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Cortical Connections of the Second Somatosensory Area and the Parietal Ventral Area in Macaque Monkeys

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ABSTRACT

To gain insight into how cortical fields process somatic inputs and ultimately contribute to complex abilities such as tactile object perception, we examined the pattern of connections of two areas in the lateral sulcus of macaque monkeys: the second somatosensory area (S2), and the parietal ventral area (PV). Neuroanatomical tracers were injected into electrophysiologically and/or architectonically defined locations, and labeled cell bodies were identified in cortex ipsilateral and contralateral to the injection site. Transported tracer was related to architectonically defined boundaries so that the full complement of connections of S2 and PV could be appreciated. Our results indicate that S2 is densely interconnected with the primary somatosensory area (3b), PV, and area 7b of the ipsilateral hemisphere, and with S2, 7b, and 3b in the opposite hemisphere. PV is interconnected with areas 3b and 7b, with the parietal rostroventral area, premotor cortex, posterior parietal cortex, and with the medial auditory belt areas. Contralateral connections were restricted to PV in the opposite hemisphere. These data indicate that S2 and PV have unique and overlapping patterns of connections, and that they comprise part of a network that processes both cutaneous and proprioceptive inputs necessary for tactile discrimination and recognition. Although more data are needed, these patterns of interconnections of cortical fields and thalamic nuclei suggest that the somatosensory system may not be segregated into two separate streams of information processing, as has been hypothesized for the visual system. Rather, some fields may be involved in a variety of functions that require motor and sensory integration. J. Comp. Neurol. 462: 382–399, 2003.

Indexing terms: S2; PV; Sylvian fissure; electrophysiology; somatosensory cortex; primates

The somatosensory cortex of primates is composed of a number of cortical fields believed to be involved in complex behaviors such as texture perception (e.g., Jiang et al., 1997; Pruett et al., 2000), haptic shape perception (Reed et al., 1999), and bilateral coordination of the hands (Disbrow et al., 2001). Unfortunately, little is known about the neural circuitry that subserves these complex behaviors. One can speculate that dual processing streams, such as the "what and where" pathways described for the visual system of primates (Ungerleider and Mishkin, 1982), also exist in somatosensory cortex. If this were the case, then different types of behaviors, including texture discrimination, object recognition, and active reaching and grasping, might be processed by cortical fields that are part of separate processing streams.

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While it is tempting to accept this hypothesis because of its simplicity, it is actually difficult to evaluate whether such processing streams exist in somatosensory cortex for several reasons. First, emerging evidence indicates that the somatosensory cortex, particularly that of the lateral sulcus, is more complexly organized than previously appreciated (see Disbrow et al., 2000, for review). Second, the paucity of neuroanatomical studies of somatosensory cortex in primates makes it difficult to determine whether there is a parcellation of information flow within the cortex. Finally, the anatomical, electrophysiological, and neuroimaging data that do exist for areas in the lateral sulcus suggest that a single field may contribute to a variety of complex behaviors, including tactile recognition, attention, and coordination of the hands.

For instance, in the lateral sulcus of nonhuman primates, electrophysiological recording studies have demonstrated that cortex traditionally termed the second somatosensory area (S2) contains multiple somatosensory cortical fields, including S2 (S2a of Whitsel et al., 1969, and S2c of Burton et al., 1995), the parietal ventral area (PV, S2p of Whitsel et al., 1969, and S2r of Burton et al., 1995), the granular insula (Ig), the ventral somatosensory area (VS), 7b, the retroinsular area (Ri), and the parietal rostroventral area (PR; e.g., Robinson and Burton, 1980a,–c; Cusick et al., 1989; Krubitzer and Kaas, 1990; Krubitzer et al., 1995; Qi et al., 2002). The somatotopic organization of two of these fields, S2 and PV has been described using electrophysiological recording techniques, and each contains a mirror symmetric representation of the body's surface joined at the representations of the face, hands, and feet (Fig. 1D; Krubitzer and Kaas, 1990; Krubitzer et al., 1995; Qi et al., 2002). In addition, neurons in the S2 region, unlike neurons in areas 3b and 1, have large receptive fields that are often bilateral (Whitsel et al., 1969; Robinson and Burton, 1980a,c). Cells in S2 have been shown to be involved in the perception of texture (e.g., Jiang et al., 1997; Pruett et al., 2000), and studies in which S2 was lesioned demonstrate that animals are impaired in discriminating texture and shape (Murray and Mishkin, 1984). Finally, neural activity in S2 is modulated with shifts in attention within and across sensory systems (Hsiao et al., 1993; Burton et al., 1997; Steinmetz et al., 2000).

Functional imaging studies of the human brain indicate that several of the features of organization of the somatosensory cortex within the lateral sulcus are similar to those described in nonhuman primates. First, S2 and PV have been identified and shown to have a similar topographic organization to that described in other primates (Disbrow et al., 2000). Second, the existence of multiple areas in addition to S2 and PV has been well established by several laboratories (Burton et al., 1993; Ledberg et al., 1995; Mima et al., 1997; Korvenoja et al., 1999; Disbrow et al., 2000). Third, S2 and PV are activated bilaterally under unilateral stimulus conditions, suggesting that neurons in S2 and PV in humans may have bilateral receptive fields (e.g., Hari et al., 1984; Burton et al., 1993; Shimojo et al., 1997; Simoes and Hari, 1999; Disbrow et al., 2000, 2001). These regions respond during active roughness and length discrimination (Ledberg et al., 1995; Binkofski et al., 1999a), as well as complex object manipulation (Binkofski et al., 1999b) and haptic shape perception (Reed et al., 1999). Finally, neuronal activation of cortex in the lateral sulcus is modulated by shifts in attention (Mima et al., 1998; Burton et al., 1999; Lam et al., 1999; Backes et al., 2000; Hämäläinen et al., 2000; Johansen-Berg et al., 2000; Eimer and Driver, 2000).

Taken together, recent evidence indicates that multiple fields exist in the lateral sulcus of human and nonhuman primates. These areas contribute to several complex behaviors, particularly behaviors uniquely associated with primates such as the sensory motor integration necessary for manual object exploration and recognition and sophis-

Abbreviations

Cortical Fields and Sulci	
1	somatosensory area 1
2	somatosensory area 2
3a	somatosensory area 3a
3b	primary somatosensory area
5	somatosensory area in posterior parietal cortex
7b	somatosensory area in the lateral sulcus and inferior parietal lobule
A1	primary auditory area
AS	arcuate sulcus
CS	central sulcus
FEF	frontal eye fields
Ig	granular insula
IPS	intraparietal sulcus
LBLS	lower bank of the lateral sulcus
LS	lateral sulcus
LuS	lunate sulcus
M1	primary motor cortex
OF	orbitofrontal
PM	premotor area
PP	posterior parietal
PR	rostroventral parietal area
PV	parietal ventral area
Ri	retroinsular area
S2	second somatosensory area
STS	superior temporal sulcus
UBLS	upper bank of the lateral sulcus
VS	ventral somatosensory area
Thalamic Nuclei	
CL	central lateral nucleus
MD	mediodorsal nucleus
Pla	anterior pulvinar nucleus
VMb	basal ventral medial nucleus
VPi	inferior division of the ventral posterior nucleus
VPs	superior division of the ventral posterior nucleus
Body Parts	
dig	digits
fl	forelimb
hl	hindlimb
sh	shoulder
tr	trunk
ul	upper lip
Anatomical Directions	
C	caudal
L	lateral
M	medial
R	rostral
Neuroanatomical Tracers	
FB	Fast Blue
FE	Fluoro-Emerald
FR	Fluoro-Ruby
NY	nuclear yellow
WGA-HRP	wheat germ agglutinin conjugated to horseradish peroxidase

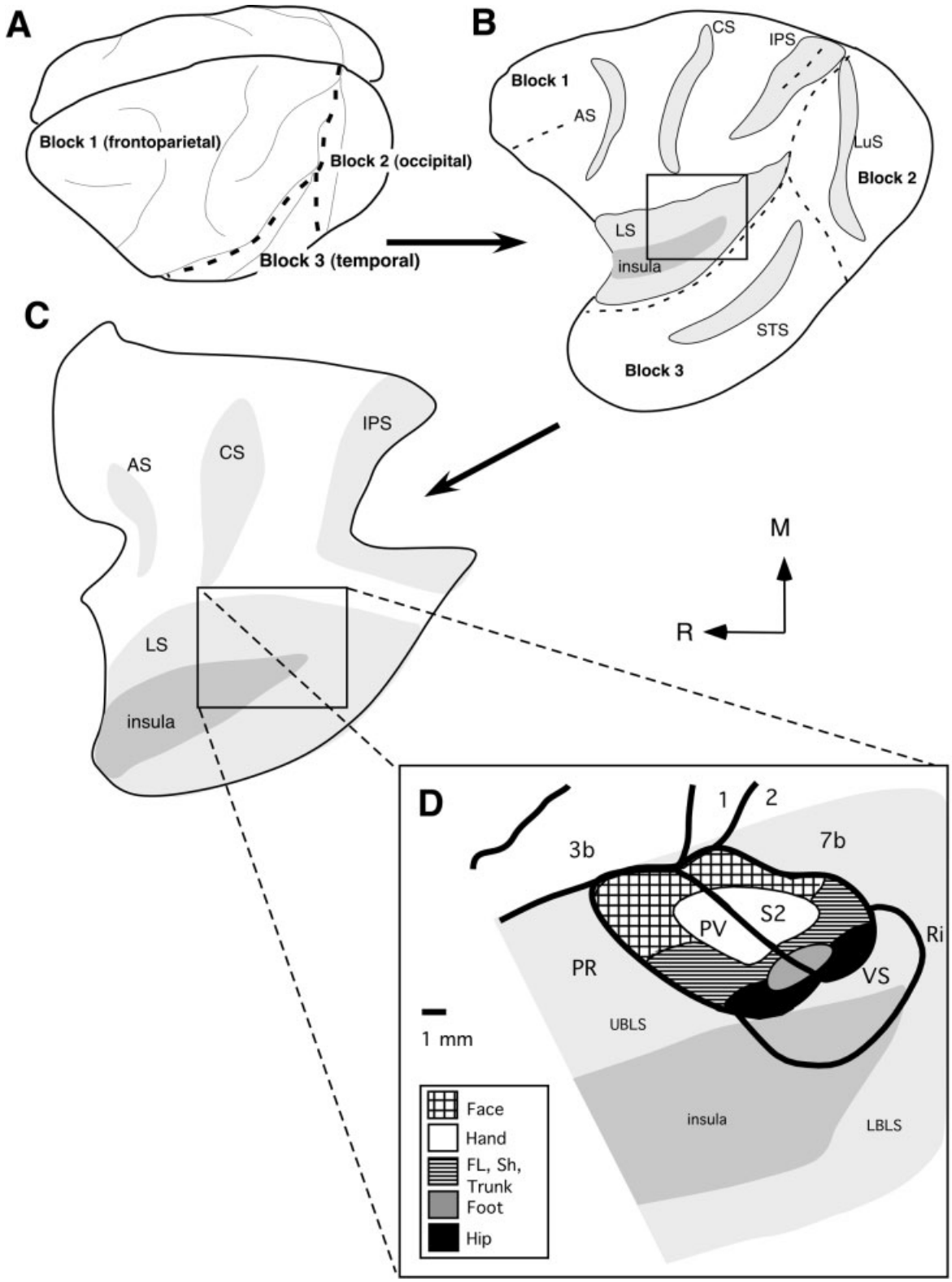


Fig. 1. A schematic of the flattening and blocking procedure used in this study (**A–C**), and an idealized summary of the topographic organization of S2 and PV in primates derived from maps of this region in several animals (**D**; Krubitzer et al., 1995). B: All sulci where gently pried apart, taking care not to tear the cortex. Several cuts were made in strategic locations, and three separate blocks were produced. C: Although only demonstrated for the frontoparietal block, the underlying white matter was gently pulled away from the underside of the cortex, and the block was then flattened. D: The cortex of interest in the lateral sulcus contains several fields, including S2 and PV examined in this study (square in C). Both fields contain a complete representation of the contralateral body surface and share a common border at the representations of the distal limbs and face. Unlike anterior parietal fields 3b and 1, which contain neurons with receptive fields on small portions of individual digits, areas S2 and PV contain neurons with large receptive fields covering, for example, much of the hand. This finding is true for all primates investigated (e.g., Krubitzer and Kaas, 1990; Krubitzer et al., 1995; Qi et al., 2002). Rostral is to the right, and dorsal is up. In D, different stipples represent different body parts (see key). For abbreviations, see list. Adapted from Krubitzer et al. 1995.

TABLE 1. Injection Site Data[1]

Case	Hemisphere	Tracer	Amount (ml)	%	Injection site	Survival time	Section thickness (mm)
98-1	R	W G A	0.025–.035	7	PV	24 hr	80
98-26	L	W G A	0.030–.050	1	S2	24 hr	40
98-33	R	N Y	Crystal	—	PV	2 weeks	60
	R	F B	Crystal	—	PV	2 weeks	60
	R	F E	0.4	7	PV	2 weeks	60
99-6	R	F R	0.4	7	S2	2 weeks	60
	R	NY	Crystal	—	PV	24 hr	60
	L	W G A	0.030–.050	7	PV	24 hr	60

[1]

ticated manual exploration. The purpose of the present investigation is to describe the specific pattern of connections of S2 and PV in an effort to appreciate the contribution of these fields to complex tactile behaviors, and cortical processing networks that ultimately give rise to tactile perception. Furthermore, this work may shed light on the hypothesis that somatosensory cortex processes information in a manner analogous to the visual system.

MATERIALS AND METHODS

Surgical preparation, tracer injections and electrophysiological recording

The connections of S2 and PV were examined in four macaque monkeys (*Macaca mulatta*) by injecting neuroanatomical tracers into somatosensory cortical fields of the lateral sulcus that were histologically, anatomically and, in some cases electrophysiologically identified. Experiments were carried out in two phases. In the first phase, five injections of fluorescent tracers were made in two hemispheres in the estimated location of S2 or PV 2 weeks before electrophysiological recording experiments to ensure adequate tracer transport. In some cases, fluorescent tracer injection sites were examined electrophysiologically in the second phase of the experiments. In three cases, wheat germ agglutinin conjugated to horseradish peroxidase (WGA-HRP) was injected during the second phase of the experiment, under electrophysiological guidance during acute recording experiments.

For fluorescent tracer injections, monkeys were initially anesthetized with ketamine hydrochloride (10 mg/kg). The animals were then intubated and cannulated, and anesthesia was maintained using the inhaled anesthetic isoflurane (1.5–2%). Body temperature, heart rate, respiration rate, and O_2 saturation and expired pCO_2 levels were monitored throughout the experiment. Animals received a constant infusion of lactated Ringer's solution (10 ml/kg per min, i.v.). When the animal was anesthetized, the skin was cut, the temporal muscle was retracted, and an opening was drilled in the skull over the lateral sulcus. The dura was cut and retracted. Fluorescent tracers were either injected through a Hamilton syringe (Fluoro-Ruby [FR] and Fluoro-Emerald[FE]; 0.25–0.4 μl of 7%, Table 1) or placed as a crystal (Fast Blue [FB], nuclear yellow [NY]; see Krubitzer et al., 1998, for details). Injections were made 500–1,000μm dorsal to the lip of the lateral sulcus at an angle tangential to the upper bank of the lateral sulcus. In none of the cases did the injection site involve areas 3b or 1. After injections were complete, a soft, sterile contact lens was placed over the opening, the dura flaps were placed over the contact lens, the skull was replaced and cemented with dental acrylic, and the muscle and skin were sutured. All surgical techniques were performed under standard sterile conditions. The animals were allowed to recover, and after 2 weeks, the electrophysiological recording experiments were performed.

For recording experiments, the surgical preparation and anesthetic dosage were similar to those described above. However, in this phase of the experiment a urinary catheter and arterial line were placed at the beginning of the experiment, and the animal was artificially ventilated. Throughout the experiment, blood gas levels were obtained from blood samples drawn from the arterial line. Once this preparation was complete, the opening in the skull was enlarged, and an acrylic well was built around the opening and was filled with silicone fluid. An image was taken of the exposed cortex with a Pixera PVC100C digital camera (Pixera Corp., Los Gatos, CA) and printed so that the placement of electrodes could be related to vascular patterns.

A tungsten electrode designed to record from multiunit clusters (5 MΩ, 0.5 mm diameter) was lowered into the cortex by using a Kopf 650 hydraulic stepping microdrive (David Kopf Instruments, Tujunga, CA). For electrode penetrations oriented perpendicular to the cortical surface, recordings were made at a depth 700–1,000 μm from the pial surface. Within the lateral sulcus, the electrode was advanced in 500-μm steps to a depth of approximately 8 mm and multiple electrode penetrations were made across the rostrocaudal extent of the lateral sulcus. Neural recordings were amplified, filtered, viewed on an oscilloscope and heard through a loudspeaker. For somatic stimulation, stimuli consisted of light taps, displacement of hairs with brushes, light brushing of skin, hard taps, and manipulation of muscles and joints. Receptive field locations and submodality were defined and documented for neurons at all recording sites. WGA-HRP injections (0.025–0.050 μl of 1–7% solution, Table 1) were made under electrophysiological guidance 24 hours prior to the termination of the experiment.

At the end of the experiment, small electrolytic lesions (10 μA for 10 seconds) were made at strategic locations, and large probes (pasta) were inserted rostral and caudal to the mapped area to help identify the electrode angle and to aid in the serial reconstructions. These electrophysiology experiments lasted from 24 to 48 hours. At the conclusion of the electrophysiological recording session, the animal was euthanized (60 mg/kg pentobarbital sodium) and transcardially perfused with 0.9% saline followed by 3–4% paraformaldehyde in phosphate buffer (pH

7.3) and then by 3–4% paraformaldehyde in 10% sucrose phosphate buffer. All protocols used in these experiments were approved by the Animal Use and Care Administrative Advisory Committee of the University of California, Davis.

Tissue preparation and histologic processing

After the animal was perfused, the brain was removed from the cranium, and in most cases, the cortex was removed from the brainstem and thalamus. Each hemisphere was then dissected into three separate blocks: A frontoparietal block, an occipital block, and a temporal block (see Fig. 1). For each piece, the sulci of the cortex were gently pried apart so that the cortex could be manually flattened. The flattened cortex was placed under a lightly weighted glass microscope slide and left to soak overnight in 30% sucrose and phosphate buffer. In one case, the brain was left intact and was sectioned horizontally. The flattened cortex was cut tangentially on a freezing microtome at a thickness of 40–80 μm (Table 1). Alternate sections of the flattened cortex were stained for myelin (Gallyas, 1979), mounted for fluorescent microscopy, or reacted for HRP using tetramethylbenzidine (Mesulam, 1978; modified by Gibson et al., 1984). In one case, the brain was sectioned horizontally at 80 μm and alternate sections were stained for Nissl, myelin, cytochrome oxidase (Carroll and Wong-Riley, 1984) and reacted for HRP.

Data analysis

Labeled cell bodies (Fig. 4A,B) in the ipsilateral and contralateral cortex resulting from injections of fluorescent tracers were plotted relative to tissue artifacts, blood vessels, lesions, portions of electrode tracks, and the outline of sections using a Zeiss axioscope with an X/Y stage encoder attached to a digitizer and computer using MDPLOT software (Minnesota Datametrics Corporation, St. Paul, MN). Labeled cell bodies and axon terminals for the WGA-HRP injections were plotted using a camera lucida attached to a Zeiss SV6 stereomicroscope. The landmarks listed above were related to plotted cell bodies and axon terminals. All sections included an outline of the injection site and the zone of uptake. The effective uptake zone has been described previously (Krubitzer et al., 1998). Reconstructed sections were collapsed onto a single section so that the total pattern of connections could be appreciated. This final reconstruction was matched to the entire series of sections stained for myelin by aligning blood vessels and other tissue landmarks, and the architectonic boundaries of cortical fields were drawn onto the reconstruction for each case. PV can be distinguished from S2 (when recording density is sufficient) by a reversal in receptive field progression across the boundary and a re-representation of body parts at distant locations. PV and S2 are readily distinguished from surrounding cortical fields by changes in responsivity of neurons or the presence of neurons in other fields that respond to multimodal stimulation.

To match the cortical reconstructions to electrophysiological recording data, the reconstructions were scaled to the digital image, which contained blood vessels and probe locations. The electrode penetrations were matched in both data sets using the pasta probes and entry sites. In flattened cortex, determining the angle of the electrode could be done with a high degree of accuracy. Because the brain was flattened and cut parallel to the surface, the entire electrode track for all of the penetrations could be viewed in a single section. The recording depths were determined from electrolytic lesions, and the receptive field and stimulus preference for neurons at the different depths were transposed onto the reconstructions. In this way, a comprehensive reconstruction was made that included the injection site and labeled cell bodies and their relation to architectonic boundaries and electrophysiological recordings.

The case cut horizontally was serially reconstructed. Labeled cell bodies and axon terminals were plotted on all sections, as well as the fiducial probes of pasta. Architectonic boundaries were added to the reconstruction in a manner similar to that described for flattened cortex. Drawings of serial sections included either cell bodies and several electrode penetrations, or architectonic boundaries, were then re-drawn at a 30-degree angle from vertical for better visualization and stacked based on the location of sulci and the surface of the brain. The electrode angle was recovered, and the location of transported tracer was related to cortical field boundaries and electrophysiological data.

In addition to electrophysiological recordings and myelo- or cytoarchitecture, patterns of thalamocortical connections were also used to identify S2 and PV (Disbrow et al., 2002). The area we define as PV receives thalamic input from lateral posterior nucleus (Vpi), anterior pulvinar nucleus (Pla), mediodorsal nucleus (MD), and central lateral nucleus (CL). S2, on the other hand, receives input from VPi, VPs, & Pla. These results came from the same animals and injection sites as those reported in the present study. Digital images of cases were taken with an RT slider spot digital camera (Diagnostic, Inc., Sterling Heights, MI) and were assembled in Adobe Photoshop 6.0.

RESULTS

Architectonic subdivisions of somatosensory cortex

There were multiple cortical fields in somatosensory cortex that could be reliably identified from flattened cortex. First, the primary somatosensory area, S1 or 3b, stained very darkly for myelin (Fig. 2A). This field resided predominantly on the caudal bank of the central sulcus. As has been reported previously, the border of the hand and face representations of area 3b was denoted by a small rostrocaudal strip that was devoid of myelination (Krubitzer and Kaas, 1990; Jain et al., 1998). Area 1 bordered area 3b caudally and was moderately to lightly myelinated. At the rostral border of area 3b, area 3a was observed to be a moderately myelinated field that resided on the fundus and the rostral bank of the central sulcus, sometimes continuing onto the caudal bank of the sulcus as well. Area 2 was located just caudal to area 1 and was lightly myelinated. Thus, the boundary between areas 1 and 2 was difficult to discern in this preparation. Area 5 was a wedge-shaped field just caudal to the medial portion of area 2. Area 5 was moderately myelinated and resided predominantly on the rostral bank of the intraparietal sulcus. Rostral to area 3a was motor cortex, or M1. M1 was a darkly myelinated field and could be readily distinguished from the caudally residing area 3a.

Cortex in the lateral sulcus has been described previously by our laboratory using a similar preparation (Kru-

bitzer et al., 1995). Two moderately myelinated fields abut the lateral boundary of area 3b (Fig. 2B). These fields, S2 and PV, each contain complete representations of the body surface (Fig. 1D; Krubitzer et al., 1995; Burton et al., 1995). Just rostral to PV, a very lightly myelinated region of cortex was observed, and we have termed this field PR, as in previous investigations in New World monkeys (e.g., Krubitzer and Kaas, 1990; Qi et al., 2002). However, PR is a large region and may contain more than a single field. The rostral boundary of PR is difficult to distinguish because cortex adjacent to this field is lightly myelinated as well. Caudal to S2 is a moderately myelinated field termed 7b (from Robinson and Burton, 1980a,b). Area 7b is bordered by lightly myelinated cortex caudally and laterally so that its boundaries can be readily distinguished in this preparation.

In cortex that has been cut horizontally and stained for Nissl, the border between S2 and PV is distinct (Fig. 2C). S2 has a darkly staining and moderately packed layer IV and VI, whereas PV contains a less densely packed and darkly staining layer IV and a thick, moderately staining layer VI. Area 3b is also readily identified as koniocellular cortex containing a dense layer IV and VI.

Ipsilateral connections of S2

Injections in S2 were made in two cases (Figs. 3B,C, 5, 6), and in one of the cases, the injection site was electrophysiologically identified (Fig. 5A,B). In this case (98-26LM, Figs. 3A, 5A), a small injection of WGA-HRP was centered in the representation of the hand (Fig. 5B) and spread into the representation of the trunk and face (Fig. 5A). In the second case (99-6RM, Fig. 6), a small injection of FR was made into the approximate location of the face representation. Both cases demonstrated dense intrinsic connections close to the injection site. In the case in which electrophysiological recordings were made (98-26LM, Fig. 5), labeled cell bodies and axon terminals were found in adjacent representations of the hand in S2 (Fig. 5A,C). Similarly, in 99-6RM (Fig. 6), labeled cell bodies were in the expected location of the adjacent hand representation medial to the injection site, as well as the representation of the face, lateral to the injection site, at the lip of the lateral sulcus (LS).

Label was also identified at locations outside of S2. In both cases, label in PV was in the electrophysiologically

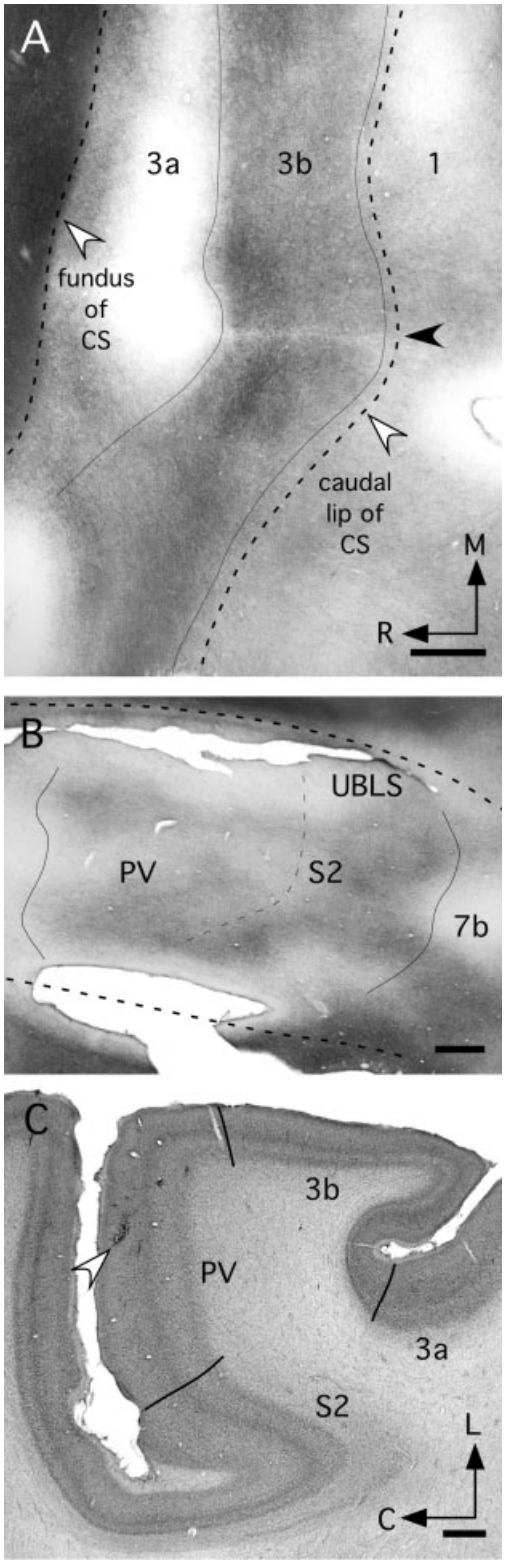
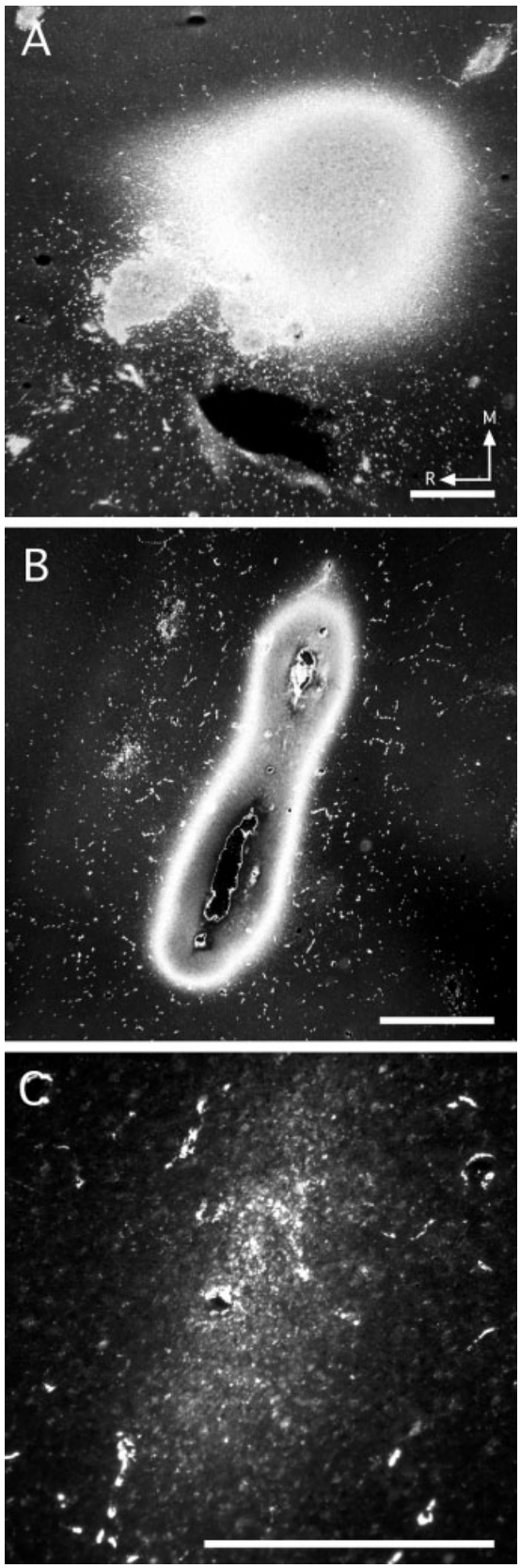


Fig. 2. Lightfield digital images of cortex that has been flattened, cut tangentially, and stained for myelin (A,B) or cut horizontally and stained for Nissl (C). **A:** Area 3b can be readily identified as a darkly myelinated region. The border between the hand and face representation is demarcated by a lightly myelinated strip of cortex (black arrowhead; see Krubitzer and Kaas, 1990; Jain et al., 1998). Area 3a is lightly myelinated, and area 1 is moderately myelinated. **B:** A lightfield digital image of S2 and PV on the upper bank of the lateral sulcus (dashed lines). To the top of the image is the lip of the lateral sulcus. Both S2 and PV stain moderately for myelin, which makes the border between the fields sometimes difficult to distinguish in a single section. However, the rostral border of PV and the caudal border of S2 is readily identified, because this region is lightly to moderately myelinated. **C:** A digital image of the 3b/S2/PV borders in cortex, which has been sectioned horizontally and stained for Nissl in case 98-1LM. Area 3b is characterized by darkly staining, densely packed layers IV and VI; PV contains a less darkly staining layer IV and a thick, moderately staining layer VI. Note the location in PV where the Hamilton syringe passed through the cortex from the injection in PV in this case (white arrowheads, see Fig. 9). Lines mark architectonic boundaries. Other conventions as in Figure 1; for abbreviations, see list. Scale bars = 1 mm in A–C.



identified or expected locations of the hand, forelimb, and face representations. For anterior parietal fields, the injection centered in the hand representation which spread into the expected location of the face representation in S2 (98-26LM, Fig. 5), resulted in transported tracer in area 3b. Transported tracer was most dense in the expected location of the face representation, which has been demonstrated to be just lateral to the unmyelinated strip of cortex, which separates the hand and face representations in area 3b (Krubitzer and Kaas, 1990; Jain et al., 1998). Label was also found in a more lateral portion of 3b, in the location of the lips and oral structure representations, and medial in 3b, in the expected location of the forelimb representation (Fig. 5C). This finding is not surprising, because the injection in S2 spread into the face and forelimb representation.

In the case with the injection located in the expected location of the face representation in S2 (99-6RM, Fig. 6), label in area 3b was at the far lateral portion of the field, in the location of the representation of the face and oral structures. Thus, label in 3b resulting from injections in S2 was in topographically matched locations. For both injections, transported tracer was also found in area 1 at the same mediolateral locations as that in 3b, suggesting that connections with area 1 are matched as well. However, label in area 1 was much less dense than in area 3b.

Just caudal to S2 and lateral to area 2, a dense patch of label was identified in the field termed area 7b. The label in 7b resulting from both injections was extremely dense (Fig. 4A,B). Finally, in one case (98-26LM, Fig. 5), labeled cell bodies and axon terminals were observed rostral to the arcuate sulcus in orbitofrontal cortex. In the other case (99-6RM, Fig. 6), a few labeled cells were observed just rostral to PV in PR.

Ipsilateral connections of PV

Six injections were made in the parietal ventral area in three different cases. In one case (99-6LM, Figs. 3A, 7A,B), WGA-HRP was injected into the electrophysiologically defined representation of the face/hand. In another case (98-33RM, Fig. 8), an injection of FB and another injection of NY were made in the expected location of the face representation. In an additional case, an injection of FE and an injection of NY were made in the expected location of the face representation (99-6RM, not shown). Finally, in case 98-1LM (Fig. 9), WGA-HRP was injected into the electrophysiologically identified bilateral trunk/forelimb representations but spread into the face representation

Fig. 3. Darkfield digital images of injections of WGA-HRP in PV (case 99-6; **A**) and S2 (case 98-26LM; **B**). The injection in PV is small, 1.5 × 1.5 mm, and is confined to its boundaries. Although the injection in S2 is somewhat larger (approximately 3.5 × 1 mm), it is restricted to S2. Electrophysiological recordings in case 99-6LM (A; Fig. 7A) demonstrate that the injection was centered in the representation of the hand and spread into the representation of the face and trunk. Electrophysiological recordings in case 98-26LM (B; Fig. 5A) demonstrate that the injection in S2 is centered in the representation of the forelimb, but spread into the representations of the hand, trunk, and face. Electrophysiological recordings in case 99-6LM (Fig. 7A) demonstrate that the injection was centered in the representation of the hand and spread into the representation of the face and trunk. **C:** A very small injection of Fluoro-Ruby was centered in S2 in case 99-6RM (see Fig. 6). Other conventions as in Figure 1; for abbreviations, see list. Scale bars = 1 mm in A,B, 500 μm in C.

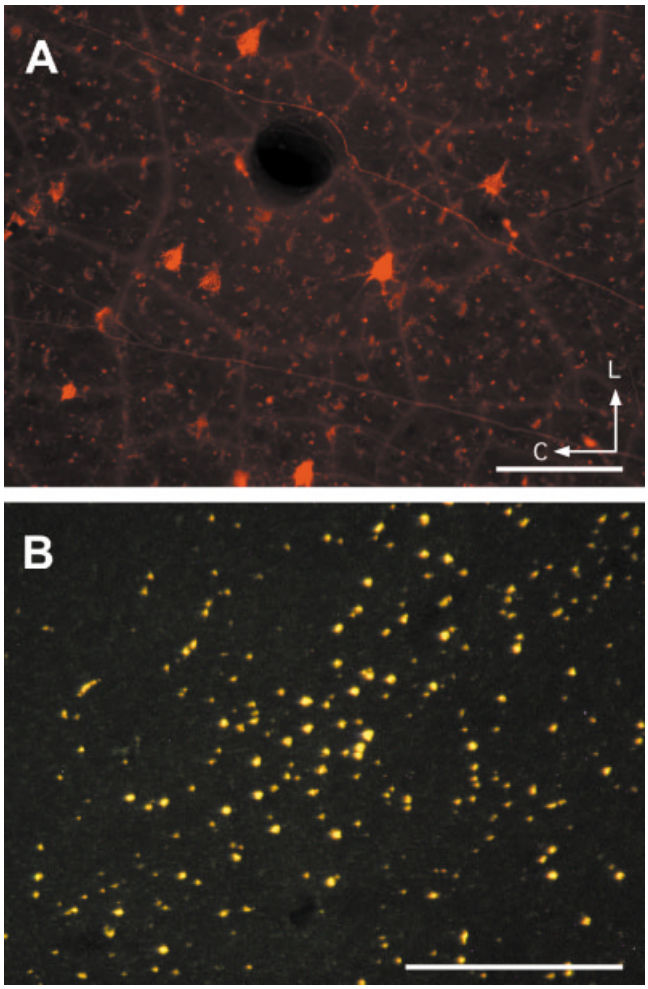


Fig. 4. Darkfield images of retrogradely labeled cells resulting from injections of different anatomical tracers into S2 and PV. **A:** A small injection of Fluoro-Ruby in S2 in case 99-6RM (see Fig. 6) resulted in labeled cells in 7b. **B:** A WGA-HRP injection in PV in case 99-6LM resulted in several labeled cells in area 7b (see Fig. 7). Labeled cell bodies in B are seen as bright, large spheres, whereas a few labeled blood cells and tissue artifact are small and irregular in shape. Other conventions as in Figure 1; for abbreviations, see list. Scale bars = 100 μm in A, 750 μm in B.

(Fig. 9A,B). In all cases, intrinsic connections with other portions of PV were most dense with regions immediately adjacent to the injection site, in matched representations (e.g., Fig. 9A).

In 99-6LM (Fig. 7A), a few labeled cells were observed in the shoulder representation in PV. In case 98-33RM (Fig. 8), labeled cells were observed in the expected location of the hindlimb representation in PV, at its far medial border. In case 98-1LM (Fig. 9A), labeled cells and axon terminals were in the electrophysiologically identified representations of the forelimb, hand, face, and oral structures.

In S2, labeled cells, and in two cases axon terminals, were predominantly at the same mediolateral location as the injection site. In case 99-6LM (Fig. 7), label in S2 was close to the S2/3b boundary, in the expected location of the face representation. In case 98-33RM (Fig. 8), an injection of NY at the rostral boundary of PV, in the expected location of the representations of the face, oral structures, and upper trunk, resulted in label in S2 at the far caudal boundary, in the expected location of matched representations. An injection of FB at the caudal boundary of PV, in the expected location of the representations of the face and hands, resulted in label in S2 at its rostral boundary. The pattern of connections from this case (98-33, Fig. 8) demonstrates the mirror somatotopic representations of S2 and PV. Finally, an injection in the face and forelimb representations in PV (98-1LM, Fig. 9A) resulted in label in the face representation in S2.

Five of the six injections resulted in label in area 3b. In all of these cases, label was in the representations of the face and oral structures. Five of the six injections in PV also resulted in label in area 1. In these cases, label was in the lateral portion of area 1, in the expected location of the face. Dense label was observed in area 7b for five of six injections. For two of these cases (99-6LM and 98-1LM, Figs. 7A, 9A), electrophysiological recordings indicated that the transported tracer in 7b was in the forelimb representation. In case 98-1LM (Fig. 9), injections in neck, chin, and forelimb representations in PV resulted in label in the representations of the dorsal limbs and trunk, and lower jaw and chin in area 7b.

There were several distinguishing features of the patterns of connections of PV compared with S2. First, for all PV injections, very dense label was observed in PR, just rostral to PV, whereas injections in S2 resulted in little or no label in PR (Figs. 7C, 8, 9C). Second, for half of the injections, label ranging from sparse to moderately dense was observed in the premotor cortex (e.g., Fig. 7C), and on the lower bank of the lateral sulcus, in cortex traditionally defined as the medial auditory belt region (Fig. 8; for review see Kaas and Hackett, 2000). Finally, label was observed in the intraparietal sulcus (Figs. 7C, 8, 9C) in four of six cases, and in the arcuate sulcus, in the location of the frontal eye field, for four of six cases. In one case, label was observed in the cingulate cortex (Fig. 8).

Contralateral connections of S2 and PV

Callosal connections were determined for one of the S2 injections (99-6LM, Fig. 10A) and for two of the PV injections (99-6RM and 98-1RM, Fig. 10 B,C). For the S2 injection in the expected location of the face/hand representation, contralateral label was observed in the middle portion of both S2 and PV, in the electrophysiologically defined representation of the hand, forelimb, and trunk representation (Fig. 10A). Label was also observed in area 7b, and in area 3b in the expected location of the face representation. The injection in PV in the electrophysiologically defined face/hand representations (99-6LM; Fig. 7), resulted in transported tracer predominantly in a middle portion of PV in the opposite hemisphere, in the expected location of the hand, forelimb, and upper trunk representations (Fig. 10B). A small patch of label was also observed near the 3b/PV border, in the expected location of the face. The PV injection in the bilateral trunk/forelimb representations (98-1LM, Fig. 9) resulted in label in the middle portion of PV, in the expected location of the hand representation (Fig. 10C).

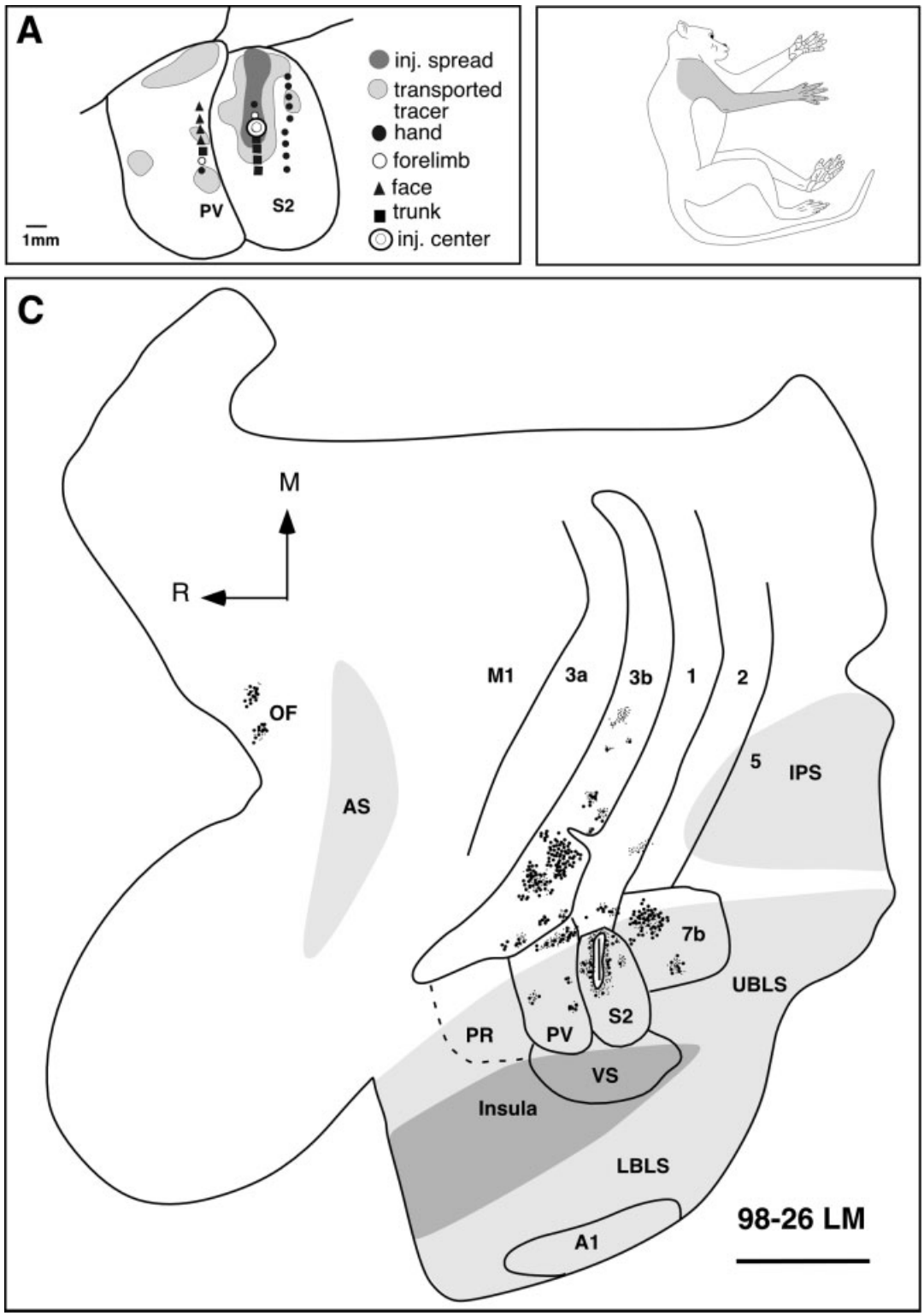


Fig. 5. A reconstruction of an injection of WGA-HRP centered in the electrophysiologically defined forelimb representation of S2 (see Fig. 3B) and transported tracer in surrounding cortical fields in the left hemispheres of case 98-26LM. **A** is an enlargement of S2 and PV, the recording sites within these regions, the location of the injection site (the recording site surrounded by a large open circle), locally transported tracer, and architectonically defined boundaries. Note that the injection site was restricted to S2. **B:** The receptive field for neurons at the center of the injection site is shown. Small patches of anterograde and retrograde label can be observed in both S2 and PV. **C:** Caudal to S2, area 7b contains a large, dense patch of transported tracer and a smaller, lateral patch of transported tracer. Although label is found throughout much of the mediolateral extent of area 3b, it is most dense in the expected location of the face and hand representations, and somewhat sparser in the expected location of the forelimb and oral structures. Label in area 1 is in the expected location of the hand and face. Finally, two small patches of transported tracer are observed in orbitofrontal cortex. In A, filled and open circles, squares, and triangles mark electrode penetrations. In B, shaded area represents the receptive field for neurons at the core of the injection site. In C, architectonic boundaries are marked by solid lines, and dashed lines mark approximate boundaries. Light gray areas mark the banks of the opened sulci, and dark gray marks the insula. Large dots mark labeled cells, and small dots mark axon terminals. Other conventions as in Figure 1; for abbreviations, see list. Scale bar = 1 cm in C.

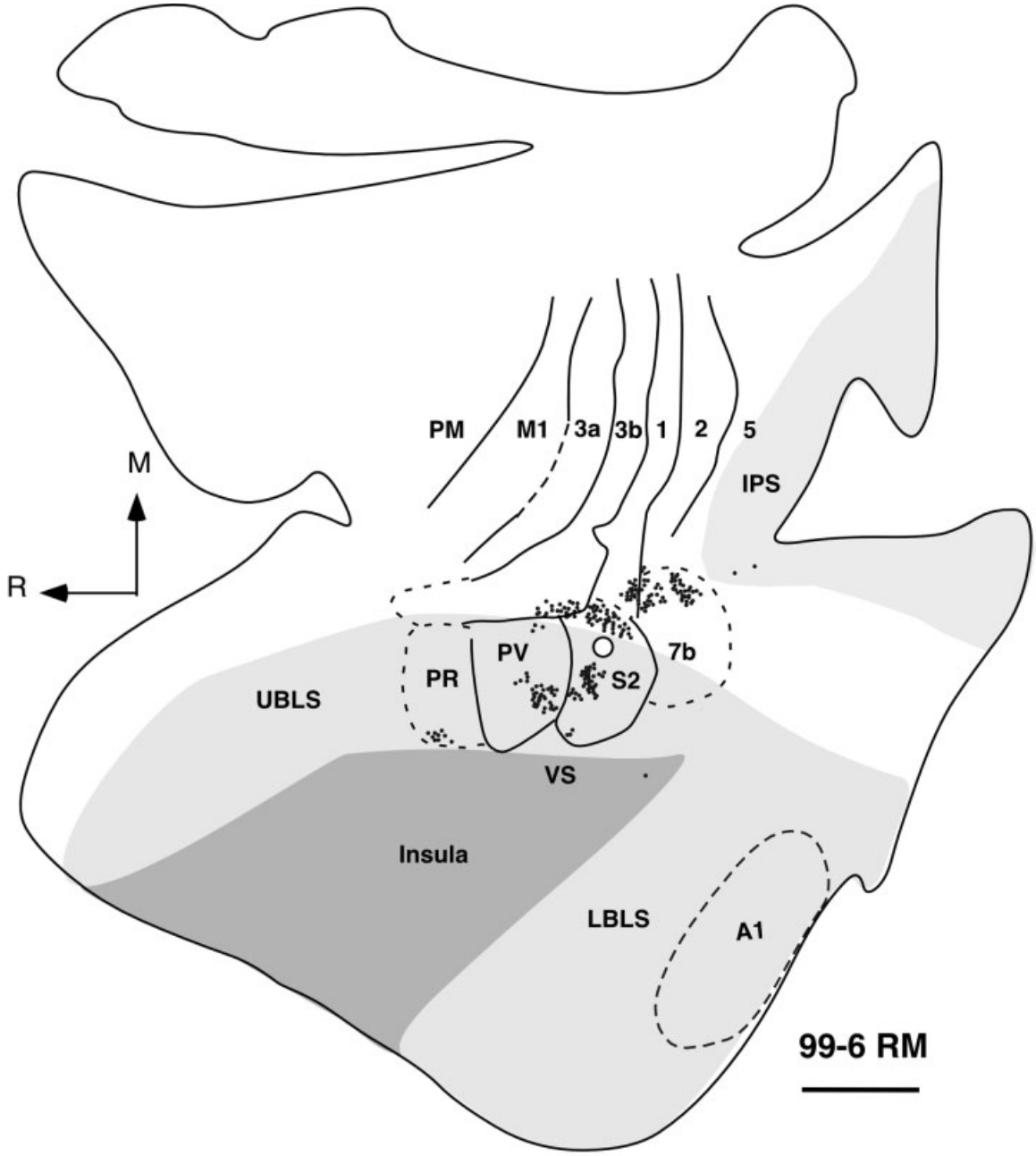


Fig. 6. A reconstruction of an injection of Fluoro-Ruby centered in the expected forelimb/face representation of S2 and transported tracer in surrounding cortical fields in the right hemisphere of case 99-6RM. Although the injection in this case is in the right hemisphere, for ease of comparison, all figures are shown in the same orientation. As in the previous case, labeled cells (filled circles) are observed locally in S2 and PV, 7b, and areas 3b and 1. A small patch of labeled cells is also located in PR. Other conventions as in Figure 1; for abbreviations, see list. Scale bar = 1 cm.

DISCUSSION

S2 has been implicated in a wide variety of tasks, including manual dexterity, bilateral integration of tactile inputs, pain perception, tactile object exploration and identification, tactile learning and memory, and attention (Mishkin, 1979; Hsiao et al., 1993; Forss et al., 1995; Burton et al., 1997, 1999; Shimojo et al., 1997; Mima et al., 1998; Oshiro et al., 1998; Watanabe et al., 1998; Baron et al., 1999; Reed et al., 1999; Simoes and Hari, 1999; Binkofski et al., 1999b; Backes et al., 2000; Hämäläinen et al., 2000; Johansen-Berg et al., 2000; Steinmetz et al., 2000; Disbrow et al., 2001). Our lack of a refined understanding of the role of S2 in any one of these tasks stems from three major sources. First, there is an inconsistency in how S2 is defined. This discrepancy is particularly problematic since recent studies indicate that several fields in addition to S2

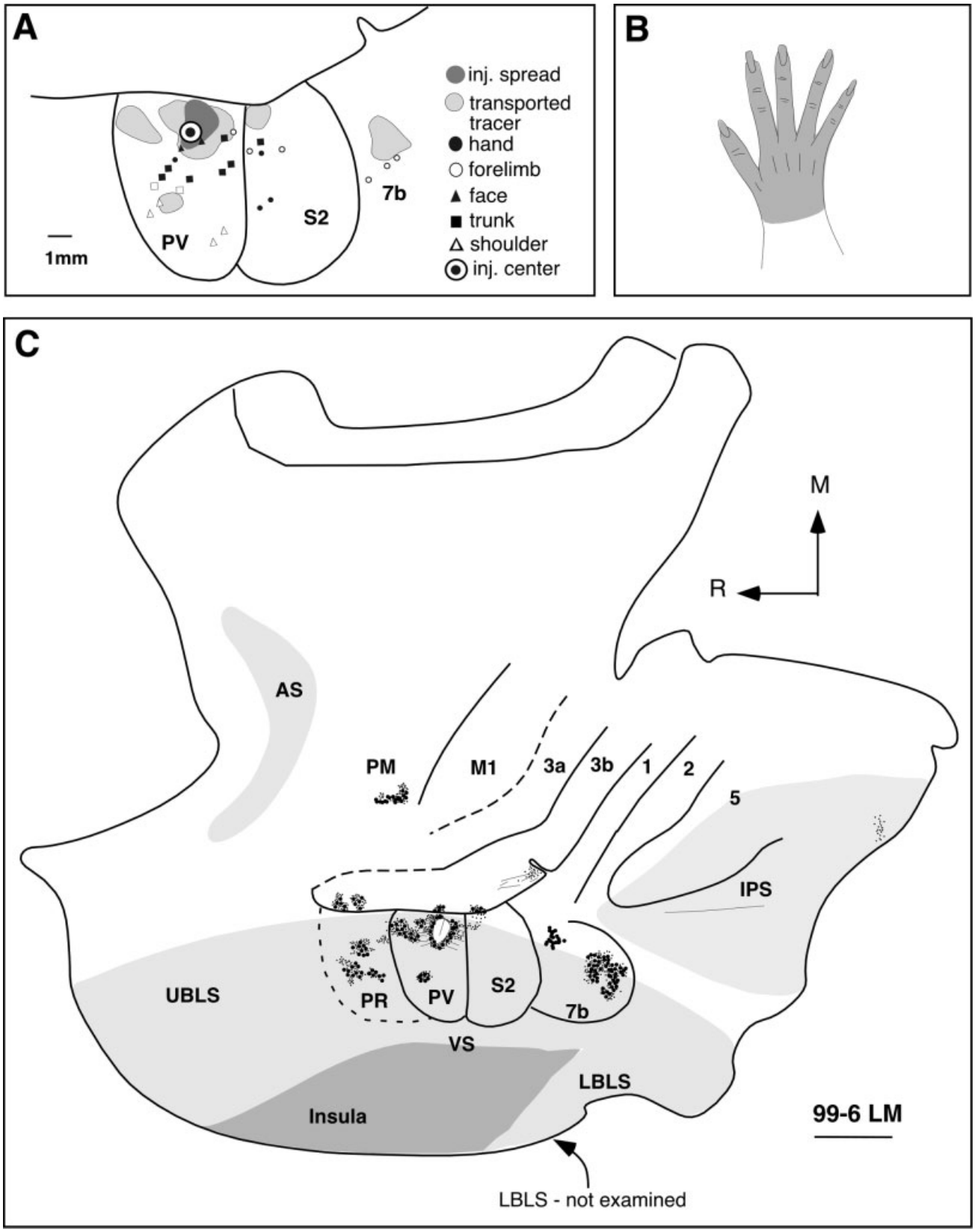


Fig. 7. A reconstruction of an injection of WGA-HRP centered in electrophysiologically defined hand representation of PV and transported tracer in surrounding cortical fields in the left hemisphere of case 99-6LM. **A** An enlargement of S2 and PV depicting the recording sites within these regions (circles, triangles, and squares), the center of the injection site (large open circle), the spread of the injection (dark gray), and architectonically defined boundaries (thin lines). Note that the injection site was restricted to PV. **B:** The receptive field for neurons at the center of the injection site is shown. Small patches of anterograde and retrograde label can be observed close to the injection site in PV and somewhat further from the injection site, in the location of the forelimb representation. Label in S2 is immediately adjacent to the 3b boundary. **C:** Label in 3b and 1 is in the expected location of the face and oral structures and near the hand/face border. Dense label is observed in PR, 7b, and PM. Sparse label is observed in IPS. Other conventions as in Figure 1; for abbreviations, see list. Scale bar = 1 cm in C.

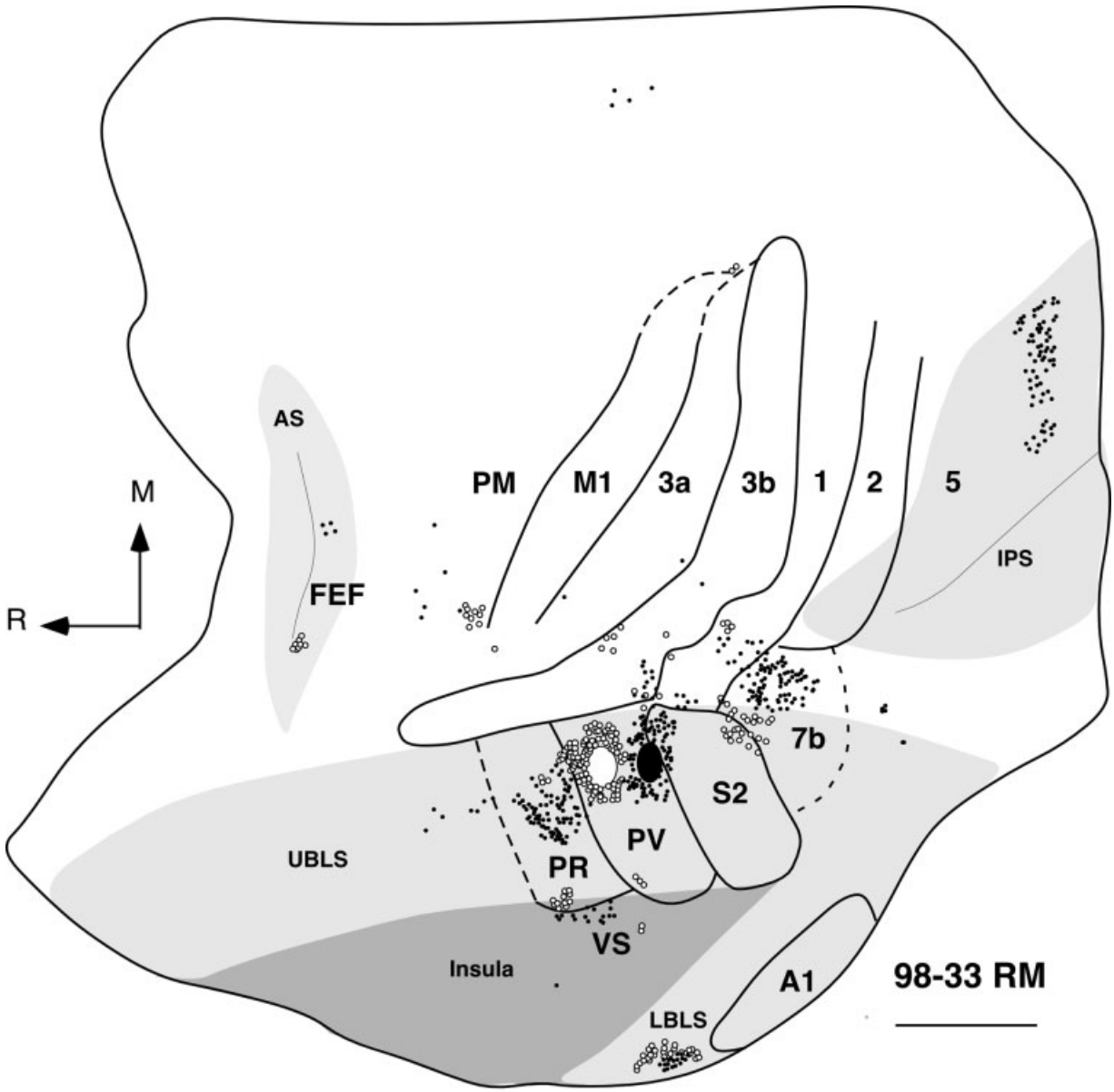


Fig. 8. A reconstruction of an injection of Fast Blue (filled circles) and nuclear yellow (open circles) centered in the expected location of the face representation of PV and transported tracer in surrounding cortical fields in the right hemisphere of case 98-33RM. The circled region denotes the injection site and local uptake. Local label in PV is observed close to the injection site. In S2, label is found close to the area 1 border, in the expected location of the S2 face representation. For the Fast Blue injection at the rostral boundary of PV, resulting label in S2 is at the caudal boundary. These injections and the pattern of transported tracer demonstrate the mirror reversal representations found in S2 and PV. In areas 3b and 1, labeled cells are located at the lateral boundary of the fields, in the expected location of the face representation of these fields. As with S2 injections, dense label is found in area 7b. Unlike S2, PV has dense connections with PR and cortex on the lower bank of the lateral sulcus, just medial and rostral to A1, in the medial auditory belt region. PV also has connections with premotor cortex and cortex in the arcuate sulcus in the expected location of the frontal eye fields. The FB injection in PV resulted in dense label in area 5, and a few scattered cells in cingulate cortex. Other conventions as in Figure 1; for abbreviations, see list. Scale bar = 1 cm.

reside on the upper bank of the lateral sulcus. Second, the anatomical connections of these fields have never been fully described. Finally, our theories about how the somatosensory system processes information are largely guided by our understanding of how the visual cortex processes sensory inputs. For instance, the ideas regarding feedforward and feedback connections and their relationship to hierarchical processing networks originated in the visual system and was rapidly incorporated into theories of somatosensory processing (e.g., Rockland and Pandya, 1979; Van Essen and Maunsell, 1983). Furthermore, as discussed below, the idea that separate, parallel processing streams exist in the neocortex also originated in the visual system and was subsequently proposed for

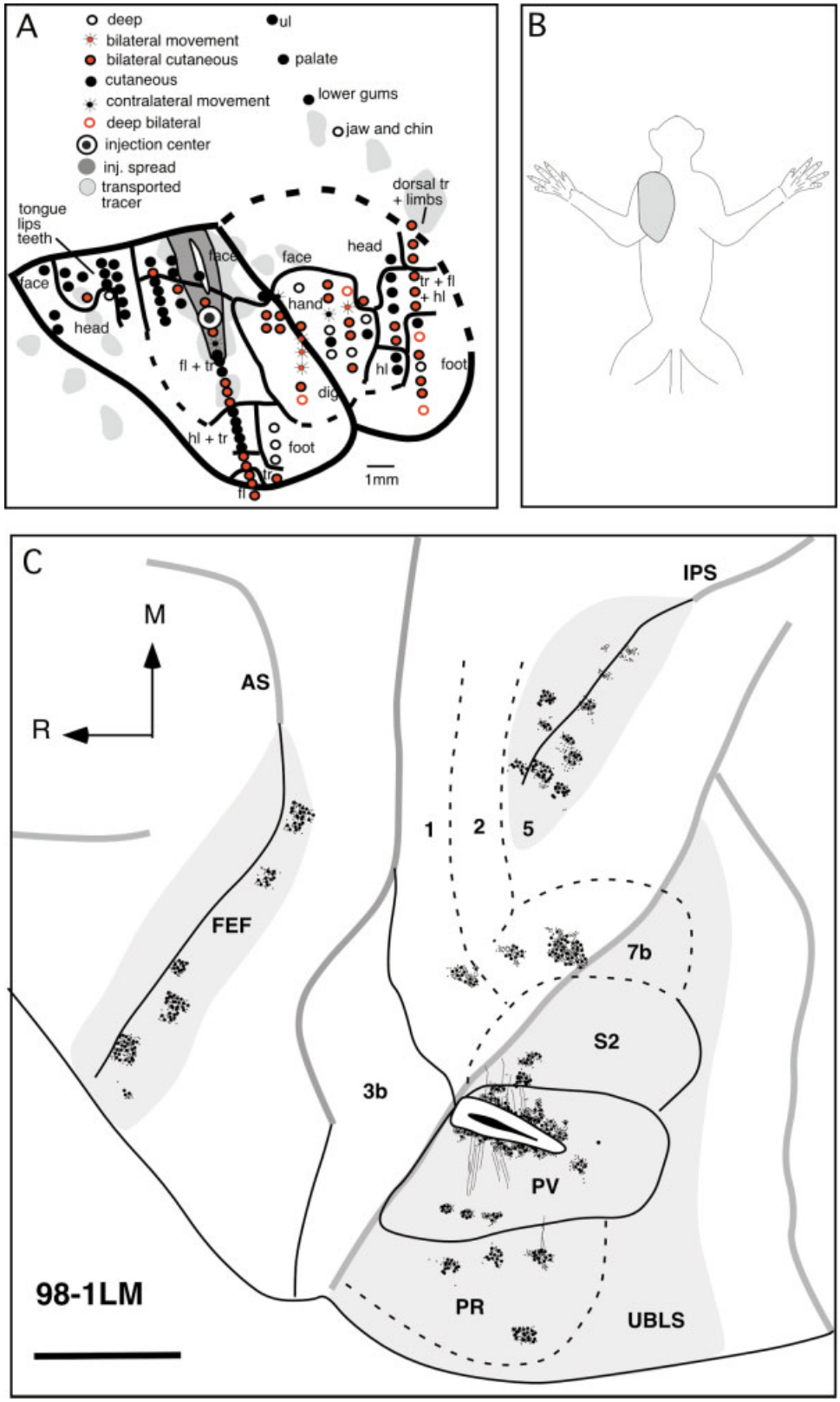


Fig. 9. A reconstruction of an injection of WGA-HRP centered in electrophysiologically defined proximal forelimb and trunk representations in PV in case 98-1LM. The injection spread into the forelimb and face representations. **A:** An enlargement of S2 and PV, the recording sites within these regions (open circles, filled circles, stars), the location of the center of the injection site (open circle around recording site), the spread of the injection (dark gray), locally transported tracer (light gray), and architectonically defined boundaries (lines). Note that the injection site was restricted to PV. **B:** The receptive field for neurons at the center of the injection site is shown. Small patches of anterograde and retrograde label can be observed close to the injection site in PV in the representations of the head, oral structures, face, and forelimb. Label in S2 is immediately adjacent to the 3b boundary in the representation of the face. Label in 7b is in the representation of the dorsal trunk and limbs and lower jaw and chin. **C:** A reconstruction of the ipsilateral connections of PV from horizontally sectioned tissue. Dense label is observed in PR, FEF, IPS, PR, and 7b. Other conventions as in Figure 1; for abbreviations, see list. Scale bar = 5 mm.

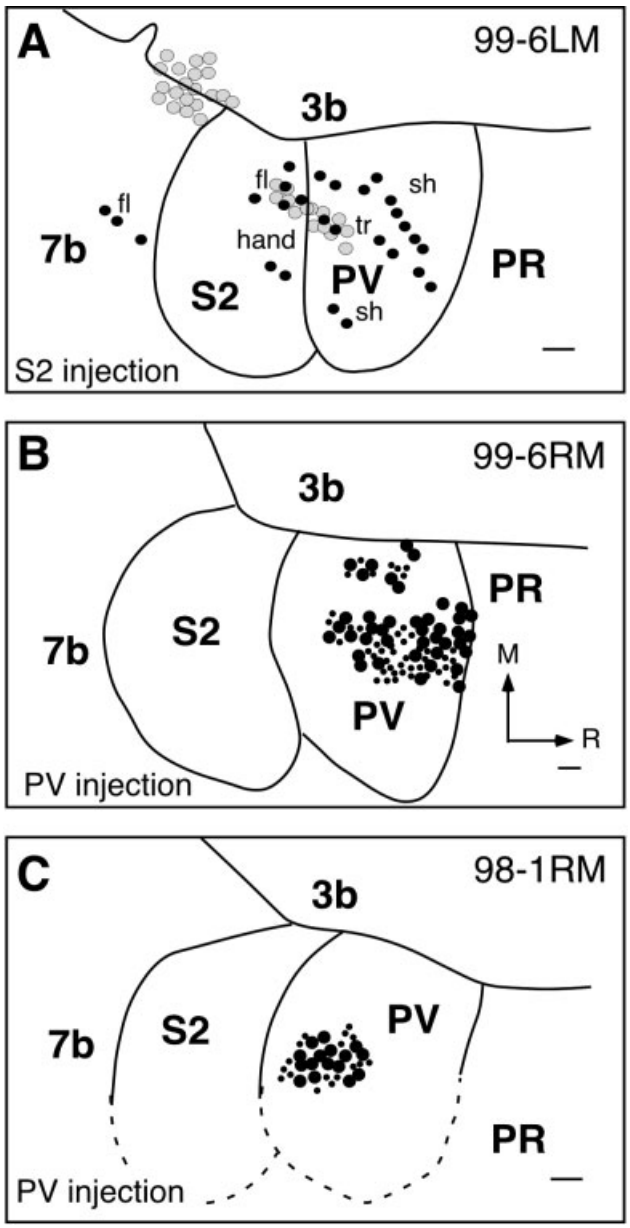


Fig. 10. Reconstruction of callosally transported tracer resulting from injections into S2 (A) and PV (B,C) in the opposite hemisphere. **A:** An injection of FR centered in the expected location of the face/hand representation of S2 resulted in labeled cells (gray circles) in the electrophysiologically identified hand, forelimb, and trunk representations of S2 and PV in the opposite hemisphere of case 99-6 (see Fig. 6 for injection site). Labeled cells were also identified in the face representation of areas 3b and 1. Although 99-6 is actually a left hemisphere, all brains are shown in the same orientation for ease of comparison. The black circles in A mark recording sites. **B:** An injection of WGA-HRP centered in the electrophysiologically defined hand representation in PV in case 99-6LM resulted in label in the expected location of the hand and forelimb representation of area PV in the opposite hemisphere. Some labeled cell bodies (large dots) and axon terminals (small dots) were located in the expected location of the face (see Fig. 7 for injection site). **C:** Finally, an injection of WGA-HRP centered in the electrophysiologically defined proximal forelimb and trunk representation in PV in case 98-1LM resulted in transported tracer in the approximate location of the hand/forelimb representation of PV in the opposite hemisphere (see Fig. 9 for injection site). A few labeled cells were also observed in area 5. Other conventions as in Figure 1; for abbreviations, see list. Scale bars = 1 mm in A–C.

the somatosensory system. Although several of these features may well be general features of cortex, others may be characteristics that are specific to the visual system.

Organization and connections of somatosensory fields in the lateral sulcus

Modern electrophysiological studies of the S2 region in primates (Krubitzer and Kaas, 1990; Krubitzer et al., 1995; Qi et al., 2002) demonstrate that the field historically referred to as S2 is actually composed of at least two separate areas, S2 and PV, each of which contains a complete, mirror symmetric representation of the body surface (Fig. 1D). This finding is further supported by our data which indicate that these fields have unique patterns of cortical and thalamic connections as well (Disbrow et al., 2002). In addition, recent studies have also shown that several additional somatosensory fields exist in this region, including Ig, PR, VS 7b, and Ri (Fig. 1D; e.g., Robinson and Burton, 1980a,–c; Friedman and Murray, 1986; Cusick et al., 1989; Krubitzer and Kaas, 1990; Schneider et al., 1993; Krubitzer et al., 1995). Thus, the upper bank of the lateral sulcus and parietal operculum contain at least seven fields. It is not surprising that a wide range of functions have been ascribed to S2, because it is likely that any particular study may have been investigating one or another of these fields.

In the current investigation, restricted injections in S2 resulted in connections with areas 3b, 1, PV, and 7b. In contrast, PV had additional connections with cortex subserving other sensory and motor systems, such as the auditory belt area, the intraparietal sulcus, and premotor cortex (Fig. 11). These findings are largely similar to previous studies in which S2 was identified electrophysiologically. For instance, injections in S2 in marmosets (Krubitzer and Kaas, 1990; Qi et al., 2002) resulted in dense connections with PV, 7b, 3b, and 1 as in the present study. However, in marmosets, connections of S2 and PV were more broadly distributed. Label was also observed in PR, M1, SMA, frontal eye fields, cingulate cortex, and medial and lateral auditory belt regions (Krubitzer and Kaas, 1990; Qi et al., 2002).

Results from the current study indicate that PV in macaques as well as marmosets (Qi et al., 2002) has ipsilateral cortical connections with 3b, 1, S2, and PR, and callosal connections with somatotopically matched locations in S2 and PV. However, in the macaque, connections were also observed with 7b, IP, and PM, whereas in the marmoset, additional connections were observed with 3a, VS, SMA, and MI. The differences in connectivity may be the result of technical differences between studies, for instance, in both previous studies of marmoset cortex injection sites were proportionally larger than in the current investigation and may have involved fields in addition to S2 or PV (e.g., see Fig. 6 of Qi et al., 2002), which could explain why connection patterns appeared more distributed. On the other hand, these differences may be a reflection of true species differences. There is some evidence that smaller brained mammals with fewer cortical fields such as marmosets have more widespread connections than animals with large brains, like the macaque, in which more local processing occurs (Ringo, 1991; Manger et al., 1998). This difference in connectivity patterns has been proposed to be the result of minimizing total connection length (Cherniak, 1994).

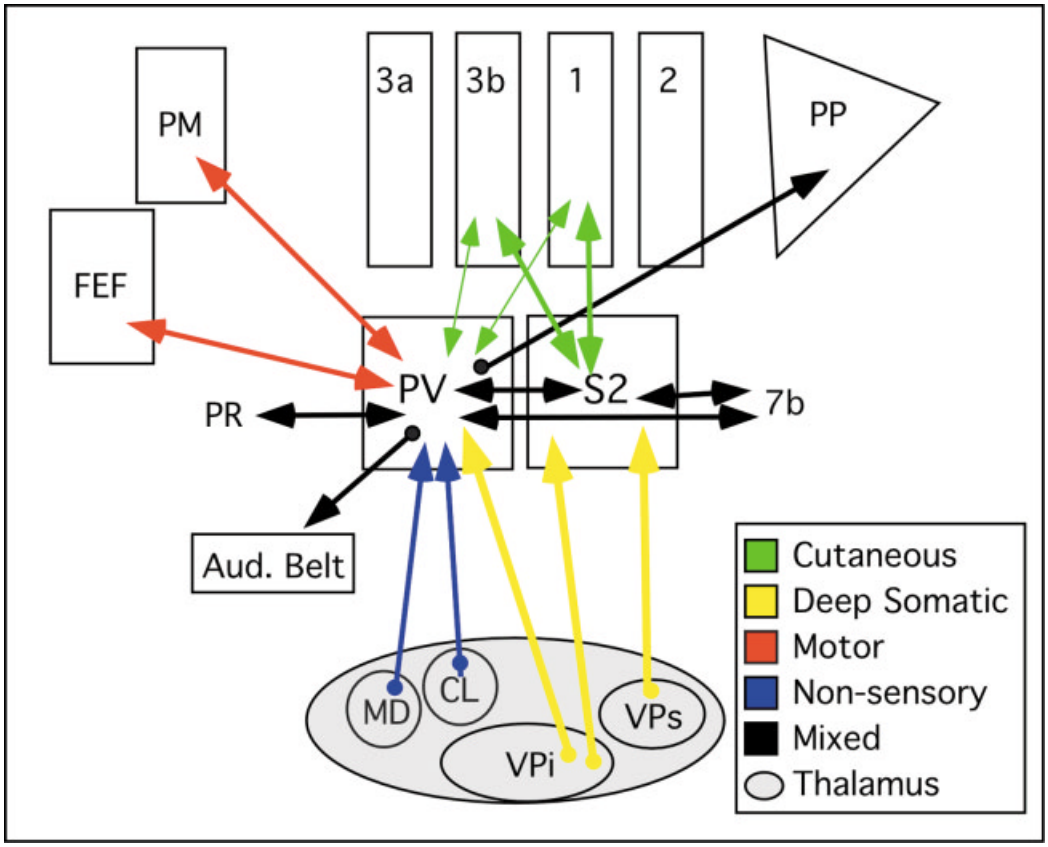


Fig. 11. A summary of cortical connections of S2 and PV observed in the present investigation and a related study of thalamic connections (Disbrow et al., 2002). PV receives several different types of inputs from both the cortex and the thalamus. Inputs from deep receptors such as muscle spindles and Golgi tendon organs arise from the inferior and superior division of the ventral posterior nucleus (VPi and VPs, respectively; Disbrow et al., 2002). PV also receives cutaneous inputs from cortical areas 3b and 1 and is interconnected with motor areas such as the frontal eye field and premotor cortex. Finally, PV has access to nonsensory inputs from the MD and CL of the thalamus. The connections of S2 from the thalamus are restricted to nuclei processing deep inputs and from cortical areas processing cutaneous inputs. Note that, rather than two separate "streams," somatosensory cortex appears to be organized into several overlapping networks. Modality of input (as depicted by different color arrows) is assumed based on receptive field properties of neurons described in previous studies of thalamic nuclei and cortical fields (Nelson et al., 1980; Robinson and Burton, 1980a,b; Dykes et al., 1981; Jones et al., 1982; Krubitzer et al., 1995; Preuss et al., 1996; Rizzolatti et al., 2002). Other conventions as in Figure 1; for abbreviations, see list.

In a previous study of connections in macaque monkeys in which the injection sites in S2 were electrophysiologically identified (Friedman and Murray, 1986), the results were similar to those in the current investigation in that connections with 3b, 1, and 7b were identified. However, the pattern of connections reported in this previous study was more broadly distributed and included areas PR, 3a, 2, 5, Ri, and portions of Ig. We believe that the discrepancies between this previous study and the present investigation may be due to differences in the definition of S2 in each study. Examination of the region of cortex injected in the Friedman and Murray (1986) study indicates that the area identified as S2 actually incorporates S2, PV, and portions of VS and 7b as described in the current study.

While there are other studies in which the connections of S2 were investigated in macaque monkeys (e.g., Jones and Powell, 1969a,b; Vogt and Pandya, 1978; Cipolloni and Pandya, 1999), these studies were done before the complex organization of the lateral sulcus was appreciated, and injections or lesions were large (sometimes including almost the entire upper bank of the LS) and probably encompassed more than a single field. Thus, direct comparisons between the present investigation and these previous studies are problematic.

Despite some of the differences in the present investigation and other connection studies in which S2 and PV have been electrophysiologically identified, all studies report that S2 and PV are interconnected with cortical fields that process cutaneous and proprioceptive inputs, with motor areas, and with other sensory areas, such as posterior parietal and auditory belt regions. Furthermore, a recent study of thalamic connections of S2 and PV in the macaque (Disbrow et al., 2002) indicates that these fields have connections with nuclei in the thalamus involved in processing proprioceptive input such as VPi and VPs, as well as with nonsensory nuclei such as CL and divisions of MD which are often associated with prefrontal and orbitofrontal cortex as well as with the vestibular system (Fig. 11; see Disbrow et al., 2002, for further discussion).

The "what" vs. "where" hypothesis

To a large extent, the interpretation of anatomical and electrophysiological results associated with studies of sensory cortex is influenced by our understanding of the visual cortex. For instance, in the visual system, there is support for the hypothesis that two largely separate, parallel processing streams exist that are associated with object recognition and visuospatial abilities. This idea originated from an elegant series of studies in macaque monkeys performed by Mishkin and colleagues (see Ungerleider and Mishkin, 1982 for review). In these experiments, lesions placed in ventral extrastriate cortical areas resulted in deficits in visual discriminations of hue, brightness, and shape as well as visual memory. Lesions placed in dorsal extrastriate visual areas resulted in deficits in visuospatial abilities. These two separate information streams—one related to object recognition (the ventral stream), and the other related to spatial perception (the dorsal stream)—have been termed the "what" and "where" streams, respectively.

Although recent evidence suggests that this dual processing stream model may be an oversimplification (e.g., Merigan and Maunsell, 1993; Gegenfurtner et al., 1994; Dobkins and Albright, 1994; Seidemann et al., 1999), this hypothesis still strongly influences the study of the visual and other sensory systems (e.g., see Mishkin, 1979; Ungerleider and Mishkin, 1982; Rauschecker, 1998). For instance, in the analogous model of the somatosensory system, it has been proposed that tactile information is initially processed in S1, sent to S2, and in turn to insular and limbic cortex of the temporal pole. This corticolimbic processing network is proposed to be similar to the ventral stream of processing or the "what" pathway in the visual cortex (Mishkin, 1979; Murray and Mishkin, 1984). In contrast, projections from S1 to other anterior parietal fields (such as areas 3a and 2), which in turn project to posterior parietal fields (areas 5, 7a, and 7b), are thought to be involved in processing information that results in movements toward objects (see Goodale, 2001, for review). This pathway is believed to be analogous to the "where" stream in visual cortex.

There is a large body of evidence that supports the idea that S2 is part of the "what" pathway. For example, despite the lack of consistency in the delineation of S2, it is clear that this region of cortex is involved in object identification and recognition, as well as the somatic and motor integration necessary for these tasks. Studies of single units in monkeys have shown that the S2 region is involved in the perception of texture (e.g., Jiang et al., 1997; Pruett et al., 2000), and lesions to this region result in impaired discrimination of texture and shape (Murray and Mishkin, 1984). In humans, activation of S2 and surrounding cortex has been reported in response to roughness and length discrimination (Ledberg et al., 1995; Binkofski et al., 1999a), hardness discrimination (Servos et al., 2001), as well as during active touch of gratings (Sinclair and Burton; 1993) and the manipulation of complex objects (Binkofski et al., 1999a,b).

The S2 region also plays a role in tactile–motor integration necessary for object exploration. In the macaque monkey, S2 and PV receive input predominantly from deep receptors of the skin, muscle, and joints (Friedman and Murray, 1986; Disbrow et al., 2002). In humans, the S2 region is active during passive finger movement (Xiang et al., 1997), electrically induced movement (Kakigi et al., 1997), and movement imagery (Kakigi et al., 1997). Furthermore, responses are enhanced during combined tactile and motor stimulation (Huttunen et al., 1996; Forss and Jousmaki, 1998; Lin et al., 2000; Hinkley et al., 2001). Thus, both tactile discrimination and the motor control necessary to manipulate objects appear to be processed by S2 and surrounding cortical fields.

Posterior parietal cortex, on the other hand, is involved in the generation of a body-centered frame of reference for directed reaching into extrapersonal space and sensory motor integration necessary for visually guided reaching and grasping in both human and nonhuman primates (Hyvaerinen and Poranen, 1974; Mountcastle et al., 1975; Faillenot et al., 1997; Kertzman et al., 1997; Binkofski et al., 1998; Jancke et al., 2001; for reviews, see Sakata and Taira, 1994; Kalaska et al., 1997; Culham and Kanwisher, 2001; Andersen and Buneo, 2002; Cohen and Andersen, 2002). In fact, the posterior parietal cortex is considered part of the "dorsal stream" or "where" pathway of the visual system as well (Ungerleider and Mishkin, 1982; Goodale and Milner, 1992).

However, as in the visual system, the "what" and "where" dual pathway model may be an oversimplification. Although more data regarding connections of posterior parietal and lateral sulcus regions are needed to elucidate these pathways, the anatomical results of the current study and previous studies (Friedman and Murray, 1986; Krubitzer and Kaas, 1990; Disbrow et al., 2002; Qi et al., 2002) indicate that S2 and PV are not solely involved in tactile recognition, since their cortical and subcortical connection patterns are with fields and nuclei that process cutaneous, proprioceptive, motor, auditory, and visual inputs. In fact, PV has connections with posterior parietal cortex, which is hypothetically part of the "where" pathway (Mishkin, 1979; Fig. 11) and which is known to be involved in reaching and grasping. There is also evidence that premotor cortex, which has connections with PV, is involved in similar functions (e.g., Binkofski et al., 1999a,b; for review see Rizzolatti et al., 2002). Furthermore, there is emerging evidence that posterior parietal cortex plays an important role specifically in object perception in human (Binkofski et al., 1999a,b; Bodegard et al., 2001; see Culham and Kanwisher, 2001, for review) and nonhuman primates (Murata et al., 2000).

If the somatosensory system were organized in a manner consistent with that of the visual system, one would expect to see a stronger segregation of connectivity between proposed ventral and dorsal streams. Rather, our data, in conjunction with previous electrophysiological, neuroanatomical, and functional imaging studies cited above, suggest that somatosensory fields in the lateral sulcus are part of several largely overlapping networks (Fig. 11). One network, composed of S2, 3b, and 1, is involved in detecting where and when an object acts upon the body. This network plays a role in processing the location of stimuli on the skin and may also be involved in texture discrimination, which requires the integration of precise tactile inputs over time. Our data also indicate that S2 and PV, along with posterior parietal cortex and premotor cortex, are part of a network involved in visually guided reaching, grasping, and tactile object perception, or how the body acts upon objects. Finally, S2 and PV are part of a network that includes the subdivisions of the mediodorsal nucleus of the thalamus, MDp and CL (Dis-

brow et al., 2002), and prefrontal cortex (present study), suggesting a role in tasks that are not specific to a particular sensory system. These networks are necessary for object acquisition, exploration, and ultimately identification.

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