The function of secondary somatosensory (SII) cortex is poorly understood, but there is evidence to suggest that one of its roles may be in multisensory integration. This study used high-resolution field potential mapping coupled with laminar field potential and multunit recording to examine the association between SII and multisensory (auditory–somatosensory) cortex in the rat. We demonstrate that while there is spatial overlap between unisensory areas of SII and multisensory regions, particularly for representations of the trunk and hind limbs, they form distinct somatotopic maps. We propose that multisensory cortex be considered functionally distinct from SII, and that SII may be more concerned with unisensory processing tasks.

Keywords: All, auditory, barrel, polysensory, SII

Introduction

The functional importance of somatosensation in the rodent, particularly from the face and vibrissae, is reflected in the disproportionate area of primary cortex (SI) devoted to this sensory modality in the parietal region (Chapin and Lin, 1990; Tracey and Waite, 1995). The auditory senses are also well developed in the rodent (Kelly, 1990), with primary auditory cortex (AI) occupying much of the more lateral and caudal parietotemporal area. In rodents, as well as in other mammalian species, cortex adjacent to these primary sensory zones reveals at least one additional region for each sensory modality, comprising secondary somatosensory (SII) and auditory (AII) cortex (Chapin and Lin, 1990; Kelly, 1990).

The functions of both SII and AII are poorly understood. Yet there is evidence that one of the roles may be in multisensory integration. Based on microelectrode recordings in the rat, Wallace et al. (2004) recently proposed a revised view of sensory cortical parcellation in which the cortical regions bordering and interposed between unisensory regions are predominately multisensory. Since the interposed cortex largely overlaps presumed SII and AII, it is not surprising that many studies of secondary sensory cortex have reported at least partially overlapping multisensory responsive zones (Woolsey and Wang, 1945; Woolsey and Fairman, 1946; Lende and Woolsey, 1956; Pinto-Hamuy et al., 1956; Woolsey, 1958; Berman, 1961a,b; Carreras and Andersson, 1963; Lende, 1963; T.A.Woolsey, 1967; Campos and Welker, 1976; Pubols, 1977; Burton et al., 1982; Clemo and Stein, 1983; Curvell and Simons, 1986). This raises the question of whether multisensory integration should be considered to be a function of secondary sensory cortex, or if multisensory cortex should be regarded as functionally and anatomically distinct, with secondary cortex performing more unisensory processing tasks.

In the present study, we used high-resolution epipial field potential mapping of somatosensory and auditory evoked potentials (SEP and AEP, respectively) in rodent lateral parietotemporal cortex to determine areas of unisensory and multisensory responsiveness. We applied multivariate statistical analysis to determine the significance and reliability of somatotopic representations in these areas, and then used the results to guide placement of a laminar microelectrode array to record localized field potentials and multiunit activity (MUA) from putative unisensory and multisensory zones.

Materials and Methods

**Animals and Surgery**

All procedures were performed in accordance with University of Colorado Institutional Animal Care and Use Committee guidelines for the humane use of laboratory animals in biological research. Adult male Sprague-Dawley rats (300–400 g) were anesthetized to surgical levels using intramuscular injections of ketamine (71 mg/kg body wt), xylazine (14 mg/kg) and acepromazine (2.4 mg/kg), placed on a regulated heating pad and maintained with subsequent injections throughout the experiment so that the eye blink reflex could be barely elicited. A unilateral craniectomy was performed over the left hemisphere extending from bregma to lambda and from the midsagittal sinus laterally beyond the temporal bone to within 0.5 mm of the rhinal sulcus, exposing a wide region of parietotemporal cortex where the dura was reflected. Animals were sacrificed by anesthesia overdose without regaining consciousness at the conclusion of the experiment.

**Stimulation**

Auditory click stimuli were delivered with a high frequency piezoelectric speaker aligned with, and ∼10 cm from, the contralateral ear. The ipsilateral ear was blocked with soft wax. Clicks were computer-controlled monophasic square-wave pulses (0.3 ms; 50 dB SPL at 10 cm). Silent stimulation of the large vibrissae on the contralateral mystacial pad was achieved using a laboratory built solenoid with attached 3 cm hypodermic tubing. In most rats, stimulation displaced the tied vibrissae as a group vertically by ∼0.5 mm. In several rats, similar stimulation was applied to four subgroups of three tied vibrissae each that were situated in the extreme rostral, caudal, dorsal and ventral regions of the contralateral vibrissa array. During vibrissa stimulation, bilateral wax earplugs were also fitted to assure no incidental auditory stimulation. Silence was verified by observing activity in auditory cortex when the solenoid was close to, but not touching, the vibrissae. Silent electrical stimulation of discrete body regions (forepaw, forelimb, midtrunk, hindpaw and hindlimb) was achieved with a bipolar stainless steel electrode (0.5 mm separation; 1 mm exposed tip) attached to a constant current source, delivering current pulses (1 ms) of minimum current (0.2–0.5 mA) required to produce a reliable evoked response with no noticeable muscle contractions when applied to the shaved skin pretreated with conductive jelly. Electrical stimulation sites were on the back of the forepaw and hindpaw, on the proximal part of the forelimb and hindlimb, and on the lateral trunk midway between the forelimb and hindlimb. While stimulation produced no noticeable muscle contractions, activation of other afferents besides cutaneous could not be ruled out.
Data Collection and Analysis

Epipial maps of AEP and SEP were recorded using a flat multi-electrode array consisting of 64 silver wires in an 8 x 8 grid (tip diameter: ~100 μm; impedance: ~1 kΩ at 1 kHz; inter-electrode spacing: 500 μm) covering a 3.5 x 3.5 mm area. Surface AEP were used to consistently align the array across animals. Laminar recordings were performed with a 16 contact (10 μm diameter; impedance: ~1 mΩ at 1 kHz; 100 μm spacing) linear array (University of Michigan Center for Neural Communication Technology), inserted perpendicular to the cortical surface to a depth where the uppermost electrode was barely visible at the cortical surface. Viability of the uppermost electrode was checked throughout the experiment. Recordings of epipial and laminar potentials were referred to a silver ball electrode secured over the contralateral frontal bone, and were simultaneously amplified (x10 000), analog filtered (band-pass cut-off = -6 dB at 0.001 to 3000 Hz, roll-off = 5 dB/octave) and digitized at 10 kHz. Trials of separately evoked epipial AEP or SEP were averaged over 100 presentations. During laminar recording, 100 single trial records of AEP and SEP were stored on disk for subsequent analysis. This consisted of simple averaging of field potentials. MUA was also computed by digitally high-pass filtering (1000 Hz) and rectifying each trial and then averaging across trials for a given stimulus condition and recording location. Given the 10 μm diameter and 1 mΩ impedance of the laminar electrode contacts, MUA was assumed to reflect activity of larger clusters of units than would be expected from higher impedance microelectrode recordings.

The location and spatial distribution of epipial evoked responses was determined from interpolated (bicubic spline) topographic maps depicting the root mean squared (RMS) power of the response at each electrode, computed within the first 13-25 ms post-stimulus so that only the initial positive deflection (P1) was included. This constraint was introduced because the earliest temporal component is the most spatially constrained and best reflects initial cortical activation, before substantial intracortical propagation that produces the later temporal components of the slow wave. Putative multisensory regions were identified by similarly mapping a function computed from the relative AEP and SEP power at each electrode location, reflecting areas where auditory and somatosensory responses overlapped and were of large amplitude, using the following equation:

\[ \text{AEP-SEP}_{\text{overlap}} = \frac{(\text{RMS}_{\text{AEP}}/\text{RMS}_{\text{AEP+SEP}}) \times \text{RMS}_{\text{SEP}}/\text{RMS}_{\text{AEP+SEP}})}{\times \text{RMS}_{\text{SEP}}} \]

this function peaks at electrodes where the total power in both stimulation conditions (\( \text{RMS}_{\text{AEP+SEP}} \)) is high and the proportion of the AEP and SEP (\( \text{RMS}_{\text{AEP}}/\text{RMS}_{\text{AEP+SEP}} \)) power to the total power are equal. The function is minimal if either the AEP or the SEP is large and the other is small, or if both are small. No attempt was made to further examine interaction patterns between the AEP and SEP using combined auditory and somatosensory stimulation because these effects are typically small and require a large number of randomized trials. The prolonged experimental time such procedures require when stimulating multiple body parts would have precluded additional laminar recordings performed here while maintaining the viability of the animal. Thus, when we refer to multisensory cortex, we mean to imply only regions that respond to both auditory and somatosensory stimulation. However, we have found in previous studies that regions where the AEP and SEP spatially overlap correspond closely to those that produce nonlinear responses during combined stimulation. To compensate for slight positional variations in the electrode array across animals, we used the maps of SEP and AEP-SEP overlap for each animal to compute the relative distances between all responses to stimulation of the different body parts. Relative distances, expressed as Cartesian coordinates, were independent of absolute locations of responses within the array and thus permitted the most accurate comparisons across animals. The two-dimensional distances between representations of pairs of body parts were evaluated using a multivariate Hotelling \( T^2 \) statistic referred to an \( F \) distribution (Tatsuoka MM, 1988). For graphical display, resulting somatotopic maps that were averaged across animals in relative coordinates were then registered to the absolute coordinate space of the array using the locus of the grand averaged response to forepaw stimulation as a reference point.

Laminar recordings were performed at field potential maxima for presumed unisensory and multisensory cortex for a given body part, as determined from epipial maps for each animal. Amplitudes of the averaged laminar AEP and SEP and corresponding MUA were compared by summing the RMS power throughout the 100 ms sampling epoch across all 16 electrode locations (\( \text{RMS}_{\text{AEP}} \) and \( \text{RMS}_{\text{SEP}} \), respectively). The relative amplitudes of the AEP and SEP at a given recording site were determined as the ratio \( \text{RMS}_{\text{AEP}}/\text{RMS}_{\text{SEP}} \times 100 \), reported as mean (± SE) percent and compared between regions using unpaired \( t \) tests with significance set to \( P < 0.05 \). The expectation was that both field potentials and MUA would show a significantly reduced auditory/ somatosensory ratio in more unisensory secondary somatosensory cortex compared with multisensory regions where the responses would be closer to equal power.

Results

A graphical template (Fig. 1A), adapted from CO stained sections through layer IV of the flattened hemisphere of an earlier study, depicts the location and spatial extent of AI and the PMBSF and was scaled to the square 8 x 8 electrode array used to record from an area of 3.5 mm\(^2\) in a single lateral and caudal placement (Fig. 1A; black dashed square). Simultaneous stimulation of the 25 major vibrissae on the contralateral mystacial pad resulted in a positive/negative slow wave in the SEP that was of maximum amplitude lateral to the PMBSF in the region of SII (Fig. 1B red traces). Acoustic stimulation produced an AEP (Fig. 1B; blue traces) that was centered on the approximate location of AI, but also spread rostrally to overlap the vibrissa evoked SEP (Fig. 1B-b; dashed box). However, the AEP only partially overlapped the SEP, leaving a more rostral area where the SEP was dominant with an attenuated or absent AEP (Fig. 1B-a; dashed box). The locus and spatial distribution of the AEP and SEP may be more clearly visualized in normalized topographic maps of RMS power (Fig. 1C; AEP and SEP, respectively) used for all subsequent illustration of epipial evoked responses. A similar map, reflecting regions of the array where both the AEP and SEP were of large power (Fig. 1C; AEP-SEP overlap) indicates that the region of overlap (Fig. 1C-b) was shifted caudally toward auditory cortex by ~1 mm from the region of maximum SEP power (Fig. 1C-a).

Maps of AEP, SEP and AEP-SEP overlap shown in Figure 1C represent responses averaged across all animals. The grand average SEP and AEP-SEP overlap maps are reproduced in Figure 1D (Vib-all) with superimposed dots reflecting the variability in peak amplitude derived from similar maps of the separate animals (n = 6). In a separate set of five animals, the somatotopic organization of unisensory and multisensory vibrissa evoked responses was explored. Stimulation of the rostral vibrissa group (Fig. 1D; Vib-rost) produced a response that was 0.79 ± 0.1 mm (\( P < 0.001 \)) rostral to that of the caudal group (Fig. 1D; Vib-caud) with no significant separation along the mediolateral axis. Responses to dorsal and ventral vibrissa stimulation (Fig. 1D; Vib-dors and Vib-vent) substantially overlapped Vib-caud and Vib-rost. However, Vib-vent was lateral to Vib-dors by 0.81 ± 0.11 mm (\( P < 0.001 \)). These results taken together suggested an upright and rostrally pointing trigeminal map at this site. Regions of overlap between the SEP and AEP were apparent for all four stimulation conditions, even for the most rostral vibrissa group. Those occupied a common site at the vibrissa representation of multisensory cortex identified for combined vibrissa stimulation (Fig. 1D; Vib-all). No further somatotopic organization was apparent in the trigeminal multisensory region.

All animals receiving stimulation of the combined vibrissae (Fig. 1D; Vib-all) also received stimulation of the forepaw,
forelimb, midtrunk, hindpaw and hindlimb (Fig. 1E; Fp, Fl, Mt, Hp, and Hl, respectively) and were studied with both epipial and laminar recordings. Spinal responses in SII were lateral to the vibrissa response, with Fp and Fl rostral to Mt, Hp and Hl. Each SEP map reflected a single representation for each body part that extended caudally to partially overlap the AEP. This caudal extension was particularly evident for Fp and Fl (Fig. 1E; arrows) where there was the greatest separation between unisensory and multisensory regions. Similar to Vib-all, regions where these responses overlapped the AEP (multisensory cortex) were shifted caudally, with Fp and Fl just lateral to Vib and Mt, Hp and Hl most lateral.

Figure 1. (A) A graphical template depicts the location and spatial extent of primary auditory cortex (AI) and the vibrissa representation of the postero medial barrel subfield (PMBSF) of primary somatosensory cortex. The approximate location of the recording array is indicated with a dashed box. (B) The vibrissa evoked SEP (red traces) was of largest amplitude just lateral to the PMBSF (a) but also extended into the rostral region of auditory cortex where it partially overlapped (b) the AEP (blue traces). (C) Interpolated topographical maps reflect the spatial distribution of root mean squared (RMS) power of the first positive wave of evoked potential. Maps were normalized to the largest response in a given condition and were therefore of arbitrary units of percent. The maps provide a more compact view of the locus and extent of the AEP over AI, the SEP just lateral to the PMBSF (a) and the region where both the AEP and SEP overlapped (b) and were of large amplitude. (D) Grand averaged power maps of the SEP and AEP-SEP overlap computed across animals for stimulation of the vibrissae. The SEP to combined vibrissa stimulation (Vib-all; n = 6) was rostral to the locus of AEP-SEP overlap (dots reflect the loci of power maxima for the individual animals). In five additional animals, stimulation of subgroups of rostral, caudal, dorsal and ventral vibrissae evoked SEP maxima (Vib-rost, Vib-caud, Vib-dors and Vib-vent, respectively) reflecting an upright and rostrally oriented somatotopic organization. Each response was accompanied by a caudally displaced locus of AEP-SEP overlap with no apparent somatosomatotopic organization. (E) SEP to forepaw (Fp) and forelimb (Fl) stimulations were located most rostrally and lateral to the vibrissa response. Note the low amplitude extension of this response in the medial and caudal direction (arrows) toward the respective loci of AEP-SEP overlap for these body parts. SEP to midtrunk (Mt), hindpaw (Hp) and hindlimb (Hl) were more caudal than Fp and Fl. Close examination of these maps suggests a somatotopic organization with Fp most medial, followed by Fl and Mt. Maps of AEP-SEP overlap show the same somatotopy but are shifted slightly caudally.

forelimb, midtrunk, hindpaw and hindlimb (Fig. 1E; Fp, Fl, Mt, Hp, and Hl, respectively) and were studied with both epipial and laminar recordings. Spinal responses in SII were lateral to the vibrissa response, with Fp and Fl rostral to Mt, Hp and Hl. Each SEP map reflected a single representation for each body part that extended caudally to partially overlap the AEP. This caudal extension was particularly evident for Fp and Fl (Fig. 1E; arrows) where there was the greatest separation between unisensory and multisensory regions. Similar to Vib-all, regions where these responses overlapped the AEP (multisensory cortex) were shifted caudally, with Fp and Fl just lateral to Vib and Mt, Hp and Hl most lateral.

To estimate the locus and extent of AI, SII and intervening multisensory cortex for the body parts stimulated here, composite maps were computed by averaged responses across animals and across all body parts stimulated (Fig. 2A; the approximate borders of each area indicated by dashed white outlines drawn along the 25% isocountour lines). Superimposed responses for each body part in SII, averaged across animals (Fig. 2A; SEP, dots), suggested a somatotopic map. The most rostral response was Fp, with the representation of Fl most medial, followed by Mt and Hl. The somatosensory organization of spinal input to SII therefore appeared inverted, with the forelimbs oriented rostrally, the paws pointing medially.

Multisensory cortex occupied much of the region between AI and SII with a somatotopic organization that was distinct from...
Figure 2. Laminar recordings from SII and multisensory cortex determined from epipial mapping. (A) The AEP averaged across all animals defines the approximate borders of primary auditory cortex (AI). The 25% isocontour line is outlined with a dashed trace. SEPs averaged across stimulation of different body parts form a composite map that defines the borders of SII (demarcated with dashed traces at the 25% isocontour lines). The distances between body parts were averaged in relative coordinates across animals to compensate for slight positional variations of the electrode array. They were then reregistered in absolute coordinates here using the averaged locus of Fp as an arbitrary reference point. The vibrissa representation (from stimulating all vibrissae simultaneously) was the most medial, just lateral to the PMBSF. Spinal representations were grouped rostral and lateral to AI and revealed an inverted somatotopy, with the head pointed rostrally and the paws pointed medially. Multisensory cortex, determined from the regions of maximum overlap between the AEP and SEP, occupied much of the region between AI and SII. Representations of Hp, Hl and Mt substantially overlapped SII but were shifted slightly toward AI. Representations of Fl and Fp were the most radically shifted toward AI compared with their respective loci in SII, with vibrissa representation the most medial. Multisensory cortex formed a distinct somatotopy, with the face pointed medially and the paws pointed caudally. (B) An example of distinct sites in SII and multisensory cortex identified from epipial power maps of the SEP to combined vibrissa stimulation. (C) In this example, and in all other laminar recordings, the surface positive/negative slow wave of the AEP and SEP reversed polarity in the cortical depth, indicating a vertically oriented dipolar current source. In multisensory cortex, the laminar AEP (blue) was 54% the amplitude of the vibrissa evoked SEP (red) throughout the depth. At a slightly more rostral location within SII, the amplitude of the SEP increased and the AEP fell to 2% of the SEP. (D) Multunit activity (MUA) showed corresponding differences, with a ratio of auditory to somatosensory responses of 66% in multisensory cortex and 5% in SII. (E) The ratio of AEP/SEP was significantly lower in SII (blue) compared with multisensory cortex (red) for all body representations. (F) Corresponding differences in MUA at these loci were similar to the field potentials, indicating cells firing to both auditory and somatosensory stimuli in multisensory cortex and primarily to somatosensory stimuli in SII. Number of animals included in the laminar recordings for the different body parts were Vib = 7, Fl = 6, Fp = 6, Mt = 6, Hl = 5, Hp = 6.
SI and rotated about the hindquarters toward auditory cortex, with the head oriented medially and the paws pointing caudally (Fig. 2A; AEP-SEP overlap). The most medial multicensory response was to vibrissa stimulation (Fig. 2A; AEP-SEP overlap; Vib), and this was shifted in the caudal direction toward the auditory cortex by 7.5 ± 0.10 mm (P < 0.001) compared with Vib in SII. The most dramatically shifted multisensory responses were Fl and Fp, which were located more caudal and mediolateral to the representations in SII at distances of 1.51 ± 0.12 mm (P < 0.001) and 1.65 ± 0.10 mm (P < 0.001), respectively. Multisensory responses for Fl and Fp were also separated on the rostrocaudal axis with the paws pointed caudally. While this separation was small (0.16 ± 0.07 mm) it was significant (P < 0.04). Multisensory Hp was also slightly closer to auditory cortex than HI (0.22 ± 0.05 mm, P < 0.01). Multisensory responses to Hp and HI were more lateral than Fl (0.91 ± 0.08 mm, P < 0.001 and 1.13 ± 0.08 mm, P < 0.01, respectively) and were shifted caudally from their corresponding positions in SII (0.24 ± 0.09 mm, P < 0.05 and 0.21 ± 0.07 mm, P < 0.05, respectively). Multisensory Mt remained the most lateral response (lateral to HI by 0.28 ± 0.08 mm, P < 0.03). It also followed the trend of the other responses and was shifted toward auditory cortex compared with the SII response (0.13 ± 0.06 mm), but this shift failed to reach significance (P > 0.05, F = 2.3, df = 5). The somatotopic organization of multisensory cortex was therefore distinct from SII and rotated about the hindquarters toward auditory cortex with the head oriented medially and the paws pointing caudally. It should be noted that it was difficult to find areas of SII that were not at least partially responsive to auditory stimulation except at the most rostral recording locations. In this light, while we refer to unisensory and multisensory cortical regions, this reflects their dominant response property.

Figure 2B displays an example of laminar field potential and MUA profiles in the unisensory vibrissa representation of SII and the more caudal region of AEP-SEP overlap. Here, and in field potential recordings of other body representations, the surface recorded P1 and subsequent negative wave (N1) reversed polarity in the depth (Fig. 2C), indicating a cortical dipolar generator. In this example, at the location where the AEP and vibrissa evoked SEP overlapped at the surface, AEP power throughout the depth was ~54% that of the SEP (Fig. 2G; right traces). In recordings performed ~0.5 mm rostral to this site in SII, the power of the laminar SEP increased while the relative power of the AEP dropped to 2% of the SEP (Fig. 2G; left traces). The relative power of AEP and SEP field potentials in SII and multisensory cortex were reflected in corresponding laminar MUA activity. At the multisensory site, total MUA power evoked by auditory stimulation was ~66% of that evoked by vibrissa stimulation (Fig. 2D; right traces). By contrast, in the vibrissa representation of SII, somatosensory MUA power nearly doubled while the relative auditory MUA power dropped to 5% of that evoked by somatosensory stimulation (Fig. 2D; left traces).

Relative powers of auditory and somatosensory responses differed in a similar way during laminar recordings in representations of the other body parts (Fig. 2E,F). In all cases, the ratio of auditory to somatosensory field potentials and MUA were significantly lower in SII compared with multisensory recording sites. The ratios of AEP to SEP in multisensory cortex were 89 ± 9, 85 ± 10, 82 ± 12, 140 ± 11, 120 ± 19 and 127 ± 13%, for Vib, Fl, Fp, Mt, HI and Hp, respectively (Fig. 2E; red bars). These ratios dropped to 29 ± 4, 49 ± 6, 45 ± 4, 98 ± 9, 71 ± 11 and 70 ± 7%, for representations of the same body parts in SII (Fig. 2E; blue bars). Laminar MUA followed the field potential responses with ratios of auditory to somatosensory equaling 73 ± 9, 73 ± 13, 66 ± 8, 100 ± 17, 92 ± 26 and 93 ± 22%, for Vib, Fl, Fp, Mt, HI and Hp representations in multisensory cortex (Fig. 2E; red bars) and 29 ± 4, 44 ± 8, 42 ± 6, 56 ± 9, 40 ± 6 and 43 ± 8%, for corresponding representations in SII (Fig. 2E; blue bars).

Discussion

Early evoked potential studies in a number of species (Bromiley et al., 1956; Lende and Woolsey, 1956; Benjamim and Welker, 1957; Woolsey, 1958) have indicated that secondary somatosensory cortex is somatotopically organized, with a secondary trigeminal representation positioned just lateral to the face region of primary somatosensory cortex and a secondary spinal representation lateral to this, displaying a rostrally oriented somatotopy. More recent high-resolution evoked potential studies (Brett-Green et al., 2004), including the present study, are in agreement with this earlier work. Based on microelectrode unit recordings, Krubitzer et al. (1986) described a single secondary somatosensory map in the parietal ventral area (PV) of the grey squirrel with an erect and rostrally pointed representation of the head congruent with the face region of SI and a more lateral and inverted body representation. The location and somatotopy of PV in the squirrel bears a striking resemblance to what we have defined as SII in the rat. Furthermore, similar to the present findings, cells in PV near the border with auditory cortex respond to both somatosensory and auditory stimuli, an observation common to other species as well (Krubitzer and Calford, 1992; Beck et al., 1996; Krubitzer et al., 1997; Catania et al., 2000). However, more recent microelectrode unit recordings (Remple et al., 2003) and anatomical studies (Fabri and Burton, 1991) in the rat have suggested not one but two rostrally oriented somatotopic representations lateral to SI. These studies describe SI as upright and just lateral to SI, whereas PV forms an inverted representation lateral to SI. Our failure to distinguish dual representations may be due to the fact that field potential recordings reflect population responses and may miss more subtle response patterns revealed by single unit recording (Pimentel-Souza et al., 1980; Carvell and Simons, 1986). In the absence of more definitive evidence, we will simply refer to this entire area as SII.

Overlap between secondary somatosensory and auditory cortex has been variously described (Woolsey and Wang, 1945; Woolsey and Fairman, 1946; Lende and Woolsey, 1956; Pinto-Hamuy et al., 1956; Woolsey, 1958; Berman, 1961a,b; Carreras and Andersson, 1963; Lende, 1963; T.A.Woolsey, 1967; Campos and Welker, 1976; Pubols, 1977; Clemo and Stein, 1983; Carvell and Simons, 1986). In light of the rostral orientation of SII, it is perhaps not surprising that the region of somatosen- sory-auditory overlap typically involves the trunk and hindquarters, which are positioned closest to auditory cortex. However, the present data suggest that multisensory cortex forms a complete and separate somatotopic map, including even the most rostral anatomical representations such as the forelimbs and rostral vibrissa group. This conclusion is further supported by laminar field potential and MUA recordings indicating a multisensory responsiveness within this region that may be distinguished from more unisensory responses even for the trunk and hindquarters where the epipial SEP and AEP almost completely overlap. In this light, the area of multisensory cortex in the rat may be analogous to multisensory cortex (SIV) in the
and Patton, 2004; Stein multisensory integration is the superior colliculus (Anasasio perhaps one of the most thoroughly studied centers for anatomically distinct, with secondary cortex performing more unisensory cortex in the rat. It has been proposed that evolutionary advances of cortical structures may be directed toward less multisensory integration and more unisensory segregation (Diamond and Hall, 1969), a process that could be justified by the challenges inherent to accurately identifying objects in a particular sensory modality compared with co-registering these objects in multisensory space. In this light, the rat may reflect a transitional phase, where the cortical processing of the face and forelimbs, most important for exploration of the environment, has become distinctly segregated into unisensory and multisensory regions of parietotemporal cortex with substantially less segregation of the hindquarters.

Notes
This research was supported by NINDS grant 1 R01 NS69811 and the University of Colorado Undergraduate Research Opportunity Program. The information provided in this material was also supported by Grant/Cooperative Agreement Number U33/CCU824219 from the Centers for Disease Control and Prevention (CDC). The contents are solely the responsibility of the authors and do not necessarily represent the official views of the CDC.

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