

# Synthesis of Multiwhisker-Receptive Fields in Subcortical Stations of the Vibrissa System

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**Timofeeva, Elena, Philippe Lavallée, Dominique Arsenault, and Martin Deschênes.** Synthesis of multiwhisker-receptive fields in subcortical stations of the vibrissa system. *J Neurophysiol* 91: 1510–1515, 2004. First published December 10, 2003; 10.1152/jn.01109.2003. This study addresses the origins of multiwhisker-receptive fields of neurons in the thalamic ventral posterior medial (VPM) nucleus of the rat. We sought to determine whether multiwhisker-receptive field synthesis occurs in VPM through convergent projections from the principalis (PrV) and interpolaris (SpVi) nuclei, or in PrV by intersubnuclear projections from the spinal trigeminal complex. We tested these hypotheses by recording whisker-evoked responses in PrV and VPM before and after electrolytic lesion of the SpVi in lightly anesthetized rats. Before the lesion PrV cells responded, on average, to  $3.2 \pm 1.2$  whiskers but responsiveness was reduced to  $1.07 \pm 0.31$  whisker after the lesion. A similar reduction of receptive field size was observed in VPM, where neurons responded, on average, to  $2.94 \pm 0.95$  whiskers before the lesion and to  $1.05 \pm 0.22$  whisker after the lesion. Thus one can conclude that intersubnuclear projections mediate surround whisker-receptive fields in PrV, and therefore in VPM. However, it has previously been shown that parasagittal brain stem transection, which severed ascending projections from SpVi, but left intersubnuclear connections intact, rendered VPM cells monowhisker responsive. We wondered whether midline brain stem lesion modified receptive field properties in SpVi. In normal rats SpVi cells responded, on average, to  $7.52 \pm 4.25$  whiskers, but responsiveness was dramatically reduced to  $1.47 \pm 1.07$  whisker after the lesion. Together these results indicate that the synthesis of surround receptive fields in subcortical stations relies almost exclusively on intersubnuclear projections from the spinal trigeminal complex to the PrV.

## INTRODUCTION

The vibrissal system of rodents consists of 2 main ascending pathways: 1) a lemniscal pathway that arises from the principal trigeminal nucleus (PrV), transits through the barreloids of the ventral posterior medial nucleus of the thalamus (VPM), and terminates in the granular zone of the cortical barrel field; and 2) a paralemniscal pathway that arises from the interpolar division of the spinal trigeminal complex (SpVi), transits through the posterior group of the thalamus, and terminates in the dysgranular zone of the barrel field. In the brain stem these parallel streams of information processing are not totally isolated from each other, in that the PrV receives abundant projections from the spinal complex (see the wiring diagram of Fig. 1A). Yet, the contribution of intersubnuclear projections to receptive field properties in the PrV remains unknown.

There is now general consensus that in lightly anesthetized animals cells forming the lemniscal pathway strongly respond

to the deflection of one whisker (the principal whisker) and more weakly to that of 1–5 surrounding whiskers (Armstrong-James and Callahan 1991; Chiaia et al. 1991b; Diamond et al. 1992; Friedberg et al. 1999; Minnery and Simons 2003; Minnery et al. 2003; Nicolelis and Chapin 1994; Simons and Carvell 1989), whereas cells in the paralemniscal pathway are equally well driven by the motion of several whiskers (Chiaia et al. 1991b; Diamond et al. 1992; Jacquin et al. 1986, 1989; Veinante et al. 2000; Woolston et al. 1982). In VPM responses to surrounding whiskers are strongly depressed by deep anesthesia, which reduces receptive field sizes to the principal whisker (Armstrong-James and Callahan 1991; Friedberg et al. 1999). Similarly, SpVi lesion was reported to reduce the receptive field of VPM cells to a single whisker (Friedberg et al. 1999; Lee et al. 1994), without respect to the state of anesthesia (Friedberg et al. 1999). In that latter study it was also shown that parasagittal brain stem transection, which severed crossed ascending projections from the SpVi, rendered VPM cells monowhisker responsive. On the basis of these results it was proposed, after others (Armstrong-James and Callahan 1991; Lee et al. 1994; Rhoades et al. 1987), that multiwhisker-receptive field synthesis occurs within VPM through the convergence of PrV and SpVi projections. This proposal was supported by earlier tract-tracing studies in which large injections of wheat germ horseradish peroxidase were used to demonstrate overlapping PrV and SpVi projections in VPM (Chiaia et al. 1991a; Peschanski 1984).

However, later anatomical studies that reexamined trigeminothalamic projections by means of various anterograde tracers (cholera toxin, *Phaseolus vulgaris* leucoagglutinin, biotinylated dextran) rather suggested that PrV and SpVi project to nonoverlapping regions within VPM (Veinante et al. 2000; Williams et al. 1994). In light of these latter studies, it appeared unlikely that SpVi inputs alone could account for the widespread presence of multiwhisker-receptive fields in VPM. As an alternative hypothesis it was proposed that multiwhisker-receptive field synthesis might occur in the PrV (Minnery and Simons 2003; Varga et al. 2002) through intersubnuclear projections from the spinal trigeminal complex (SpV; Jacquin et al. 1990). Yet, this hypothesis was hardly reconcilable with the demonstration that parasagittal brain stem sections, which left intersubnuclear connections intact, reduced the receptive field of VPM cells to a single whisker (Friedberg et al. 1999). It had never been shown, however, that after that type of lesion SpVi cells still responded to whisker deflection as in normal rats.

In the present study we recorded whisker-evoked responses

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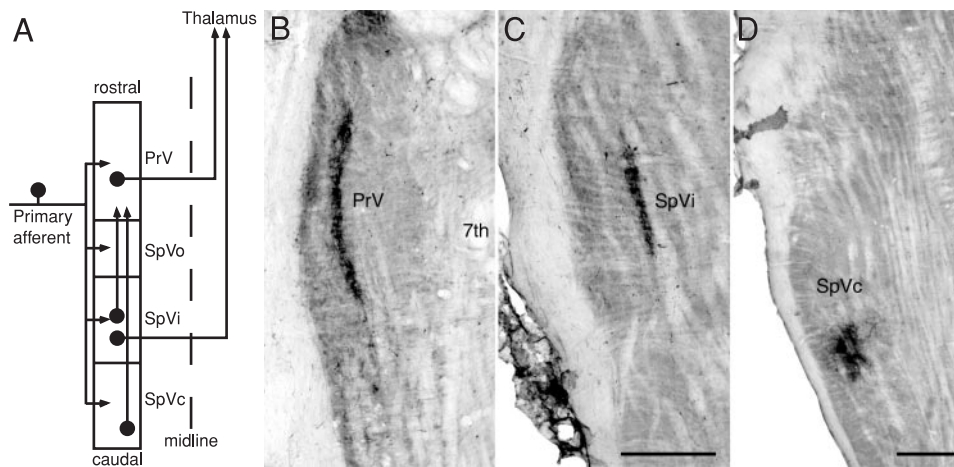


FIG. 1. Interconnections between vibrissa responsive regions in the brain stem trigeminal complex. Wiring diagram in *A* summarizes anatomical features relevant to the present study. Vibrissa primary afferents distribute several clusters of terminations in each division of the trigeminal complex; the main stream of vibrissa information to ventroposterior medial nucleus (VPM) arises from the principal trigeminal nucleus (PrV) and spinal trigeminal complex (SPVi); intersubnuclear projections to the PrV arise principally from the SpVi and SpVc. Latter projections are illustrated in the horizontal brain stem sections shown in *B–D*. An iontophoretic injection of biotinylated dextran into the caudalis nucleus (*D*) led to a columnar pattern of anterograde labeling across the whole trigeminal complex. Note that intersubnuclear axons travel through the trigeminal complex (*B, C*) to reach the PrV. Scale bars: 500  $\mu\text{m}$ ; same scale in *B* and *C*.

in the PrV and VPM before and after electrolytic lesion of the SpVi in lightly anesthetized rats. We also examined how SpVi cells respond to whisker stimulation before and after midline brain stem lesions. Altogether results show that the synthesis of surround receptive fields in subcortical relay stations relies almost exclusively on intersubnuclear projections from the SpV to the PrV.

## METHODS

### Animal preparation

Experiments were carried out in 18 male rats (Sprague Dawley, 250–300 g) in accordance with federally prescribed animal care and use guidelines. Rats were initially anesthetized with pentobarbital (50 mg/kg), supplemented as needed by a small amount of xylazine (1 mg/kg), and the left facial nerve was cut. The nape of the neck and resected tissue were infiltrated with a long-lasting local anesthetics (Marcaine 1%). Throughout the experiment the animal breathed freely, and body temperature was maintained at 37.5°C with a thermostatically controlled heating pad. During the recording sessions animals frequently displayed spontaneous twitches of the right whiskers and briskly reacted to a moderate pinch of the hindlimb, but otherwise remained motionless, indicating that they did not experience any discomfort. Electroencephalograms (recorded in 2 rats) displayed spindles and a dominance of 5- to 7-Hz activity. Together, these signs are indicative of a light anesthesia stage (stage III-2; Friedberg et al. 1999). An additional dose of anesthetics (ketamine/xylazine, 20/0.5 mg/kg) was given when small-amplitude whisking motion of the right whiskers was noticed.

### Recordings and brain stem lesions

Glass micropipettes (1  $\mu\text{m}$ ) filled with potassium acetate (0.5 M) were used to record single units in the PrV and VPM before and after lesion of the SpVi in the same animals. Signals were amplified, band-pass filtered (150 Hz–3 kHz), sampled at 20 kHz, and stored on hard disks for off-line analysis. An unilateral electrolytic lesion of the SpVi was made with a tungsten electrode (tip diameter  $\sim$  200  $\mu\text{m}$ , deinsulated over 500  $\mu\text{m}$ ). The electrode was lowered through the cerebellum (12 mm behind the bregma, 3.2 mm lateral to the midline;

Paxinos and Watson 1986) until the floor of the brain stem was reached. Then the electrode was retracted in steps of 500  $\mu\text{m}$ , and DC current (3 mA, 4 s) was applied at 4 depths. At the end of the recording sessions animals were perfused under deep anesthesia with saline followed by a solution of 4% paraformaldehyde and 0.5% glutaraldehyde in phosphate buffer (0.1 M, pH 7.4). The brain stem was coronally cut at 70  $\mu\text{m}$ , and the extent of the lesion was visualized after processing sections for cytochrome oxidase histochemistry.

In another series of experiments single interpolaris units were recorded in normal rats and in rats after midline brain stem lesion. Electrolytic lesions were made 11–13 mm behind the bregma (Paxinos and Watson 1986) by passing DC current (2 mA, 3 s) through a tungsten electrode at 4 depths spaced by 500  $\mu\text{m}$  (deepest lesioned site,  $-10$  mm). After the recording session, rats were perfused as described above, and the extent of the lesion was assessed after processing horizontal brain stem sections for cytochrome oxidase histochemistry.

### Whisker stimulation

The receptive field size of the units was determined by manual whisker deflection under a dissecting microscope. Because in lightly anesthetized rats central neurons respond to several whiskers, it was found impractical to further assess receptive field sizes by means of controlled deflection of individual whiskers. In the context of the present study the important issue was rather to ascertain whether cells identified as single-whisker responsive by manual deflection indeed responded to a single whisker. This test was carried out in a subset of cells by using air-jet stimuli to simultaneously deflect a large number of vibrissae. First, the responsive whisker was cut at 2 cm from the pad, and a peristimulus time histogram (PSTH) was built by compiling 20 responses (bin width, 2 ms) to air-jet stimuli. Then, the principal whisker was inserted into a 2-mm glass capillary, and a second PSTH was compiled. The capillary gently pressed against the pad to completely mask the principal whisker. Air jets were generated by a Picospritzer (General Valve, Brookshire, TX) connected to a broken micropipette (tip diameter  $\sim$  200  $\mu\text{m}$ ). The delay between the command voltage and the actual motion of the vibrissae was measured by placing a piezoelectric film (Measurement Specialties, Fairfield, NJ) at the same distance from the tip of the micropipette. This delay ( $\sim$  13 ms) was subtracted from the recordings to build PSTHs of

sensory-evoked responses. Data analysis was carried out with the Neuroexplorer (Plexon, Dallas, TX) and Excel (Microsoft, Redmond, WA) softwares.

Anatomical data were obtained from previous experiments in which biotinylated dextran (BDA) was used to map projections from the SpV to the thalamus (see Veinante et al. 2000 for methodological information).

## RESULTS

### Projections from the SpV to the PrV

Previous tract-tracing studies have shown that most inter-subnuclear projections to PrV arise from the interopolaris and caudalis divisions of the SPV (Jacquin et al. 1990). Fewer projections were seen to arise from the oralis division. Inter-subnuclear axons travel in deep bundles within the trigeminal complex, although some may also ascend through the trigeminal spinal tract. The former route is clearly depicted in the photomicrographs of Fig. 1, B–D, which show the columnar, barrelette-like pattern of projections after a BDA injection in the whisker-responsive region of the caudalis nucleus. Similar columns of projections were observed after BDA injections in the SpVi, suggesting that primary afferent and intersubnuclear axons overlap in their regions of termination (see also Jacquin et al. 1990). Therefore lesions made in the rostral pole of the SpVi should prevent the activation of PrV cells by intersubnuclear projections after sensory stimulation.

### Receptive field size before and after SPV lesion

In our recording conditions spontaneous activities in the PrV and VPM were low (<2 Hz) and consisted of a mixture of single spikes (in the PrV and VPM) and bursts (in the VPM). The low level of spontaneous activity, likely ascribable to facial nerve cut, allowed us to clearly identify evoked responses both from the computer display and the sound monitor.

As previously reported, in unlesioned animals the receptive field of most PrV units was composed of one principal and 1–4 adjacent whiskers (Minnery and Simons 2003). Some units were equally well driven by the motion of several whiskers (>5). These units, which represent 15 and 7% of the samples in normal and lesioned rats, respectively, likely correspond to the large-size cells that have been classified as multiwhisker responsive in deeply anesthetized animals and principally project to the posterior group of the thalamus (Veinante and Deschênes 1999). If one excludes latter units, PrV cells responded, on average, to  $3.2 \pm 1.2$  whiskers ( $n = 59$ ) before the lesion, but responsiveness was reduced to  $1.07 \pm 0.31$  whisker after the lesion ( $n = 76$ ) (Fig. 2, A and C). The reduction of receptive field size was also assessed by air-jet stimulation before and after masking the principal whisker (Fig. 2D). In normal rats population PSTH ( $n = 15$  units) to combined deflection of the principal and adjacent vibrissae exhibited a prominent peak at stimulus onset followed by a conspicuous decrease in the response. Adjacent whisker deflection alone produced a somewhat delayed ON response, the magnitude of which was about 25–30% of that evoked when principal and adjacent whiskers were codeflected. In contrast, after SpVi lesion population PSTHs ( $n = 18$  units) show that adjacent whisker responses were absent, and the decline in principal whisker response was markedly attenuated.

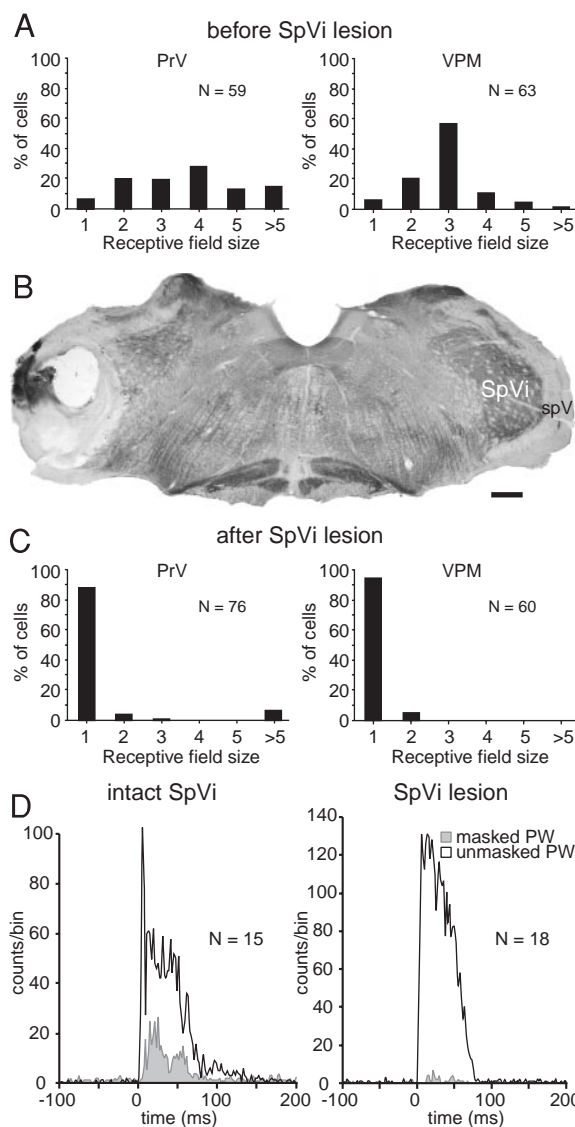


FIG. 2. Reduction of receptive field sizes of PrV and VPM cells after lesion of the SpVi. Histograms show for each cell group the distribution of receptive field sizes before (A) and after (C) the SpVi lesion shown in B (SpV, trigeminal spinal tract; scale bar in B, 500  $\mu$ m). Population *peristimulus time histograms* (PSTHs) in D show responses evoked by air-jet stimuli (duration, 50 ms) in PrV cells before and after SpVi lesion (white PSTHs, principal and adjacent whiskers were codeflected; gray PSTHs, principal whisker was masked within a glass capillary).

As expected, a similar reduction of receptive field size was observed in VPM, where neurons responded, on average, to  $2.94 \pm 0.95$  whiskers before the lesion ( $n = 63$ ) and to  $1.05 \pm 0.22$  whisker after the lesion ( $n = 60$ ) (Fig. 2, A and C). Histological controls confirmed that lesions completely destroyed the ventral portion of the SpVi (e.g., the whisker-responsive region; Henderson and Jacquin 1995), and a large part of the trigeminal tract (Fig. 2B). Lesions also involved the caudal part of the oralis nucleus but they never extended rostrally beyond the emergence of the facial nerve. Thus these results not only confirm that SpVi lesion reduces the receptive field size of VPM cells to a single whisker, but they also suggest that this reduction might be ascribable to that of receptive field sizes in the PrV after severing intersubnuclear connections.

### Effect of parasagittal brain stem transection on SpVi receptive fields

That intersubnuclear projections might mediate multiwhisker-receptive field synthesis has been disproved in a prior study in which it was shown that parasagittal brain stem transections that sever crossed ascending axons from the SpVi, but preserve intersubnuclear connections, rendered VPM cells single-whisker responsive (Friedberg et al. 1999). Yet, it remained possible that such a lesion had modified responses properties in the SpVi. We thus repeated these experiments and found that midline brain stem lesion dramatically reduce receptive field sizes in the SpVi. In normal rats ( $n = 2$ ) interparietal cells responded, on average, to  $7.52 \pm 4.25$  whiskers ( $n = 103$ ; Fig. 3A), whereas in lesioned rats ( $n = 3$ ) receptive field sizes were reduced to  $1.47 \pm 1.07$  whisker ( $n = 119$ ; Fig. 3B). As for PrV units single-whisker responsiveness was also assessed by air-jet stimulation before and after masking the effective whisker. Population PSTHs ( $n = 16$  units; Fig. 3D) show that in lesioned rats cell responses were completely obliterated after masking the responsive vibrissa. Histological controls revealed that brain stem lesions involved the core of the brain stem through which interparietal axons travel to reach the contralateral thalamus (Fig. 3C).

### DISCUSSION

The main finding of the present study is that multiwhisker-receptive field synthesis in the vibrissa lemniscal pathway occurs at the first relay station through intersubnuclear projections from the SpV to the PrV. Recordings from VPM in SpVi-lesioned rats demonstrate no further convergence at the thalamic level. In addition, our results show that midline brain stem lesion renders SpVi cells monowhisker responsive.

### Methodological considerations

In the present study a handheld probe was used to assess the receptive field size of neurons. This approach permits a rapid scan of receptive field by deflecting a number of single vibrissae in different directions, but it may yield to an underestimate of receptive field size, particularly when spontaneous activity is high and responses weak. However, in our recording conditions spontaneous activities were low, and considering the lack of responses to adjacent whisker after the lesions there was no point to attempt a quantitative assessment of receptive field by using controlled deflection of noneffective whiskers. Moreover, changes observed in the VPM were quantitatively similar to those previously reported by Friedberg et al. (1999) who used controlled whisker deflections. Finally and more important, single-whisker-receptive fields were also assessed in subsets of PrV and SpVi neurons by means of air-jet stimuli. Because air-jet stimuli represent a very effective way to drive cell discharges in the vibrissa system (Ahissar et al. 2000; Sosnik et al. 2001), the lack of responses when principal whisker was masked strongly supports results obtained after manual whisker deflection.

Although we did not use antidromic invasion to identify PrV cells that project to the VPM, it is known that these cells constitute the majority (70–90%) of neurons in the nucleus (Jacquin et al. 1988; Minnery and Simons 2003; Veinante and Deschênes 1999). A minority of PrV cells are of large size, and

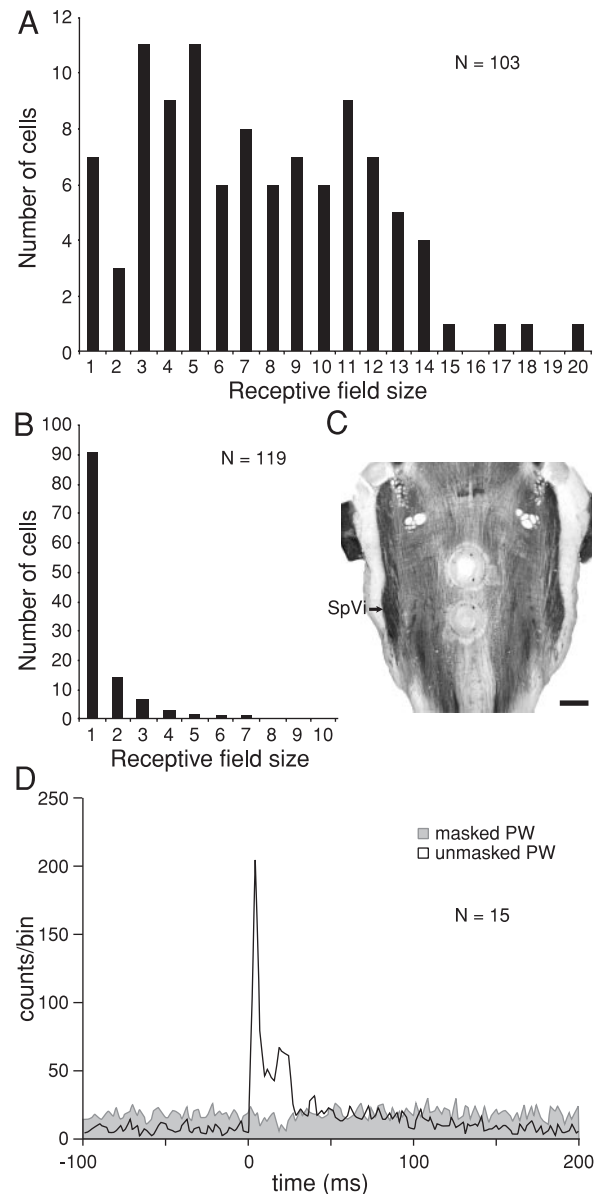


FIG. 3. Reduction of receptive field sizes in the SpVi after midline brain stem lesion. Histograms show the distribution of receptive field sizes before (A) and after (B) the lesion shown in C (scale bar, 1 mm). Population PSTHs in D show responses evoked by air-jet stimuli (duration, 30 ms) in lesioned rats before (white PSTH) and after (gray PSTH) inserting the effective whisker into a glass capillary.

project to the superior colliculus and posterior group (Bruce et al. 1987; Veinante and Deschênes 1999). The latter neurons demonstrate strong responsiveness to the deflection of multiple vibrissae even in deeply anesthetized animals. In lesioned rats we indeed found a small proportion of PrV cells (7%) that were still strongly driven by  $>5$  whiskers, and that likely belonged to the class of large-size neurons. That result was expected because the synthesis of multiwhisker-receptive field in these units is believed to result from their extensive dendritic arbors across the barrelettes (Jacquin et al. 1988; Veinante and Deschênes 1999).

Lesions of the spinal trigeminal complex were performed at the rostral level of the interparietal nucleus so as to interrupt most ascending intersubnuclear projections to the PrV. Inter-

subnuclear axons were shown to most frequently travel in the deep bundles within the trigeminal column and the trigeminal spinal tract (Jacquin et al. 1990; present study), 2 regions that have been severely damaged by the lesions. Remaining projections from the oralis nucleus were presumably intact, but had apparently little impact on receptive field sizes in the PrV, likely because of their low density and/or because of their low synaptic efficacy.

#### *Synthesis of multiwhisker-receptive fields*

Controversy about the origins of multiwhisker-receptive fields in VPM was partly fostered by conflicting results obtained in tract-tracing studies. Although all studies agreed on the fact that both PrV and SpVi axons innervate VPM, the main discrepancy related to whether interpolaris axons terminate in the barreloids. After massive injections of wheat germ horseradish peroxidase in either PrV or SpVi anterograde labeling was observed throughout VPM (Chiaia et al. 1991a; Peschanski 1984). In these studies, however, it was not clear whether SpVi injections did not actually spread rostrally into the PrV, and neither was it clear whether SpVi labeled profiles in dorsal VPM were axons “*de passage*” en route toward the posterior group. In the study by Chiaia et al. (1991a) much smaller injections of *Phaseolus vulgaris* leucoagglutinin were also used to map the terminal fields of SpVi axons in the thalamus. Interestingly, drawings in Fig. 11 of that paper clearly suggested that SpVi terminal fields were principally restricted to the ventral lateral and caudal parts of VPM. In later studies it was indeed found that PrV and SpVi axons project to nonoverlapping regions within VPM (Pierret et al. 2000; Veinante et al. 2000; Williams et al. 1994). Principalis axons innervate the dorsomedial portion of VPM and target the barreloids, whereas SpVi terminals are principally restricted to the ventral lateral portion of VPM, where barreloids taper into cytochrome oxidase-poor “tails” (Pierret et al. 2000; Williams et al. 1994). Thus in light of these results it appeared unlikely that SpVi inputs alone could account for the widespread presence of multiwhisker-receptive fields in the barreloids.

Confusion was also fostered by the assumption that under light anesthesia most PrV cells responded to a single whisker, as reported in earlier studies conducted in deeply anesthetized animals (Jacquin et al. 1988; Shipley 1974; Veinante and Deschênes 1999). Only recently was it shown that in fentanyl-sedated rats most VPM-projecting PrV units responded to several whiskers (Minnery and Simons 2003). This finding raised the possibility that multiwhisker-receptive field synthesis might occur in the PrV. Given that the PrV receives extensive intersubnuclear projections (Jacquin et al. 1990), and that none of the SpV neurons retrogradely labeled after tracer injections in the PrV are immunoreactive for GABA or GAD (Haring et al. 1990), it was proposed that intersubnuclear input could serve an excitatory role and represent a potential source of multiwhisker input to the PrV (Minnery and Simons 2003; Varga et al. 2002). The present results directly confirm this hypothesis, and thus provide an explanation for changes previously observed in the receptive field size of barreloid cells after lesion of the SpVi. The sensitivity of adjacent whisker responses to anesthetic conditions and the latency difference between adjacent and principal whisker responses in the PrV (~2.7 ms; Minnery and Simons 2003) are also consistent with

the notion that adjacent whisker input arrives to the PrV by a di- or oligosynaptic intersubnuclear pathway. For the moment the respective contribution of caudalis and interpolaris cells to receptive field structure in the PrV remains unknown, but anatomic and physiologic evidence clearly indicate that the synthesis of surround receptive fields in subcortical relay stations relies almost exclusively on intersubnuclear projections from the SpV to the PrV.

#### *Effect of midline brain stem lesion on SpVi neurons*

It appears unlikely that axotomy per se could explain the dramatic reduction of receptive field sizes in SpVi after midline brain stem lesion. Such lesions, like the parasagittal sections performed in the study by Friedberg et al. (1999), might have deprived spinal trigeminal circuitry of neuromodulatory inputs that are essential for the expression of multiwhisker responses. This raises the intriguing possibility that brain stem modulatory systems might control the efficacy of synaptic transmission between primary vibrissa afferents and their targets in the trigeminal nuclei.

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