavior.

The prairie vole (*Microtus ochrogaster*) is a burrowing, terrestrial rodent with a well-developed social system. This mammal is unusual in that it is one of approximately 3% of mammalian species that are considered to be monogamous (Kleiman, 1977). As with other monogamous mammals, individual prairie voles form long-term associations or pair bonds between one male and one female, and both parents contribute to protecting and rearing their offspring. Such behaviors seem to be associated with increased vocalizations during conspecific interactions. For example, young prairie voles call more often when separated from adults and vocalize at much higher rates (up to 15 times more), both in isolation and with a parent present, compared with their closest rodent relative, the montane vole (Rabon et al., 2001; Shapiro and Insel, 1990). Audition may also play a large role in prairie vole mating behavior. Male prairie voles produce vocalizations

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at higher rates compared with other rodents during all stages of the mating sequence, suggesting that auditory signals are a large part of copulatory signaling in voles, possibly a signal of gender and availability for reproduction (Lepri et al., 1988). Thus, compared with a number of other rodents and other mammals, these animals seem to rely a great deal on audition for mating and parent/offspring interactions (Shapiro and Dewsbury, 1990; Shapiro and Insel, 1990).

The issue of how aspects of nervous system organization are related to social behaviors, including monogamy, is interesting, but relatively few animal models are available in which to study this relationship. Furthermore, in the models that do exist, such as the prairie vole, research is often focused on hormonal interactions or the role of neuropeptides and their receptors in initiating and maintaining specific behaviors (Bales and Carter, 2003; Bielsky and Young, 2004; Carter, 1998). The current study is one of a series from our laboratory aimed at appreciating the relationship between neocortical organization, connections, and social behaviors associated with monogamy and cooperative breeding in the prairie vole.

In this investigation, multiunit electrophysiological recording techniques combined with cortical myeloarchitecture were used to explore the organization, size, and geographic relationship of the primary visual area (area 17/V1), auditory cortex (AC) including A1, and primary somatosensory area (area 3b/S1) in the prairie vole (for abbreviations see list). Our overall goal was to determine whether the social behaviors mediated by audition in the prairie vole were reflected in their neocortical organization. This study focuses predominantly on the allocation of different sensory systems on the cortical sheet, the relative size of sensory cortical fields, and the topographic organization of S1.

Abbreviations

17	area 17
AC	auditory cortex
3b	area 3b
Aud	auditory
C	chin
CO	cytochrome oxidase
DT	dorsal trunk
FL	forelimb
FP	forepaw
HL	hindlimb
M	medial
MM	multimodal cortex
N	naris
P	perioral
PV	parietal ventral area
R	rostral
S1	primary somatosensory area
S2	secondary somatosensory area
SN	snout
SS	somatosensory
T	tail
TA	temporal auditory region
TR	trunk
V1	primary visual area
Vib	vibrissae
Vis	visual
VT	ventral trunk

MATERIALS AND METHODS

In total 12 prairie voles (nine females and three males) weighing between 30 and 60 g were used in this study. Nine were used for mapping, in which 673 recording sites in total were obtained (see Table 1). All of these cases were sectioned and processed for myelin and/or cytochrome oxidase. The remaining three cases were processed for cytochrome oxidase and/or myelin. All procedures were approved by the Institutional Animal Care and Use Committee (IACUC) and conformed to NIH guidelines.

Electrophysiological recordings

At the beginning of each experiment, animals were anesthetized with an initial dose of 15% urethane diluted in phosphate-buffered saline (600 mg/kg; pH 7.5; IP), followed by supplemental doses of urethane (120 mg/kg) administered 45 and 90 minutes after the initial induction, and one final dose of urethane (60 mg/kg) administered 135 minutes after induction. To maintain surgical levels of anesthesia, supplemental doses of ketamine hydrochloride (17–33 mg/kg) were administered intramuscularly every 45–60 minutes throughout the recording session. Subcutaneous injections of lactated Ringer's solution were administered every 3–4 hours to maintain hydration. Body temperature was maintained, and heart rate and respiration were monitored continuously throughout the experiment. Once animals were anesthetized, the skin was cut and the temporal muscle over the left hemisphere retracted. A small screw was placed on the right side of the skull both as an electric ground and to immobilize the animal's head. The screw was secured by acrylic to a magnetic base attached to the surgery table. A craniotomy was performed to expose the entire left hemisphere, and the dura was left intact. The exposed cortex was imaged with a digital camera (PVC100C; Pixera Corporation, Los Gatos, CA) attached to a surgical microscope (Optronics Engineering; Zeiss). This image was used as a reference map to relate the electrode penetrations to cortical vasculature. A tungsten electrode (5 MΩ, 0.02-in. diameter) designed to record from multiple units was lowered into the cortex. Multiunit recordings were amplified, filtered, viewed on an oscilloscope, and heard through a speaker. At each recording site, responses to visual, auditory, and/or somatosensory stimulation were recorded.

Visual stimulation consisted of full-field flashes of light and moving bars of light. Auditory stimulation consisted of broadband clicks presented in a free field. Somatosensory stimulation consisted of light taps, displacement of hairs, light brushing of skin, hard taps, and manipulation of muscles and joints. Descriptions of the receptive fields and the type of stimulus required to elicit a response were documented. For somatosensory stimulation, receptive fields for neurons at each site were determined and drawn on illustrations of the vole body.

Particular care was taken to ensure that we did not inadvertently stimulate nontargeted sensory systems. For example, in small animals, it is possible to stimulate the auditory system inadvertently with tactile stimulation of the face and head. When neurons within a recording site responded to an auditory and somatosensory stimulus, we ensured that the somatosensory stimulation was not generating the auditory response through carefully and systemically stimulating other areas equidistant from the ear. Visual flashes and auditory clicks were performed out

of the immediate space of the animal so that vibrissae would not be inadvertently touched and so that small changes in air flow around the head would not be made.

Upon completion of electrophysiological recording, fluorescent probes (Fluororuby and Fluoroemerald, 7% concentration; Molecular Probes, Eugene, OR) were placed in the cortex, and the placement of each probe was marked on the digital image of the cortex to aid with reconstruction of the tissue. Each recording session lasted for 2–5 hours.

Histological processing and data analysis

At the end of each recording session, the animal was euthanized with an overdose of sodium pentobarbital (60 mg/kg) and perfused transcardially with 0.9% saline, followed by 4% paraformaldehyde in phosphate buffer (pH 7.4) and 4% paraformaldehyde in 10% sucrose in phosphate buffer. After fixation, the brain was extracted from the skull; the two hemispheres were removed from the thalamus, weighed, and then flattened between two glass slides. The thalamus and cortex were immersed in 30% sucrose overnight. The flattened cortex was sectioned at 20–60 μm thickness in a plane parallel to the cortical surface. In all cases, sections were stained for myelin (Gallyas, 1979) and, in two cases (05-79 and 05-87), for cytochrome oxidase as described by Wong-Riley (1979). In three additional cases, cortex was processed for CO and/or myelin (see Table 1). Minimal alterations in Adobe Photoshop were made in the brightness and contrast of all photomicrographs.

Relating electrophysiological maps and myeloarchitecture

For each case in which electrophysiological recordings were made, camera lucida reconstructions of individual myelin sections for the entire series were made with a stereomicroscope (Zeiss Stemi SV6). Whereas individual sections can contain many of the boundaries, to determine accurately the extent of each cortical field, the entire series of sections has to be examined and combined into a single, comprehensive reconstruction to determine the full extent of cortical field boundaries. Each reconstruction contained the outline of the section, blood vessels, tissue artifacts, probes, visible electrode tracks, and myeloarchitectonic borders. Sections were aligned using these landmarks and compiled into one composite image. Architectonic boundaries and electrophysiological recordings were combined by aligning probes marked on the photograph of the brain with those visible in sectioned tissue to produce a comprehensive reconstruction.

The topographic organization of the primary somatosensory area was determined by examining the receptive fields for neurons at each electrode penetration and then grouping them by body part. Lines were drawn around these sites through interpolation with adjacent sites representing other body parts. By correlating receptive field progressions for neurons with electrode penetrations, topographic maps of S1 were generated.

Data analysis

The percentages of recording sites in which neurons responded to a particular modality of stimulation were calculated for each composite image. For V1, AC, and S1, the total number of electrode penetrations and the type of response for neurons at each penetration were counted. Responses were grouped by type (visual, auditory, somatosensory, multimodal, and no response), and each group was divided by the total number of electrode penetrations, yielding a percentage of electrode penetrations in which neurons responded to a particular type of stimulation for each of the three cortical areas. For multimodal cortex (MM) similar calculations were made. Calculations for the percentage of neocortical area occupied by each of these areas were made using methods described previously by Hunt et al. (2006) and Karlen and Krubitzer (2006).

TABLE 1. Summary of Data Cases

Case No.	Histology		Electrophysiological recordings				
	CO	Myelin	V1	AC	S1	Outside	Total
05–29		X					
05–33	X	X					
05–40		X	17	14	55	33	119
05–44		X	3	8	26	12	49
05–59		X	12	11	58	31	112
05–79	X	X	7	7	23	24	61
05–87	X	X	6	7	28	34	75
05–89	X	X					
05–131		X	0	5	67	31	103
05–191		X	2	1	61	16	80
05–196		X	11	18	1	8	38
06–03		X	1	0	29	6	36
Totals			59	71	348	195	673

RESULTS

The goal of the current study in the prairie vole was to investigate the amount of neocortex occupied by different sensory systems and to correlate this sensory allocation with architectonically distinct features of the neocortex. We first describe the general location and appearance of three architectonically distinct cortical fields, areas 17, AC, and 3b, in both myelin- and CO-stained tissue. Then, we describe the allocation of cortex to different sensory systems, how these functional distinctions are related to architectonic distinctions, and the topographic organization of the primary somatosensory area.

Cortical architecture

In all cases in which electrophysiological recordings were made, a series of cortical sections was stained for myelin. Three additional cases were used for histochemical processing alone (Table 1). In these cases, CO stains were used to examine the barrel field within area 3b/S1. For tissue that was stained for myelin or for CO, the entire series of sections was used to determine cortical field boundaries.

When myelin-stained tissue was examined, several consistent features were observed across all cases, and, in most cases, architectonic boundaries directly correlated with functional boundaries obtained from electrophysiological recordings (see below). First, a relatively small, darkly myelinated wedge of cortex was observed at the caudomedial pole of occipital cortex and corresponded to area 17 described in other mammals (Fig. 1A; Kaas et al., 1989; Kahn et al., 2000). Second, lateral to area 17, in the temporal pole of the cortex, a large, heavily myelinated circular area of cortex was identified and corresponded to AC (A1 and surrounding auditory fields: Fig. 1A), defined architectonically in other rodents, such as mice (Caviness,

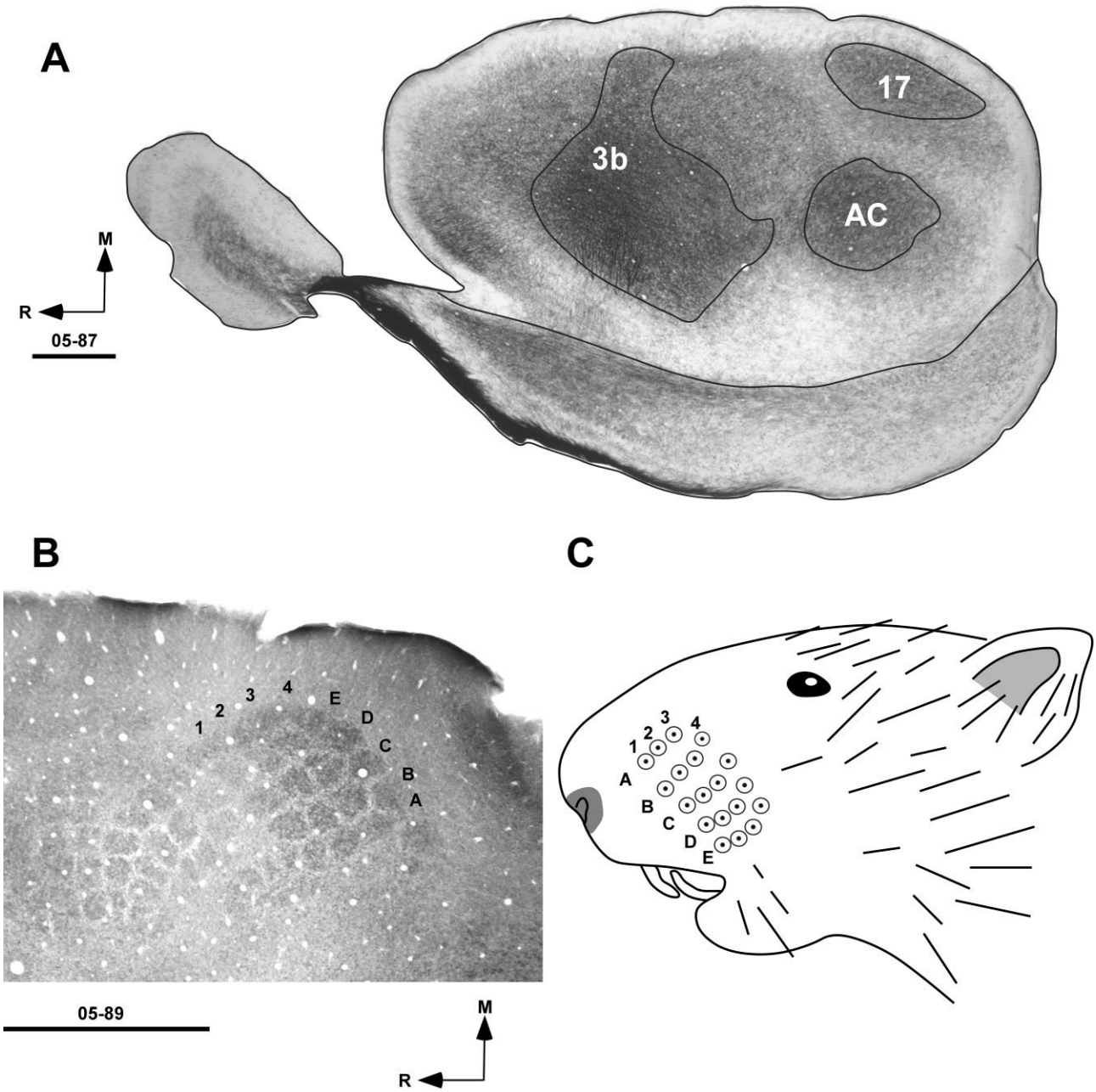


Fig. 1. Lightfield digital images of cortex that has been flattened, sectioned parallel to the cortical surface, and stained for myelin (**A**) and cytochrome oxidase (**B**). Whisker arrangements on the prairie vole are depicted in **C**. By examining the entire series of sections, architectonic boundaries can be accurately drawn. In myelin-stained sections (A), three architectonically distinct fields were observed: areas 17, AC, and 3b (denoted by thin lines). Electrophysiological recordings indicate that these fields are coextensive with the primary areas V1 and S1 and with several known auditory fields encompassed within AC. Compared with that in other mammals, AC is relatively large and assumes almost the entire temporal pole of the cortex. In B, a distinct barrel field was observed and corresponds to the representation of the vibrissae. In both B and C, the letters A–E represent the five rows of vibrissae and the numbers 1–4 represent the vibrissae within each row. Medial is to the top and rostral is to the left. For abbreviations see list. Scale bars = 1 mm.

1975) and squirrels (Luethke et al., 1988; Merzenich et al., 1976). AC in the prairie vole was notably larger than a homologous area described from other species with approximately the same size neocortex, such as in the mouse (Hunt et al., 2006), in the opossum (Karlen and Krubitzer, 2006), and in a number of insectivores (Catania, 2005; Catania et al., 1999, 2000). Finally, a darkly myelinated region, located midway between the rostral and the caudal poles of the neocortex was observed and corresponded to architectonic area 3 of Brodmann (1909), now recognized as area 3b described for all mammals (Felleman et al., 1983; Kaas, 1983; Krubitzer et al., 1986; Sur et al., 1980b).

In most cases, area 3b was irregular in shape and was quite broad laterally and narrowed medially (Fig. 1A).

In four cases, tissue stained for CO was correlated with tissue stained for myelin, and some distinctions in the neocortex could be observed with CO. Within area 3b, the CO stains revealed a characteristic barrel cortex (Fig. 1B) composed of a caudal region with large barrels and a rostral region with smaller barrels, corresponding to the posteromedial barrel subfield and anteromedial barrel subfield, respectively (Woolsey and Van der Loos, 1970). The caudal field identified in S1 corresponded structurally to the whisker arrangement on the snout with the dorsal three whiskers of the face represented rostrolaterally in the field and the ventral rows of whiskers represented progressively caudomedially in the field (Fig. 1B,C). This organization is similar to that described for other rodents via a variety of staining techniques (Land and Simons, 1985; Maier et al., 1996; Welker and Woolsey, 1974; Wong-Riley and Welt, 1980; Woolsey and Van der Loos, 1970).

Electrophysiological recordings

In nine animals, 673 recordings sites in total were obtained. Neurons in the neocortex of the prairie vole were extremely sensitive to slight fluctuations in temperature and anesthetic, which sometimes resulted in a low number of recording sites in which neurons were responsive. Thus, the number of sites ranged from 36 to 119 sites per animal (Table 1). This sensitivity sometimes resulted in a lack of neural response in a number of regions where vigorous responses would be expected.

Allocation of sensory cortex and determination of cortical fields

Our studies demonstrate that most of the cortical sheet is devoted to processing sensory inputs from one of three tested modalities (visual, auditory, and somatosensory) and that the majority of the sites contained neurons that responded to only one modality of sensory stimulation. Neurons located in the caudomedial aspect of the cortex, in the occipital pole, were predominantly responsive to visual stimulation, and most of these neurons were coextensive with area 17 (V1; Figs. 2, 3, yellow dots). Neurons in the temporal pole were predominantly responsive to auditory stimulation, and a subset of these neurons was coextensive with AC (Figs. 2, 3, green dots), as in other rodents and mammals (Bizley et al., 2005; Catania, 2005; Luethke et al., 1988; Merzenich et al., 1976; Stiebler et al., 1997). Finally, neurons located rostrally in cortex were predominantly responsive to somatosensory stimulation, and most of these neurons were coextensive with the architectonically defined area 3b (S1; Figs. 2, 3, pink dots).

To quantify these results, the percentage of recording sites at which a particular sensory stimulus produced a neural response was calculated. We found that, within V1, 51% of recording sites contained neurons that responded to visual stimulation alone, 8% contained neurons that were responsive to auditory stimulation alone, and 24% contained neurons that responded to multimodal stimulation (Fig. 4A). The remaining recording sites contained neurons that were unresponsive to any type of sensory stimulation delivered. In AC, 66% of the recording sites contained neurons that responded only to auditory stimulation, 10% of recording sites contained neurons that responded to multimodal stimulation, and under 3% of the recording sites contained neurons responsive to visual or somatosensory stimulation alone (Fig. 4A). The remaining recording sites contained neurons that were unresponsive to any type of sensory stimulation delivered. In S1, 57% of the recording sites contained neurons that were responsive only to somatosensory stimulation, 10% of the recording sites contained neurons that were responsive to multimodal stimulation, and under 4% of recording sites contained neurons that were responsive to either visual or auditory stimulation alone (Fig. 4A). Within V1, AC, and S1, most recording sites that contained neurons responsive to multimodal stimulation were responsive to auditory stimulation plus either visual or somatosensory stimulation (Fig. 4B). Specifically, in V1, 86% of the recording sites with neurons responsive to more than one modality, contained neurons that were responsive to auditory and visual stimulation, 7% of sites contained neurons that were responsive to auditory and somatosensory stimulation, and 7% of sites contained neurons that were responsive to all three modalities. Within AC, 71% of the recording sites with neurons responsive to more than one modality contained neurons that were responsive to audi-

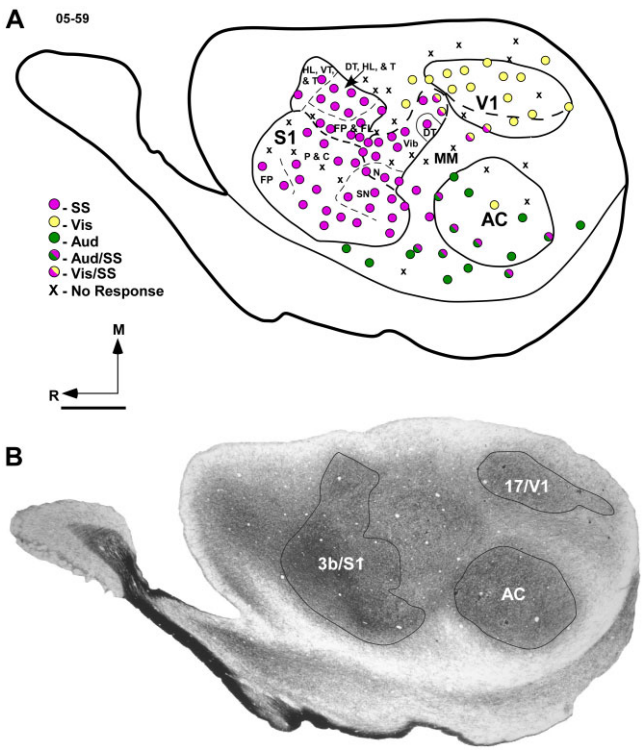


Fig. 2. Multiunit electrophysiological recording sites (**A**) and their relation to architectonic boundaries (**B**). The cortical field boundaries in A (thick lines) are determined by reconstructing an entire series of sections stained for myelin (B). In V1, neurons responded to visual stimulation. This functionally defined region of cortex was coextensive with a darkly myelinated wedge of cortex located in the occipital pole (B; area 17/V1). In AC, neurons responded to auditory stimulation or to auditory stimulation and stimulation of another modality. AC corresponds to a large, circular, heavily myelinated field identified in B. Within S1, most neurons responded to cutaneous stimulation of the contralateral body. In this case, the trunk is represented far medially followed laterally by the representation of the forepaw, perioral areas, and the snout. Conventions as in Figure 1. For abbreviations see list. Scale bar = 1 mm.

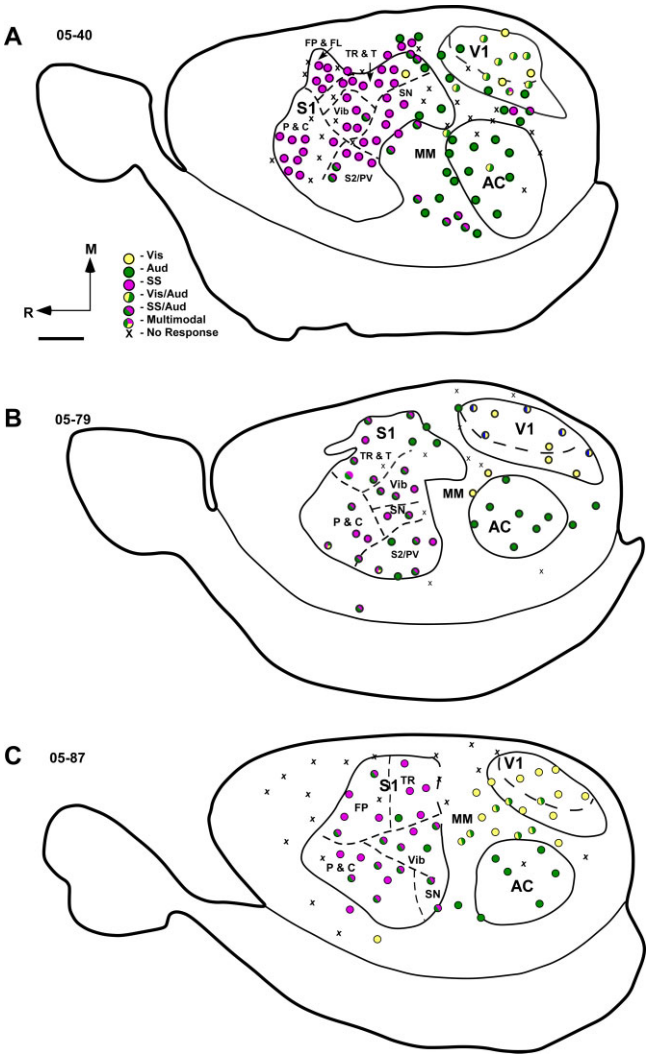


Fig. 3. Three composite images of sensory neocortex generated from multiple recording sites made in the neocortex of three separate cases (05-40, 05-79, and 05-87). These cases illustrate the distribution of responses from electrophysiological recordings and their relationship to architectonically defined primary areas. **A** depicts a case with numerous recording sites. In this case, most neurons in the sensory areas responded to stimulation of one sensory modality. **B** depicts a case with considerably fewer penetrations and more neurons that responded to stimulation of more than one modality. **C** depicts a case with a moderate number of recording sites. In this case, neurons in the sensory areas responded to unimodal stimulation or bimodal stimulation. From these examples, a clear, overall pattern of functional organization can be distinguished. Neurons responsive to visual stimulation are located in the occipital pole. Neurons responsive to auditory stimulation are located across the entire caudal half of the cortex and can sometimes extend rostrally into S1. Finally, neurons responsive to somatosensory stimulation are located rostrally. Furthermore, a topographic progression of body part representations can be distinguished in S1. Conventions as in previous figures. For abbreviations see list. Scale bar = 1 mm.

tory and somatosensory stimulation, 14% of sites contained neurons that were responsive to auditory and visual stimulation, and 14% of sites contained neurons that were responsive to somatosensory and visual stimulation. In S1, 85% of the recording sites with neurons responsive to more than one modality contained neurons responsive to auditory and somatosensory stimulation, whereas only 12% of sites contained neurons that were responsive to somatosensory and visual stimulation. A small percentage of sites (about 3%) in S1 contained neurons that responded to all three modalities.

Electrophysiological recordings were also made outside of V1, AC, and S1 in what we term the *multimodal cortex* (MM; Figs. 2, 3). Results from these recordings were also quantified and are depicted in Figure 4C,D. Many neurons outside of these three areas were unresponsive to any type of sensory stimulation (43% of recording sites; Fig. 4C, shown in black). However, 40% of these sites contained neurons that responded to unimodal stimulation: 8% of sites contained neurons that responded to visual stimulation alone, 17% of sites contained neurons that responded to auditory stimulation alone, and 15% of sites contained neurons that responded to somatosensory stimulation alone. The remaining recording sites contained neurons that responded to more than one modality of stimulation, and, among these sites, the majority (93%) contained neurons that were responsive to auditory stimulation plus either visual or somatosensory stimulation (Fig. 4D). Taken together, these results demonstrate that, both within and outside of V1, AC, and S1, a preponderance of neurons is responsive to auditory stimulation alone or to auditory stimulation and some other modality of stimulation. Thus, at least half of the sensory cortex is devoted to the auditory system.

Topography of S1

In all but one case (see Table 1), most of the recording sites were in S1. Neurons at recording sites in S1 that responded to cutaneous stimulation had receptive fields on the contralateral body. Receptive field sizes for neurons in S1 varied from being relative large on the trunk, to being extremely small on portions of the face (Fig. 5). By examining the receptive field progressions for neurons in S1, we were able to generate topographic maps of body part representations, as has been done in a variety of other mammals (Kaas, 1983). As in other mammals, the hindlimb and trunk representations were located most medially in S1, followed by the representation of the forelimb and face laterally (Fig. 5). We were unable to identify a separate region of S1 devoted solely to representing the hindlimb or the tail. However, we did observe sites containing neurons with large receptive fields that encompassed portions of the trunk plus the tail or the hindlimb (e.g., Fig. 5, recording sites 1–4). Within the trunk representation, receptive fields for neurons were large. The ventral trunk was represented rostral to the dorsal trunk (Fig. 5A,B, recording sites 1–4), and the lower trunk was represented medial to the upper trunk (Fig. 5A,B, recording sites 4–6).

The representation of the forelimb and forepaw varied slightly in location but in most cases was lateral to the representation of the trunk (Figs. 2A, 3A, 5A) and in some cases was located at the rostral border of S1 (e.g., Fig. 4A). Within the representation of the forepaw, receptive fields for neurons usually encompassed several digits (Fig. 6A,B, receptive fields 2–4), although, at a few recording sites, receptive fields for neurons were restricted to an individual digit (Fig. 6A,B, receptive field 1). There appeared to be a gross topographic order within the forepaw representation, with digit 5 represented caudally and digit 1 rep-

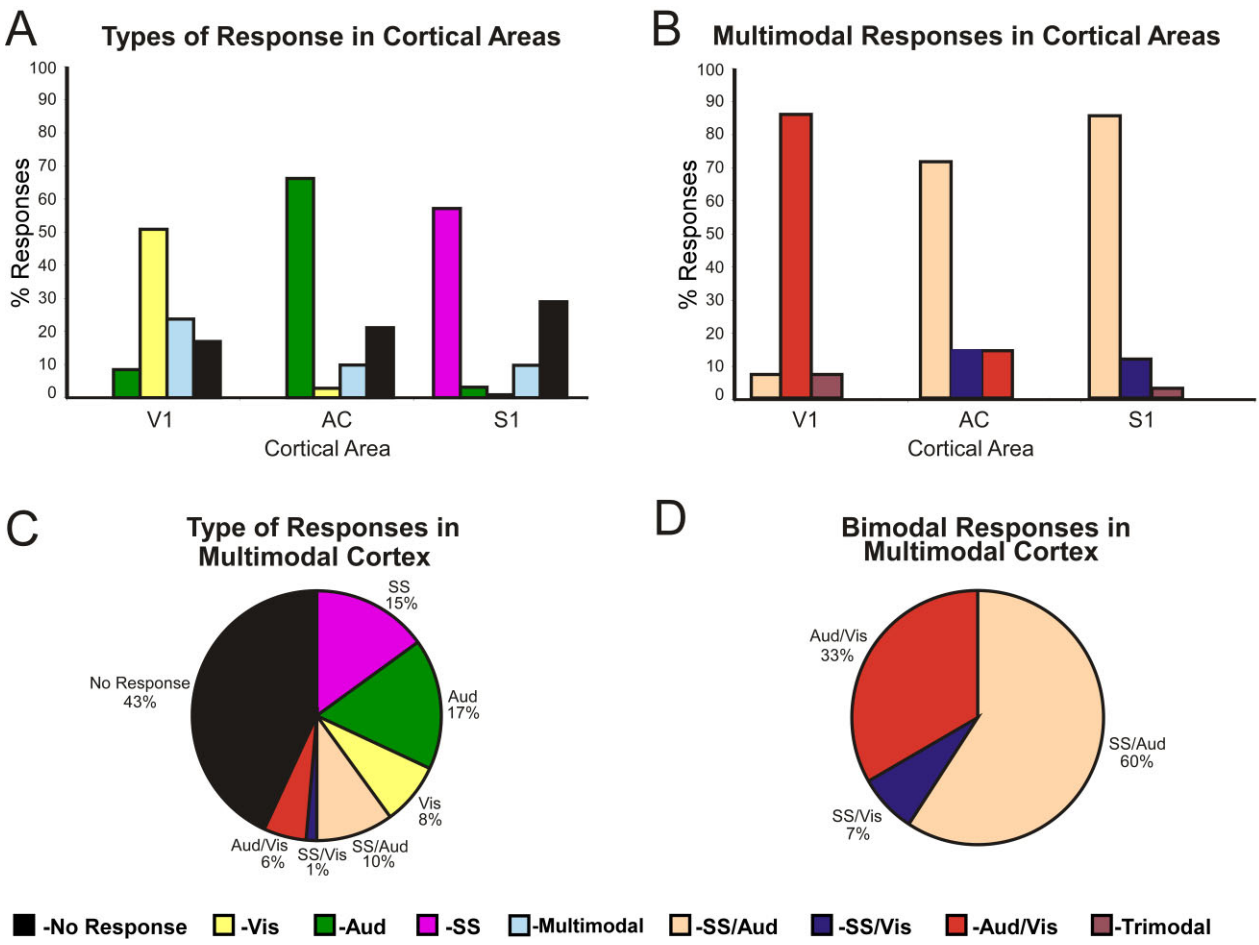


Fig. 4. Summary of the percentages of recording sites that contained neurons that responded to either one or two modalities of stimulation sorted by type of response and cortical area. The graph in **A** illustrates the percentage of recording sites in cortical fields V1, AC, and S1 in which neurons were responsive to visual, auditory, somatosensory, and bimodal stimulation, as well as sites that contained neurons that were unresponsive to any type of stimulation. The graph in **B** illustrates the percentage of recording sites within each area that contained neurons that responded to more than one modality of stimulation and demonstrates a prevalence of neurons responsive to auditory stimulation in combination with the other modalities. The pie chart in **C** depicts the percentage of recording sites outside of the primary areas in which neurons were responsive to unimodal and bimodal stimulation, organized by the type of sensory stimulation needed to elicit a neural response. The pie chart in **D** depicts the percentage of recording sites outside of primary areas in which neurons responded to stimulation of more than one modality, organized by the type of sensory stimulation needed to elicit a neural response. Specifically, this graphic demonstrates the prevalence of neurons responsive to auditory stimulation in combination with another modality. For abbreviations see list.

resented rostrally, but this was not a consistent observation. The lack of individual digit representations within the forepaw representation and the lack of precise topographic organization may be due to our inability to isolate individual digits on the very small forepaw to localize receptive fields. In some cases, the representation of the forepaw corresponded to a small, darkly myelinated island located rostromedially in S1 (Fig. 6A,C).

Over half of S1 was devoted to representing portions of the face. Caudolateral to the forelimb representation, a relatively large portion of S1 was devoted to representing the vibrissae. In these experiments, we did not attempt to define the precise representation of individual vibrissae in the cortex, but during mapping we found that receptive fields were small and were often restricted to one or two vibrissae (e.g., Fig. 5A,B, recording site 8). In cases in which CO stains were made, a clear barrel field representing the facial vibrissae could be identified (see above for detailed description). Immediately lateral to the representation of the forepaw and rostrolateral to the representation of the vibrissae was the large representation of the perioral region. Electrophysiological recordings in this region indicate that receptive fields were very small and that there was an orderly representation, with the naris being represented caudally within S1, the snout represented rostrolaterally, and the upper lip to the corner of the mouth represented rostrally in the field (Fig. 5A,C, recording sites 9, 10, and 12–15; Fig. 6A,C, recording sites 5–8). Within the representation of the perioral region, the upper lip was represented medial to the lower lip. Finally, caudal to the perioral and vibrissae representation was the representation of the snout (Figs. 3A, 5A). Receptive fields for neurons on the snout were relatively small (Fig. 5A,B, receptive field 9, 10). Several recording sites cau-

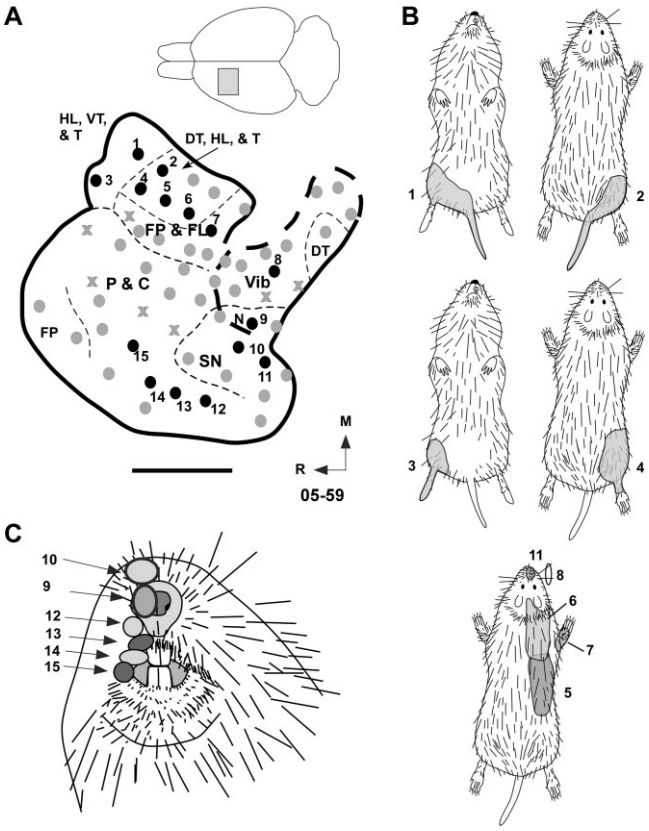


Fig. 5. Map of S1 from case 05-59 with selected recording sites (**A**) and the corresponding receptive fields for those sites (**B,C**) drawn on illustrations of the prairie vole body. The ventral trunk is represented medially in S1 (recording sites 1, 3), and the dorsal trunk is represented caudally (recording sites 2, 4). Within the trunk representation, the lower trunk is represented rostromedial to the upper trunk (recording sites 5, 6). The representation of the forelimb and forepaw is lateral to the trunk (recording site 7). A relatively large portion of S1 is devoted to the vibrissae, and the receptive fields are often small and restricted to one or two vibrissae (recording site 8). In the large perioral mouth representation, receptive fields are small and progress from the naris to the corner of the mouth as recording sites move from caudal to rostral in the field (recording sites 9, 10, and 12–15). Although progressions within body part representations are continuous, there is a discontinuity in the receptive field progression when moving from one body part representation (naris) to another (snout and perioral). Conventions as in previous figures. For abbreviations see list. Scale bar = 1 mm in A.

dolateral to S1 also contained neurons responsive to cutaneous stimulation or to cutaneous and auditory stimulation. Although there was not enough data to demarcate clearly other somatosensory areas, such as the secondary somatosensory area (S2) or parietal ventral area (PV), in every case, we did observe neurons lateral to the perioral representation in S1 that had receptive fields on the trunk and neurons that were responsive to both somatosensory and auditory stimulation, both characteristics of areas S2/PV (Krubitzer et al., 1986, 1997). The location of these sites and the size of receptive fields for neurons at these sites suggest that they are in the S2/PV area of cortex (see Fig. 3A,B).

DISCUSSION

In the present series of studies in the prairie vole, the allocation of neocortex to the visual, auditory, and somatosensory system was determined via electrophysiological recording techniques, and these results were directly related to architectonically distinct features of the neocortex. Thus, the overall functional organization, as well as the size and geographic relationship of V1, AC and S1 could be appreciated. The results of our study demonstrate that most of the neocortex is occupied by V1, AC, and S1. We also demonstrate that AC is disproportionately large in the prairie vole and that the neocortex is functionally dominated by the auditory system. Finally, within S1, a disproportionate amount of cortex is devoted to representing the perioral area. We compare our findings in the prairie vole with those described for other rodents and other mammals and discuss the possible ways in which small-brained animals, such as the prairie vole, generate the unique behaviors that are associated with their specialized life styles.

Organization of neocortex in rodents

Multiunit electrophysiological recording techniques combined with studies of cyto- or myeloarchitecture have been used in a variety of other rodents to define primary sensory areas. For example, other studies have demonstrated that a complete visuotopically organized representation of the contralateral hemifield is coextensive with a darkly myelinated region (area 17) at the caudal pole of the neocortex in other rodents, such as squirrels (Hall et al., 1971; Kaas et al., 1972a; Paolini and Sereno, 1998; Van Hooser et al., 2005), mice (Schuett et al., 2002; Wagor et al., 1980), and rats (Espinoza and Thomas, 1983; Montero et al., 1973), as well as other mammals, such as primates (Rosa et al., 1997; Tootell et al., 1988), cats (Palmer et al., 1978; Tusa et al., 1978), tree shrews (Kaas et al., 1972b), flying foxes (Rosa et al., 1993), and marsupials (Kahn et al., 2000; Rosa et al., 1999). Although we did not map the visual receptive fields of neurons in this study, we were able to identify an area 17 in prairie voles and we found that in all of the cases we examined, about 50% of recording sites in V1 contained neurons that were responsive to visual stimulation alone. However, unlike reports of neural responses in other mammals and other rodents (except for the mouse; see Hunt et al., 2006), the present study demonstrated that the remaining neurons in area 17 responded to auditory, auditory and visual, or auditory and somatosensory stimulation.

A relatively large, darkly myelinated region in the temporal pole of cortex was identified as AC, which contains A1 as well as auditory belt regions (see below). The majority of neurons in AC responded to auditory stimulation. However, some neurons responded to other modalities of stimulation as previously described in the mouse (Hunt et al., 2006). A similar, darkly myelinated region has been identified in other rodents, including the mouse (Stiebler et al., 1997), squirrel (Luethke et al., 1988; Merzenich et al., 1976), gerbil (Thomas et al., 1993), and rat (Rutkowski et al., 2003), and, in all of these rodents, this region was coextensive with the primary auditory area and other auditory regions, such as the rostral field (R) or the anterior auditory field (AAF) and the ultrasonic field. In rodents, as in other mammals, A1 contains a tonotopically organized representation of the cochlea, with different

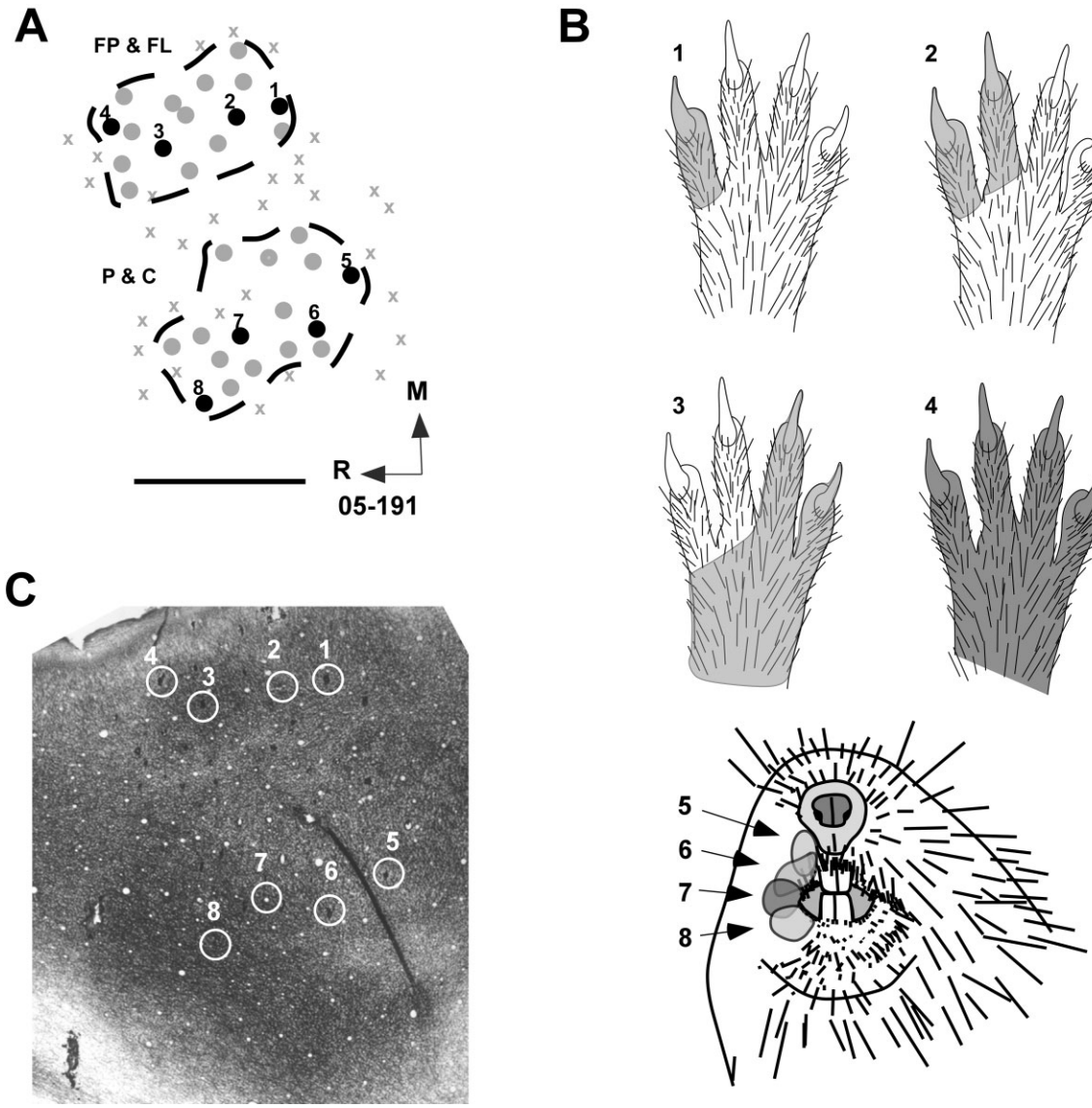
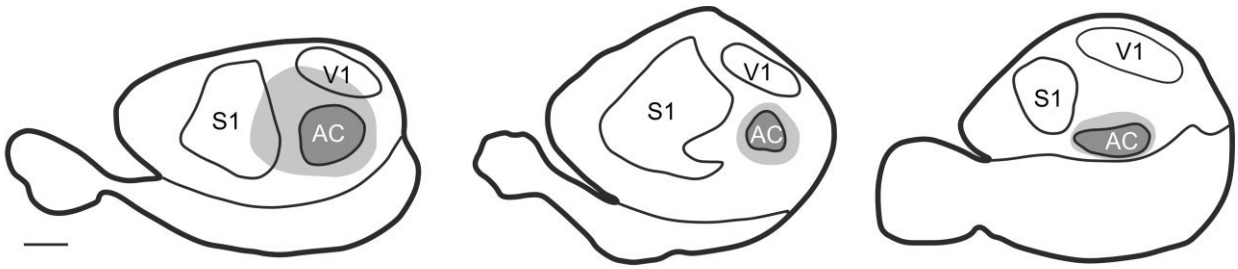


Fig. 6. An enlarged view of case 05-191 with selected recording sites (**A**), and the corresponding receptive fields for neurons at those sites (**B**) drawn on illustrations of the prairie vole body. A digital image of a myelin-stained section from this case, with visible electrode tracks is depicted in **C**. Although a few receptive fields for neurons in the forepaw representation are limited to an individual digit (recording site 1), most receptive fields for neurons in the forepaw representation usually encompass several digits (recording sites 2–4). Dense recording sites in the perioral mouth representation reveal a progression of receptive fields for neurons at those sites from the naris to the corner of the mouth as recording sites move from caudal to rostral in the field (recording sites 5–8). Receptive fields for neurons in this representation were very small. This case illustrates the precise relationship between the forepaw representation (A) and the darkly myelinated island at the rostral portion of S1 (C). Conventions as in previous figures. For abbreviations see list. Scale bar = 1 mm in A.

frequencies arranged as isofrequency bands. It will be interesting in future studies to examine the tonotopic representation of different auditory fields within AC in the prairie vole to determine whether, in fact, neurons here are tuned to frequencies associated with socially relevant calls of adult and young conspecifics.

The organization and histological appearance of S1 have been well described in mice (Woolsey, 1967; Woolsey and Van der Loos, 1970) and other rodents (Chapin and Lin, 1984; Krubitzer et al., 1995; Remple et al., 2003). As in the present investigation in the prairie vole, S1 in all rodents has been described as having a complete representation of the contralateral body surface coextensive with dark myelination or granular cortex. The representation of S1 is inverted, and receptive fields for neurons in specialized body part representations are relatively small. Furthermore, behaviorally relevant body parts, such as the vibrissae in murine rodents and the cheek pouches in squirrels, occupy a large portion of cortical space compared with other body parts. Such cortical magnification has been demonstrated for specialized body parts in S1 in all mammals examined (Catania and Kaas, 1995; Johnson, 1990; Nelson et al., 1980; Sur et al., 1980a). Taken together, the results from the present studies support previous obser-



	Prairie Vole		Mouse		Opossum	
% Neocortex devoted to:	Mean	SD	Mean	SD	Mean	SD
V1	4.85%	1.27%	8.96%	2.31%	9.10%	2.11%
AC	9.43%	0.87%	4.35%	0.90%	6.94%	1.14%
S1	23.43%	3.19%	32.71%	2.32%	18.85%	3.32%

Fig. 7. A comparison of composite images from the prairie vole, the mouse, and the short-tailed opossum. V1, AC, and S1 are outlined in black. AC is filled with dark gray, and the light gray shading represents the area of cortex in which neurons that respond to auditory stimulation are found. Prairie voles have an enlarged AC and auditory sensory allocation as compared with the other two species. The mean percentages of neocortex devoted to AC for all three species are given at the bottom. Data for the mouse are based on Hunt et al. (2006), and data for the opossum are based on Karlen and Krubitzer (2006). Scale bar = 1 mm.

vations in other rodents and other mammals that sensory areas, including V1, AC, and S1, are homologous across lineages but do vary in their relative size across species and in the magnification of different body parts in S1 (Krubitzer, 1995).

The auditory system dominates the neocortex

In the present investigation, we found that the AC was disproportionately larger in the prairie vole compared with other rodents. For example, when AC in the prairie vole is compared with AC in other mammals with about the same size neocortex, such as the mouse or the opossum, the amount of neocortex that AC assumes, relative to that of the total cortical sheet, is greater. Specifically, AC occupies 9.43% of the neocortex in the prairie vole, 4.35% in the mouse, and 6.94% in the opossum (Fig. 7; Hunt et al., 2006; Karlen and Krubitzer, 2006). The dominance of the auditory system over other sensory systems is also evident by the preponderance of neurons responsive to auditory stimulation in the primary and multimodal regions of the neocortex. For example, in the prairie vole, V1 and S1 in addition to AC contained neurons that responded to auditory stimulation (Figs. 3, 4). Thus, a large percentage of recording sites in S1 and V1 contained neurons that responded either exclusively to auditory stimulation or to auditory stimulation plus some other type of stimulation (Fig. 4A,B). In addition, multimodal cortex was dominated by neurons responsive to auditory stimulation (Fig. 4C,D).

The amount of neocortex occupied by a particular sensory system has been demonstrated to vary across mammalian species, some with extreme sensory specializations, such as the echolating bat or the duck-billed platypus, and others with what might be considered more moderate derivations, such as primates. In the echolating bat, A1 is unusually large, and the auditory system dominates the neocortex. Likewise, in the duck-billed platypus, the somatosensory system is dominant, and, in primates, the visual system occupies a relatively large proportion of neocortex. We have argued that sensory system allocation is an organizational feature of the neocortex that can vary markedly between species (Krubitzer, 1995; Krubitzer and Kahn, 2003) and that this feature is invariably linked to peripheral morphological alterations, and the enhancement of behaviors mediated by the derived sensory system. In the case of the prairie vole, the domination of the auditory system is likely associated with their social system, which may be largely dependent on acoustic signaling. Although olfaction likely plays a large role in a number of the behaviors unique to prairie voles, this sensory system was not examined in our study.

Disproportionate representation of perioral hairs in S1

In this study, we found that within S1 there was a disproportionate amount of cortex devoted to representing the perioral hairs and the snout. We believe that this magnification of the perioral representation may be related to behaviors associated with the specialized life style of prairie voles. Several studies have demonstrated these voles spend a large amount of time in contact or licking and grooming their mate as well as pups (Carter and Getz, 1993; Hammock and Young, 2005; Lonstein and De Vries, 1999). Examination of the perioral region reveals a number of densely packed rows of hairs, differing in length. As with other specialized sensory structures in other mammals, such as the vibrissae of murine rodents (Welker and Woolsey, 1974; Woolsey and Van der Loos, 1970), and the fovea of primates (Azzopardi and Cowey, 1993; Wassle et al., 1989), these hairs may be highly innervated and thus contribute to the cortical magnification observed in these animals. Alternatively, increased use of and dependence on a structure (Catania and Remple, 2004; Merzenich et al., 1996) can also contribute to cortical magnification, and

this may be the case with the specialized perioral hairs in the prairie vole.

How do small brains generate big behaviors?

In recent years, studies on mammals with relatively little neocortex, such as moles (Catania, 2005), shrews (Catania et al., 1999), mice (Hunt et al., 2005; Woolsey, 1967), marsupials (Beck et al., 1996; Kahn and Krubitzer, 2002), hedgehogs (Catania et al., 2000), and tenrecs (Krubitzer et al., 1997), indicate that few fields outside of the primary fields are present. For example, there is compelling evidence only for a second visual area and possibly an additional visual field in rodents, such as mice (Rosa and Krubitzer, 1999; Wagor et al., 1980), and in marsupials, such as *Monodelphis domestica* (Kahn and Krubitzer, 2002). There is good evidence for four areas other than A1 in mice, including the secondary auditory field, anterior auditory field, dorsoposterior field, and ultrasonic field (Stiebler et al., 1997). Finally, only one or two fields other than S1 (e.g., S2 and PV) have been consistently identified in marsupials (Beck et al., 1996; Huffman et al., 1999), mice (Carvell and Simons, 1986), hedgehogs, moles, and shrews (Catania et al., 1999). In a few cases, for the prairie vole, we found some evidence for area S2/PV (see Fig. 3A,B). As in other small-brained mammals, there was a limited amount of space between primary sensory areas that was considered MM. In prairie voles, this appeared to be functionally dominated by the auditory system. The observation that mammals with small brains have relatively few cortical fields seems at odds with some of the complex, precise, and rapidly executed behaviors that these animals exhibit (see, e.g., Catania and Remple, 2004; Suga et al., 1987).

It is possible that different strategies for increasing behavioral flexibility are adapted by animals with small brains and a small neocortex. One strategy appears to be a relative enlargement in the size of cortical fields associated with the dominant or specialized sensory system. Thus, rather than increasing the number of fields, small-brained species appear to increase the amount of cortical territory occupied by existing fields, in particular the primary areas. This enlargement is often accompanied by modularization within the field, such that different inputs are highly segregated and form isomorphs (e.g., barrels, nose follicles, and digit modules; see Catania, 2002; Catania and Kaas, 1997; Krubitzer et al., 1995; Woolsey and Van der Loos, 1970).

Another potential strategy is to co-opt existing sensory fields for multisensory functions. This appears to be the case for the vole, in which primary sensory areas other than A1 (incorporated within AC) often contain neurons responsive to auditory stimulation. The observation that neurons in primary sensory areas respond to modalities of stimulation other than that expected for that system is different from observations in most other mammals, particularly those with small brains. However, the techniques used to elicit a neural response are different in other studies, as described in their Materials and Methods sections, which indicate that only one type of stimulation was applied when a recording site was believed to be within a certain area. That is, the strict unimodal nature of primary fields as previously described may be due to the fact that other modalities of stimulation were not applied when a particular sensory area (e.g., S1 and V1) was being investigated. Thus, it has not been demonstrated that other animals do not have neurons within primary fields responsive to more than one modality of stimulation; it may be that such responsiveness has not been tested using multiple types of stimulation, as we used in the current investigation.

There are a few studies in other mammals, such as mice (Hunt et al., 2006), tenrecs (Krubitzer et al., 1997), and rats (Wallace et al., 2004), in which more than one modality of stimulation elicits a response within primary areas. The latter study in rats demonstrates that neurons that are bimodal have receptive field overlaps of the two systems represented and that there is a multisensory enhancement when these modalities are temporally correlated. This suggests that the multisensory representation in rats, and potentially that observed in voles, within the primary fields is functionally adaptive and may serve to heighten sensory-mediated behaviors associated with particular sensory systems.

It should be noted that, although small-brained mammals appear to exhibit unique and sophisticated behaviors (Catania and Remple, 2005; Suga et al., 1987), the range of the type of behavior exhibited by a particular species is limited. For example, small-brained mammals such as bats can be excellent echo locators but are more limited in their tactile and visual discrimination abilities. Star-nosed moles can rapidly detect and feed upon small prey items by an amazing manipulation of nose follicles, but they have poor vision and audition. In short, mammals with a small neocortex can do one or two things very well, but often at the expense of other sensory systems. Thus, a small neocortex could endow a particular mammal with remarkable sensory abilities within a limited behavioral repertoire (Kaas, 2000).

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