Relationship Between Physiological Response Type (RA and SA) and Vibrissal Receptive Field of Neurons Within the Rat Trigeminal Ganglion

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Leiser, Steven C. and Karen A. Moxon. Relationship between physiological response type (RA and SA) and vibrissal receptive field of neurons within the rat trigeminal ganglion. J Neurophysiol 95: 3129–3145, 2006. First published January 18, 2006; doi:10.1152/jn.00157.2005. Cells within the trigeminal ganglion (Vg) encode all the information necessary for the rat to differentiate tactile stimuli, yet it is the least-studied component in the rodent trigeminal somatosensory system. For example, extensive anatomical and electrophysiological investigations have shown clear somatotopic organization in the higher levels of this system, including VPM thalamus and SI cortex, yet whether this conserved schema exists in the Vg is unknown. Moreover although there is recent interest in recording from vibrissae-responsive cells in the Vg, it is surprising to note that the locations of these cells have not even been clearly demarcated. To address this, we recorded extracellularly from 350 sensory-responsive Vg neurons in 35 Long-Evans rats. First, we determined three-dimensional locations of these cells and found a finer detail of somatotopy than previously reported. Cells innervating dorsal facial features, even within the whisker region, were more dorsal than midline and ventral features. We also show more cells with caudal than rostral whisker receptive fields (RF), similar to that found in VPM and SI. Next, for each vibrissal cell we determined its response type classified as either rapidly (RA) or slowly (SA) adapting. We examined the relationship between vibrissal RF and response type and demonstrate similar proportions of RA and SA cells responding to any whisker. These results suggest that if RA and SA cells encode distinct features of stimuli, as previously suggested, then at the basic physiological level each whisker has similar abilities to encode for such features.

INTRODUCTION

The somatotopic organization of the whisker somatosensory system in the rat brain is well known and has, in part, made it easy to study somatosensory processing in this system. The somatotopic organization that exists in structures from the brain stem trigeminal nuclei to the primary somatosensory cortex mirrors how the whiskers are arranged on the face. On the rats’ face, whiskers are arranged in rows, labeled A (most dorsal) to E (most ventral), and columns, labeled with numbers, the most caudal whiskers labeled Column 1 and increasing in number rostrally. At each level in the brain, cells with the same principal receptive field (whisker) are physically next to each other forming clusters of like-responding cells. Just as the whiskers on the face are arranged in rows and columns, these clusters of cells with the same RF are arranged in rows and columns with relative positions similar to the position of their receptive fields on the face. These clusters of vibrissae-responsive cells are known as barrelettes in the brain stem, barreloids in the thalamus, and barrels in the cortex. Moreover, within this somatotopy it has been shown that there is a “receptive field gradient” such that the larger, more caudal whiskers are represented by more cells than the rostral whiskers at each level in the brain including brain stem trigeminal nuclei (Ma 1991; Ma and Woolsey 1984), VPM thalamus (Van der Loos 1976), and layer IV of the somatosensory cortex (Chapin and Lin 1984; Killackey et al. 1995; Woolsey and Van der Loos 1970).

However, much less is known about the somatotopic organization of the cells whose axons innervate the receptors on the face, including the whiskers, and whose cell bodies lie outside the brain in the trigeminal ganglion (Vg). For example, the extent or area of the vibrissae-responsive cells within the Vg is unknown. Although it is likely that the somatotopic organization of the whisker somatosensory system of the brain originates with organization in the Vg, this is not known. Moreover, knowledge of the somatotopic organization of the Vg will help to better target appropriate groups of cells during physiological studies examining the response properties of these cells. Although little information is available about the somatotopy of cells within the ganglion, there is information about the relative position of the three branches of the trigeminal nerve that carry the axons of Vg cells from the nerve endings in the face to the brain stem. The mandibular branch (V3), which innervates the temporomandibular joint, mandibular skin, and lower lip, is situated posterior and lateral to both the ophthalmic branch (V1), which innervates supraorbital vibrissae, eye, and nose, and the maxillary branch (V2), which innervates the cheek, upper lip, and mystacial vibrissae (Waite and Tracey 1995) (see Fig. 1A). Therefore several important questions arise. Is there somatotopy at the level of the trigeminal ganglion? If so, is the somatotopic organization of cells within the Vg similar to the relative position of the branches of the trigeminal nerve? Or is there an additional level of somatotopy that mimics the arrangement of peripheral receptors on the face similar to that found centrally in the trigeminal system?

It has been suggested previously that a crude somatotopy exists in the ganglion (Arvidsson 1982; Beaudreau and Jerge 1968; Dorfl 1985; Erzurumlu and Jhaveri 1992; Gregg and Dixon 1973; Killackey et al. 1995; Klein et al. 1988; Lichtenstein et al. 1990; Maklad et al. 2004; Pali et al. 2000; Renehan et al. 1989; Rhoades et al. 1990; Scott and Atkinson 1999;
Waite and Tracey 1995; Zucker and Welker 1969). However, these reports are not without discrepancy. For example, cells whose receptive fields are in the eye region of the face were reported to be positioned in the ganglion either dorsomedially (Jacquin et al. 1986) or anteromedially (Waite and Tracey 1995) or just medially (Renehan et al. 1989). Likewise, cells with receptive fields that are in the lower lip and jaw region of the face have been placed posterolaterally (Waite and Tracey 1995) and dorsolaterally (Jacquin et al. 1986; Renehan et al. 1989). In addition to the somatotopic organization, Zucker and Welker (1969) suggested the possibility of a receptive field gradient (i.e., the number of cells with receptive fields in a whisker column increases from the smaller, more rostral whiskers, to the larger more caudal whiskers) by demonstrating that there are more cells with caudal whisker receptive fields compared with cells with rostral whisker receptive fields.

It is critical to clarify these findings of somatotopic organization in the Vg. This is important for understanding the relationship between the organization in the Vg and the organization of structures in the rest of the brain. Therefore the first goal of this study was to perform a complete mapping of the Vg to determine its somatotopic organization and the relative position of vibrissae-responsive cells compared with cells that respond to other facial features.
to a particular whisker is the same across whiskers on the mystacial pad or if a particular whisker group (row or column) have more SA than RA type cells.

The functional differences in encoding properties of RA and SA cells have been best clarified in the primate glabrous skin (i.e., fingertips) where research supports the idea that RA cells generally code for object location by detecting low-frequency skin motion while SA cells generally discriminate the object, coding for object form and texture (Blake et al. 1997a,b; Dodson et al. 1998; Goodwin and Wheat 2002, 2004; Johnson 2000, 2001; Johnson et al. 1995, 2000; LaMotte et al. 1998; Nishiura et al. 2000; Wheat and Goodwin 2000, 2001). In support of this, LaMotte et al. (1998) demonstrated that RA cells’ responses outlined the spatial locations and velocities of the indentations and retractions of skin surrounding the object rather than provide an outline of the shape itself, whereas SA cells provided a consistent spatial rate distribution that represented a third dimension of shape in addition to the outline of the shape in contact with the skin. These data, combined with evidence from more than three decades of psychophysical and neurophysiological research, support the idea that RA- and SA-type cells serve a distinctly different sensory function (for review, see Johnson et al. 2000).

The functional differences in encoding properties of RA and SA cells in the rat have not received such attention despite the fact that studies have demonstrated that the rodent trigeminal somatosensory system is comparable to the primate tactile system. For example, it has been shown that rats utilize their whiskers during active vibrissal palpation in a comparable manner to primates using their hands during active touch and further that the velocity of rat whisker motion across objects is within the range of velocities for optimal texture discrimination in primates (Carvell and Simons 1990). It has been shown through extracellular recordings of Vg cells in anesthetized rats that SA cells code for whisker position (amplitude) and RA cells code for whisker velocity or acceleration (Shoykhet et al. 2000). These results have prompted speculation that during rats’ awake exploratory behaviors RA and SA cells in the trigeminal ganglion, possibly acting in a comparable manner to RA and SA cells in the primate hand, encode for distinct aspects of the tactile stimuli. Perhaps, RA and SA cells code for object location and object form and texture, respectively. This remains to be tested.

Knowing the relationship between the distribution of RA and SA cells and the somatotopic organization of the Vg is important because it has also been proposed that caudal whiskers (whiskers in the most caudal columns) encode different tactual features of the environment than rostral whiskers (Carvell and Simons 1990; Harvey et al. 2001; Neimark et al. 2003; Sachdev et al. 2002) and their suggested roles can be related to the known functions of RA and SA cells. For example, it is possible that the rostral most whiskers gauge the location of the surface, whereas caudal whiskers discriminate its form and texture (Carvell and Simons 1990; Sachdev et al. 2002). Given these theories about whisker and cell-type function, one could hypothesize a correlation between a particular receptive field (whisker column) and a particular physiological response type (RA or SA). To fully address this hypothesis, we performed a map of the trigeminal ganglion to determine the extent of the vibrissae-responsive region and its somatotopic organization and, by sampling cells with receptive fields from each whisker, quantitatively assessed the distribution of RA- and SA-type cells across receptive fields.

**Methods**

To evaluate the somatotopic organization of the sensory-responsive cells recorded within the trigeminal ganglion, stereotaxic coordinates were recorded for each cell and electrophysiological techniques were used to identify the cells’ receptive field (RF). Using the RF, cells were grouped by their association with one of the three branches of the trigeminal nerves. Between-group comparisons of the stereotaxic coordinates along each of the three axes (mediolateral, anteroposterior, and dorsoventrally) were made and significant differences between the coordinates were evaluated (see Data analysis). If a cell was responsive to whisker stimulation, its single whisker RF and its cells type (either RA or SA) were determined. These vibrissae-responsive cells were then grouped into whisker row groups (rows A-E) or whisker column groups (columns 1–6). For the five row groups, between-group comparisons of the stereotaxic coordinates were made along each of the three axes. For the six column groups, between-group comparisons of the stereotaxic coordinates were made along the same three axes. Significant differences between the coordinates associated with each group were evaluated (see Data analysis). Finally, the presence of a RF gradient was determined by comparing the number of cells with caudal RFs to rostral RFs. Finally, the relationship between cell type (RA or SA) and RF (whisker) was studied (details in the following text).

**Animal preparation and recording**

To record the activity from single cells within the ganglion, animals were anesthetized and an electrode was lowered into the ganglion. A total of 35 adult male Long-Evans rats (230–280 g), obtained from Harlan (Indianapolis, IN), were used to complete this study. All procedures were approved by the Institutional Animal Care and Use Committee at Drexel University and followed National Institutes of Health Guidelines. Each animal was anesthetized by an intraperitoneal injection of pentobarbital sodium (45 mg/kg) and placed in a stereotaxic frame (Cartesian Research, Sandy, OR). A stereotaxic alignment system was used to ensure the rat’s skull was planar both dorsoventrally and mediolaterally. A large trephination used for the electrode insertions was created in the skull from 0 to 5 mm posterior and 0 to 4 mm lateral from bregma. Appropriate electrode design is critical for stable recordings (Moxon et al. 2004a,b). Because the ganglion is surrounded by dura and the electrode must exit the brain and penetrate a second dural layer surrounding the ganglion (Fig. 1B), a high-impedance (10 MΩ) epoxylite-insulated tungsten microelectrode with shank diameter of 250 μm, and a sharp tip (FHC#: UEWSGGSE011E, FHC, Bowdoinham ME) was used to ensure minimal resistance when penetrating these dural layers. A ground wire was then inserted superficially in a brain region distant from the electrode, secured to a screw on the skull and connected to the electrode headstage. Finally, the electrode was mounted vertically in the stereotaxic electrode manipulator, then digitally aligned to bregma, and moved above the craniotomy to predetermined coordinates (based on a grid, defined in the following text). The electrode was lowered to the surface of the dura and all ventral coordinates were considered relative to this position.

To identify the somatotopic organization of the trigeminal ganglion, a grid was defined to help select the position of electrode penetrations. The grid extended from 1.0 to 3.0 mm lateral from Bregma (2 mm mediolaterally) and 0.0 to 4.5 mm posterior to Bregma (4.5 mm rostrocaudally; Fig. 1, E and F). Resolution within the grid was 0.5 mm in the anteroposterior and mediolateral directions and intersections on the grid defined the electrode penetration sites. Serial electrode penetrations were made in each animal at randomly selected sites on the grid. Responses from the neurons recorded by the
electrode during each penetration were also used to define the boundary of the vibrissae-responsive region of the Vg. To identify the somatotopy within the vibrissae-responsive region, the resolution of the grid was reduced to 0.25-mm spacing between electrode penetrations within this vibrissae-responsive region of the Vg.

Recordings from trigeminal ganglion

Extracellular recordings were continuously performed while the electrode was lowered through the brain to the ganglion. Signals were amplified and band-pass filtered (154 Hz to 13 kHz) by conventional means (Chapin et al. 1999; Nicolelis and Chapin 1994; Nicolelis et al. 1995), and analog signals were digitized at 40 kHz (MAP System, Plexon, Dallas, TX), displayed on an oscilloscope, and played over an audio speaker as the electrode was advanced. The electrode was lowered at ~100 μm/min to 9.0 mm. In previous studies (Leiser and Moxon 2003; Schneider et al. 1981), Vg cells were not evident >9.0 mm. The electrode was then lowered more slowly (10 μm/min) until the first signs of sensory-responsive cells appeared. Because ganglion neurons are unresponsive unless their RF was stimulated, at each interval, the presence of a cell was checked by manually stimulating the whiskers and surrounding facial features with a cotton-tipped probe while monitoring the signal on the oscilloscope and through audio speakers. Facial areas included the eye and supraorbital vibrissae, nose, upper lip, and the lower lip and jaw. Occasionally, odontocereptive (tooth-responsive) units were encountered but not included. Each area, except the eye, received steady pressure to indent the skin regions. The eye was contacted gently but with sufficient pressure to drive responsive units; however, most “eye-responsive” units responded to stimulation of the supraorbital vibrissae. Each vibrissa, including the supraorbital, mystacial, and rostral microvibrissae, received multi-directional stimulation.

When the action potential of a single discriminable neuron was elicited in response to tactile-stimulation, the electrode advancement was halted, the coordinates noted and the RF identified in the following way. A wooden probe was moved across the skin and hairs (including whiskers), and the response of the cell was monitored on the oscilloscope and computer screen and through audio-speaker. The location relative to stimulation of the supraorbital vibrissae. Each vibrissa, including the supraorbital, mystacial, and rostral microvibrissae, received multi-directional stimulation.

To determine if there was a somatotopic organization of cells within the Vg, cells were grouped by their RFs. Branch groups were generated by grouping cells with axons that were associated with one of the three branches of the trigeminal nerve, the ophthalmic branch (V1), maxillary branch (V2), and mandibular branch (V3). Row and column groups were generated for cells with RFs in the vibrissae-responsive region by grouping cells with RFs in the same whisker row or column. For example, cells with RFs corresponding to the most dorsal whisker row (A1, A2, A3, A4, etc) were grouped into the A-row group. Likewise, when assessing columns, cells with RFs corresponding to the most caudal whisker column (A1, B1, C1, D1, and E1) made up the column 1 group. Refer to Fig. 1A for a description of how the whiskers are arranged on the face.

Recording from vibrissae-responsive region of the Vg

When a cell responded to gross stimulation of the whiskers on the mystacial pad, the coordinates were noted, its RF was identified, and a peristimulus time histogram (PSTH) was generated for later analysis to determine if the cell was an RA- or an SA-type cell (see Identifying RA and SA cells). To identify the cells’ RF and preferred direction, each whisker was deflected manually with a hand-held probe (Shoykhet et al. 2000; Simons 1983). PSTHs provide a robust means to study how neurons code for discrete sensory stimuli even on a single-trial basis (Foffani and Moxon 2004; Foffani et al. 2004, 2006; Tutunculer et al. 2005). To generate PSTHs, the firing activity during sustained whisker deflection was recorded. First, a template based on the spike amplitude and waveform shape (Fig. 1, C and D) was used to identify the neuron from background activity (Devibiss and Waterhouse 2002, 2004). Sustained whisker deflections were applied by moving the whisker ~5° in its preferred direction and maintaining the whisker in its preferred direction for 500 ms using a precision stepper motor (Gemini GV6) controlled by a servo drive (Parker Hannifin Corporation, Compumotor Division, Rohnert Park, CA). For comparison to other studies, this ramp-and-hold stimulus (rise time <1 ms) was similar to previous studies (i.e., 5° in preferred direction for 500 ms) (Shoykhet et al. 2000). Seventy-five to 100 stimuli were applied at a rate of 0.5 Hz. The spike waveforms were digitized (40 kHz) and, along with the spike times using commercial software (RASPUTIN, Plexon, Dallas, TX) to generate poststimulus time histograms (described in the following text). Our goal was to record only from the cell body of these cells, and the waveform shape (negatively going) suggests that these recording were indeed made from the cell body (Fig. 1 C and D). The motor was mounted onto an adapted Kopf stereotaxic frame so that it was held firmly in place but could be precisely positioned to deliver the stimulus to only one whisker. A pulse was sent to the MNAP hardware to indicate the onset of stimulation.

Histology

To determine if there was a somatotopic organization of cells within the Vg, cells were grouped by their RFs. Branch groups were generated by grouping cells with axons that were associated with one of the three branches of the trigeminal nerve, the ophthalmic branch (V1), maxillary branch (V2), and mandibular branch (V3). Row and column groups were generated for cells with RFs in the vibrissae-responsive region by grouping cells with RFs in the same whisker row or column. For example, cells with RFs corresponding to the most dorsal whisker row (A1, A2, A3, A4, etc) were grouped into the A-row group. Likewise, when assessing columns, cells with RFs corresponding to the most caudal whisker column (A1, B1, C1, D1, and E1) made up the column 1 group. Refer to Fig. 1A for a description of how the whiskers are arranged on the face.

Data analyses

To determine if there was a somatotopic organization of cells within the Vg, cells were grouped by their RFs. Branch groups were generated by grouping cells with axons that were associated with one of the three branches of the trigeminal nerve, the ophthalmic branch (V1), maxillary branch (V2), and mandibular branch (V3). Row and column groups were generated for cells with RFs in the vibrissae-responsive region by grouping cells with RFs in the same whisker row or column. For example, cells with RFs corresponding to the most dorsal whisker row (A1, A2, A3, A4, etc) were grouped into the A-row group. Likewise, when assessing columns, cells with RFs corresponding to the most caudal whisker column (A1, B1, C1, D1, and E1) made up the column 1 group. Refer to Fig. 1A for a description of how the whiskers are arranged on the face.

For each group, we first determine whether or not our samples were normally distributed using a Kolmogorov-Smirnov one-sample test (K-S test) and found that for all analyses, the data were not normally distributed. The analysis was applied to the recorded coordinates for all cells (n = 350) in each of the three coordinate planes, dorsoventral, mediolateral, and anteroposterior. The analysis was performed for branch groups and for whisker groups (row and columns) to determine if the samples were normally distributed. In each case, the K-S test was statistically significant (P < 0.05), hence the observed data did not follow the hypothesized (normal) distribution and non-parametric tests were chosen to assess statistical differences.

To determine if there were significant differences in the recorded coordinates between different branch groups or if there were significant differences in the recorded coordinates between the different
whisker groups in the dorsoventral, mediolateral, and anteroposterior coordinates, the nonparametric Kruskal-Wallis test was used. The test was applied separately for each of the three coordinate axes (dorsoventral, mediolateral, and anteroposterior). When the Kruskal-Wallis test was significant ($P < 0.05$), the Mann-Whitney $U$ test with the Bonferroni correction was used to evaluate which group’s coordinates were significantly different from each other in each of the three coordinate planes. The Bonferroni correction is a highly conservative approach and was applied because multiple Mann-Whitney $U$ tests were used. The idea behind the Bonferroni correction is that if one is testing $n$ independent hypotheses, one should use a significance level of $0.05/n$. So, for example, when comparing the locations of cells separated by whisker row (5 rows), there were 10 comparisons between groups (1 axis), thus the $P$ value is reduced to $0.05/10$, or $P = 0.005$, and only comparisons with a $P$ value less than this was considered significantly different. In the text, $P$ values corresponding to the Mann-Whitney $U$ test are reported unless otherwise stated.

To determine if there was a RF gradient [i.e., increasing number of cells with RFs in a whisker column (row) as one moves from the more rostral (dorsal) whiskers, to the more caudal (ventral) whiskers], the number of cells with the same whisker RFs was assessed by considering the number of cells corresponding to each individual whisker or whisker group (either row group or column group) as a sample and using the Mann-Whitney $U$ test with Bonferroni correction to assess significant differences between groups (see preceding text).

The percentage of cells responding to each whisker was then compared with the innervation of each whisker follicle to determine if there was a correlation. The percentage of axons for each whisker (data from Welker and Van der Loss 1986) was correlated to the percentage of cells with the same whisker RF determined from this study using the Gamma correlation with a $P < 0.05$ considered significant. The Gamma correlation statistic was preferred to the Spearman $R$ correlation because the fact that we were collecting multiple data points (i.e., sets of coordinates) from a single penetration meant that our coordinates were not completely independent from each other. Therefore our data contained tied observations and the Spearman $R$ would be inappropriate. However, in terms of the underlying assumptions and interpretation, Gamma is equivalent to Spearman $R$. All analyses were performed in Statistica (StatSoft, Tulsa, OK) unless otherwise noted.

Classification of RA and SA cells

All single vibrissae-responsive units were classified as either RA or SA. The method for classifying each cell as either an SA or RA was based on previous studies (Lichtenstein et al. 1990; Shoykhet et al. 2000, 2003) in which a neuron was classified as slowly adapting if activity during a well-defined period of sustained stimulation (the plateau response, defined next) significantly exceeded spontaneous activity of the cell (Mann-Whitney $U$, $P < 0.05$). All other neurons were classified as rapidly adapting. To evaluate the plateau response, for each cell, a standard peristimulus time histogram (PSTH) was produced by summing the number of spikes recorded during presentation of the 75–100 sustained whisker deflections using 100 1-ms bins before the stimulus and 600 1-ms bins after the stimulus. Time 0 represented time of stimulus onset. Spontaneous activity was measured from the standard PSTH during the 100-ms period immediately preceding stimulus onset. The plateau response was the activity of the cell measured from the standard PSTH between 200 and 300 ms poststimulus. Significant differences between spontaneous activity and the plateau response were evaluated using the nonparametric Mann-Whitney test because the activity of the cell (during both spontaneous and plateau periods) were not normally distributed. If a significant difference was found, the cell was classified as SA, otherwise it was classified as RA. However, to be consistent with previous studies, significant differences between spontaneous activity and the plateau response were also evaluated using a Student’s $t$-test (Lichtenstein et al. 1990; Shoykhet et al. 2000, 2003). No difference in the classification of cells (i.e., the number of RA or SA) was found between the two tests.

Cells were then grouped based on their classification as RA or SA, and their coordinates were compared to determine if these cells were positioned in the ganglion in separate locations or if they were intermingled. The posterior, lateral, and ventral coordinates of the RA cells were separately compared with the corresponding coordinates of the SA cells to evaluate any significant differences using the same procedure as in the preceding text (Mann-Whitney $U$ with Bonferroni correction, $P < 0.05$ as significant). Finally, the relationship between RF (whisker row or column) and cell type (RA or SA) was examined. The two proportions test (NCSS, Kaysville, UT) was used to test the differences between the ratio of RA- to SA-type cells for each whisker group (individual rows and columns) compared with the population ratio. The probability level (group versus population) determined by the Fisher’s exact test was used to test significance with a value of $P < 0.05$ considered significant.

RESULTS

Overall, we found a somatotopic organization within the Vg that extended within the vibrissae-responsive region. To examine the somatotopic organization of the trigeminal ganglion, 350 sensory-responsive cells were recorded from the trigeminal ganglion of 35 Long-Evans rats. The whisker region of the trigeminal ganglion was targeted, and therefore 240 of these cells responded to stimulation of one and only one whisker on the ipsilateral mystacial pad. The remaining 110 cells responded to tactile stimulation of facial regions adjacent to the mystacial pad and included 45 that responded to the region of the lower lip, 31 to the nose, 24 to the eye and supraorbital vibrissae, and 10 to the upper lip and microvibrissae. Three-dimensional stereotaxic coordinates were noted for each cell to assess the somatotopic organization of the Vg and identify the position and extent of the vibrissae-responsive cells within the Vg (Figs. 1F and 2).

Vibrissae-responsive cells ($n = 240$) were found medially in the Vg. The extent of the vibrissae-responsive cells spanned from 1.0 to 2.5 mm lateral (median = 2.0) and 0.5 to 4.5 mm posterior (median = 1.5) from bregma, with an average location of $2.03 \pm 0.44$ (SD) mm lateral and $1.66 \pm 0.79$ mm posterior from bregma ($n = 240$; Fig. 1F). The ventral locations of vibrissae-responsive cells within the Vg were between 9.10 and 10.95 mm (median = 10.0) with an average depth of $10.10 \pm 0.36$ mm ventral from the dural surface, yet the average depth of the first and last vibrissae-responsive cell across all penetrations was $9.81 \pm 0.29$ and $10.27 \pm 0.38$ mm ventrally from the dural surface, respectively (Table 1). The dorsal and ventral extent of vibrissae-responsive cells varied slightly in both the anteroposterior and mediolateral axes with the greatest difference between the most ventral and the most dorsal coordinates being in the most lateral locations (Table 1 and Fig. 2). These coordinates were verified histologically (refer to METHODS). To better understand the probability of encountering a particular RF in a given penetration, the number of times a RF was encountered for each penetration is provided in Fig. 2. One can see a trend for the dorsal to ventral organization and the medial to lateral separation of the cells associated with the ophthalmic or maxillary branches of the trigeminal nerve, which is discussed in detail next.

In summary, we show that the greatest possibility of encountering vibrissae-responsive cells in the Vg lies within an area of...
TABLE 1. Dorsal to ventral extent of vibrissae-responsive cells within the trigeminal ganglion

<table>
<thead>
<tr>
<th>A. First Vibrissa-Responsive Cell</th>
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<tbody>
<tr>
<td>LAT.</td>
<td>1.00</td>
</tr>
<tr>
<td>POST.</td>
<td>9.72</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>B. Last Vibrissa-Responsive Cell</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>LAT.</td>
<td>1.00</td>
</tr>
<tr>
<td>POST.</td>
<td>10.15</td>
</tr>
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</table>

| C. Range | 0.43 | 0.25 | 0.56 | 0.64 | 0.55 | 0.52 | 0.17 | 0.68 | 0.8 |

The dorsal to ventral extent of the vibrissae-responsive cells are shown for each penetration on the grid (see METHODS). A: most dorsal coordinate for which vibrissae-responsive cells were identified. B: most ventral coordinate for which vibrissae-responsive cells were identified. C: distance that vibrissae-responsive cells can be found along the dorsoventral axis, derived by subtracting, for each lateral and posterior coordinate the most dorsal coordinate from the most ventral coordinate.

~2 mm wide in the anteroposterior axis and 1.25 mm in the mediolateral axis, and, as one passes through the ganglion, from dorsal to ventral, vibrissae-responsive cells will be encountered for <1.85 mm.

Somatotopic organization consistent with organization of the branches of the trigeminal nerve

When cells were grouped by the branch of the trigeminal nerve that their axons are associated with, there were significant differences along all three coordinate axes (Kruskal Wallis, P < 0.001 for each of the 3 major axes, medial-lateral, anterior-posterior, and dorsal-ventral). The first major organizational trend was that cells with axons that are within the mandibular branch of the trigeminal nerve (V3—lower jaw) were situated more posterolaterally than the cells with axons that are within either the ophthalmic (V1—eye region) or maxillary (V2—nose, upper jaw, whiskers) branches. The second major organizational trend was that as one passes through the ganglion from dorsal to ventral cells innervating the more dorsal facial features (V1) are encountered first, followed by midline features (V2) and finally ventral facial features (V3).

When examining the position of cells within the Vg along the mediolateral axis and the anteroposterior axis in detail, several of these trends were significant. Cells with axons that are within the mandibular branch of the trigeminal nerve (V3—lower jaw) were significantly more lateral and more posterior in the Vg than cells with axons that are within either the ophthalmic (V1—eye region) or maxillary (V2—nose, upper jaw, whiskers) branches. The second major organizational trend was that cells within the trigeminal ganglion were found in similar lateral and posterior coordinates (Fig. 3A, Mann-Whitney U, P < 0.001, for both). Cells responding to features innervated by the ophthalmic (V1) and maxillary (V2) branches of the trigeminal nerve were found in similar lateral and posterior coordinates (Fig. 3A, Mann-Whitney U, P = 0.59 and 0.73, respectively). Therefore along the mediolateral and anteroposterior axes, the somatotopic organization of cells within the Vg was consistent with the relative position of their axons within the trigeminal nerve.

The significant differences observed in the mediolateral direction for cells associated with the different branches of the trigeminal nerve were also observed for subgroups of cells with the same RF. For example, cells that responded to stimulation of the lower lip and whose axons reside in the mandibular branch of the trigeminal nerve were significantly more lateral than cells responding to the vibrissae (Mann-Whitney U, P < 0.001), whose axons reside in the maxillary branch. Lower-lip cells were also significantly more lateral than cells responding to either the eye or nose (Mann-Whitney U, P < 0.001) the axons of which reside in the ophthalmic branch of the trigeminal nerve (Fig. 3B). Thus there is a distinct medial-lateral separation of cells whose axons are in the mandibular branch from cells with axons that are in the ophthalmic or maxillary branches of the trigeminal nerve.

The significant differences observed in the anterior-posterior direction for cells associated with the different branches of the trigeminal nerve were also observed for subgroups of cells with the same RF. For example, the lower-lip-responsive cells were significantly more posterior than eye-responsive cells and more posterior than both vibrissae- and upper-lip-responsive cells (Mann-Whitney U, P < 0.001; Fig. 3B). These differences show a division along the anterior-posterior axis separating cells within the Vg the axons of which lie in the mandibular branch from cells whose axons lie in ophthalmic and maxillary branches.

The second major organizational trend was that cells innervating the more dorsal facial features (i.e., the eye; V1) were encountered more dorsally, whereas the cells innervating the ventral facial features (i.e., the lower lip; V3) were found more ventrally, and cells innervating the midline facial features (i.e.,
the nose, whiskers, and upper lip; V2) were found in between.

Eye-responsive cells (V1—ophthalmic branch) were found significantly more dorsal than both lower-lip-responsive cells (V3—mandibular) and vibrissae-responsive cells (V2—maxillary; Mann-Whitney U, P < 0.001; Fig. 3, C and D). As a group, although only the position of the eye-responsive cells was significantly more dorsal than cells responding to the lower lip, a dorsoventral alignment of cells that matches the dorsoventral location of their RF on the face was found. In fact, the first cells typically encountered during an electrode penetration through the Vg responded to the skin surrounding the eye and supraorbital vibrissae. This dorsal to ventral somatotopy observed throughout the Vg was consistent with the dorsal to ventral position of the trigeminal nerves innervating the ganglion and extended to the vibrissae-responsive cells associated with the maxillary branch of the trigeminal nerve, as examined in the following text.

To show the probability of encountering a particular RF for a given set of penetration coordinates (mediolateral and anteroposterior), the preceding findings were converted into a contour plot (Fig. 4). Therefore for example, if one was most interested in locating vibrissae-responsive cells, penetrations between 1.0 and 2.0 mm posterior and 2.0 and 2.5 mm lateral would be used (Fig. 4).

Cells within the vibrissae-responsive region of the Vg demonstrated a dorsal-to-ventral somatotopy

To assess the somatotopic organization of cells within the vibrissae-responsive region of the trigeminal ganglion, these cells were grouped into their respective whisker column and row, and the stereotaxic coordinates of each group were compared. The main result was that there was no significant
FIG. 4. Probability of encountering a receptive field within the trigeminal ganglion. Contour plots showing the probability of finding cells with a particular receptive field. For all plots, the posterior position relative to bregma is along the x axis (0–4.5 mm posterior), and the lateral position relative to bregma is along the y axis (1.0–3.5 mm posterior). The color coding is unique for each plot and presents the probability distribution of finding the receptive field at any particular location. For example, vibrissae-responsive cells (C) are most likely to be found between 1.0 and 2.5 mm posterior and 1.5 and 3.0 mm lateral to bregma. A: eye responsive cells; B: nose-responsive cells; C: vibrissae-responsive cells; D: upper-lip-responsive cells; E: lower-lip-responsive cells. Dorsal to ventral coordinates are not shown.
difference in the locations of cells along any of the axes when they were grouped by columns, but there were significant differences when cells were grouped by rows. When cells were grouped by columns, cells that responded to whiskers in the most rostral columns (columns 5 and 6) were found anteromedially (Fig. 5A) and ventrally (Fig. 5B) compared with cells that responded to caudal whiskers (column 1), but none of these differences were significant (Kruskal-Wallis $P = 0.30$ mediolateral, and $P = 0.42$ anteroposterior, and $P = 0.06$ dorsoventral). To further test the possibility of columnar somatotopic organization, cells were further grouped into rostral and caudal whiskers, but no differences were found. Finally, organization within animals was examined. Animals were most likely to demonstrate a trend of transitioning from columns 1 to 5 (caudal to rostral) as the position in the ganglion moved from more anterior to more posterior (4 of 6 animals, Table 2) and also exhibited a trend of transitioning from columns 1 to 5 as the position in the ganglion moved from more dorsal to more ventral (7 of 16 animals, Table 2), but there was no consistent trend along the mediolateral axis. Therefore a weak somatotopy within the vibrissae-responsive region of the Vg. A dorsoventral somatotopy of vibrissae-responsive cells that matches the placement of their receptive field on the face was found. A and B: there was no significant difference in the locations of cells grouped by column in either the lateral (A, y axis) or posterior (A and B, x axis) coordinate or along the dorsoventral axis (B, y axis). There was also no significant differences in the locations of cells grouped by row in either the lateral (C, y axis) or posterior (C and D, x axis) coordinate. However, there was a significant difference between the ventral locations (D, y axis) of the cells and their respective row. When cells were grouped by their responses to dorsal whiskers (rows A and B, $n = 86$) and ventral whiskers (rows D and E, $n = 62$), dorsal whisker cells were significantly more dorsal than ventral whisker cells (black line with asterisk, Mann-Whitney $U$, $P = 0.007$). Plotted are the mean locations of cells (center boxes) and SDs (radial arms). Straddler vibrissae, not included on this graph (see text), had a mean location of $1.54 \pm 0.7$ mm posterior, $1.94 \pm 0.3$ mm lateral and $10.06 \pm 0.32$ mm ventral from dural surface.

### TABLE 2. Within-animal trends of somatotopic organization for the vibrissae-responsive cells

<table>
<thead>
<tr>
<th>A. Anterior → Posterior</th>
<th>No. of animals</th>
<th>A row → E row</th>
<th>E row → A row</th>
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<table>
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<tr>
<th>B. Medial → Lateral</th>
<th>No. of animals</th>
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<th>E row → A row</th>
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<table>
<thead>
<tr>
<th>C. Dorsal → Ventral</th>
<th>No. of animals</th>
<th>A row → E row</th>
<th>E row → A row</th>
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<td>Grouped by column</td>
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<td>7</td>
<td>4</td>
<td>5</td>
</tr>
</tbody>
</table>

Trends within each animal were examined to determine if there was any somatotopic organization that was lost by averaging across animals. The 1st column lists whether cells where grouped by row or column. The 2nd column lists the number of animals for which vibrissae-responsive cells were found in more than one penetration along the axis studied. The 3rd column lists the number of animals that had trends along the direction indicated for that group (A: anterior to posterior; B: medial to lateral; and C: dorsal to ventral). Column 4 list the number of animals that had a trend in the opposite direction. The last column lists the number of animals that showed no trend.
topic organization for the whisker columns may exist along the anteroposterior or dorsoventral axis within the ganglion. There was a substantial somatotopic organization of cells within the ganglion when they were grouped by whisker row. Despite no significant differences between the posterior or lateral locations of the cells (Kruskal-Wallis ANOVA, $P = 0.18$ and $P = 0.72$, respectively; Fig. 5C), even when organization within individual animals was examined (Table 2), there was a significant difference in the ventral locations of the cells (Kruskal-Wallis ANOVA, $P < 0.05$; Fig. 5D). Cells responding to the most dorsal whiskers (rows A and B, $n = 86$) were significantly more dorsal than cells responding to the most ventral whiskers (rows D and E, $n = 62$; Mann-Whitney $U$, $P = 0.007$). This was confirmed by examining the organization within individual animals where 14 of 17 animals showed this same dorsal to ventral organization (Table 2). Thus the dorsoventral somatotopy seen for the gross anatomy above (refer to Fig. 3, B and D) is maintained within the vibrissae-responsive region of the Vg.

More cells responded to larger, caudal whiskers than the smaller rostral whiskers

While each whisker row was equally represented in the sample of cells, there were significantly more cells with caudal whisker RFs than cells with rostral whisker RFs. This was determined by grouping cells by their RF (whisker) into row groups (cells with RFs in the same row) and column groups (cells with RFs in the same column) in our sample of vibrissae-responsive cells ($n = 240$; Fig. 6, A and B). When cells with RFs that were in the same row were grouped, each row was equally represented, and there were no significant difference

![Fig. 6. Rostrocaudal innervation gradient of vibrissae-responsive cells in the Vg. We recorded 240 vibrissae-responsive cells and ≥2 cells from each whisker on the mystacial pad (A and B). B: number of recorded units for each whisker is given as a percent relative to the total number of vibrissae-responsive cells. This chart allows visualization of the receptive field gradient (see text). Cells are arranged by row (color coded) and presented clockwise in orientation from dorsal, A row, to ventral, E row. Numbers inside the pinwheel are column numbers and are presented clockwise in orientation from caudal, column 1, to rostral, column 5. Straddler vibrissae are placed in between rows. C and D: total number of cells for each whisker row (C) or column (D) was relatively the same; however, a significant difference between the numbers of cells in each whisker column was seen (D). The number of cells for each whisker in column 1 was significantly greater than the number of cells for each whisker in columns 4 and 5–6, and the number of cells for the Straddler vibrissae was significantly greater than the number of cells in columns 5–6 (asterisked black lines, Mann-Whitney $U$, $P < 0.01$). Although there was no other significant differences, a trend of increasing cell numbers can be seen progressing from the smaller, more rostral whiskers to the larger, more caudal whiskers. Also presented are the ratio of SA (light gray) to RA (dark gray) cells innervating each whisker row (C) or column (D). Although there was some variability in the ratio of SA- to RA-type cells innervating each whisker row or column, there was no significant difference between the ratio of SA to RA-type cells of any whisker row or column compared with the population ratio (58% SA, 42% RA, 2 proportions test, $P > 0.05$). Black lines with asterisks stretch between groups that were significantly different from each other (Mann-Whitney $U$ test, $P < 0.01$ as stated in the preceding text).
between the numbers of cells with RFs in on whisker row compared with the number of cells with RFs in any other whisker row (Fig. 6C) (Kruskal-Wallis ANOVA, $P = 0.42$). Conversely, when cells were grouped by columns, there were significantly more cells responsive to caudal whiskers than rostral whiskers (Kruskal-Wallis ANOVA, $P = 0.015$; Fig. 6D). Therefore the composition of the different trigeminal somatosensory regions of the brain having more cells with caudal whiskers RFs than rostral whisker RFs is also present in the trigeminal ganglion.

Furthermore, a significant trend was observed such that as one moves from the more rostral whiskers toward the more caudal whiskers, each successive whisker column is represented by more cells. On a column-by-column basis, the number of cells with RFs that were in column 1, the most caudal column, were significantly greater than the number of cells the RFs of which were in column 4, a column in the middle (Mann-Whitney $U$, $P = 0.01$), and the number of cells the RFs of which were in columns 5 and 6, combined, the most rostral columns (Mann-Whitney $U$, $P = 0.01$; $n = 5$ whiskers for each column group). Likewise, the number of cells with RFs in the straddler vibrissae, more caudal than column 1, were significantly greater than the number of cells with RFs in columns 5 and 6 combined (Mann-Whitney $U$, $P = 0.01$, $n = 4$ and 5 whiskers, respectively). We define this phenomenon of increasing number of cells with RFs in a column when progressing from the smaller, more rostral whiskers to the larger, more caudal whiskers as a RF gradient. This trend or RF gradient was significant ($\Gamma = -0.58$, $P < 0.001$; Fig. 6D). Therefore the larger, more caudal whiskers have more cells available to process information than the smaller, more rostral whiskers.

This RF gradient describing the greater representation of caudal whiskers than rostral whiskers by cells in the Vg is consistent with a previous study reporting the number of axons innervating each whisker follicle (Welker and Van der Loos 1986). When the percentage of cells responding to stimulation of each whisker was compared with the percentage of axons innervating each whisker, the same “pipe-organ” pattern reported by Welker and Van der Loos was observed for the cells in the Vg (Fig. 7A). In fact, the number of cells recorded for a particular whisker observed in our study correlated significantly with the number of axons innervating that whisker ($\Gamma = 0.51$, $P < 0.001$, straddler vibrissae not included because axon numbers were not reported; Fig. 7D). The comparison between cells and axons could be seen more clearly when they were grouped by the row or the column that they innervated. Therefore our data are in agreement with the innervation data that there are no differences in the number of axons innervating each row (Fig. 7B), but there are more axons innervating the caudal whiskers than the rostral whiskers (Fig. 7C).

**FIG. 7.** Receptive field gradient of vibrissae-responsive cells correlate to axonal innervation. The data reporting the number of axons innervating each whisker follicle [light gray, $r$, axon numbers from Welker and Van der Loos (1986)] was compared with the distribution of cells in our sample (dark gray) that responded to movement of that whisker. $A$: axon and cell numbers are plotted as a percentage of the total number of axons and cells observed, respectively. Note the distinct “pipe-organ” pattern first described by Welker and Van der Loos (1986). $B$ and $C$: this trend is not noted for whisker rows ($B$) but is clear for whisker columns ($C$). The larger, more caudal whiskers had more axons innervating their follicles and more cells recorded than the smaller, more rostral whiskers. $D$: number of cells recorded for a particular whisker, given as a percent (number of cells/total $n$) observed in our study correlated significantly with the relative axon numbers innervating that whisker [solid line, $R = 0.72$, $\Gamma = 0.51$, $P < 0.001$]. Individual whisker names replace points on the graph.
RA and SA cells equally distributed across both rows and columns

We next studied the location of RA and SA type cells within the vibrissae-responsive region of the Vg and their distribution among cells with different whisker RFs. The response properties of each of the 240 vibrissae-responsive cells to passive whisker deflection were evaluated and each cell was categorized as either SA or RA (see METHODS). Nearly 60% (58.3%, n = 140) of the vibrissae-responsive cells were classified as SA, whereas the remaining 41.7% (n = 100) were RA. This particular ratio of SA to RA cells has been documented before in the Vg yet its functional meaning is not known.

We first assessed whether SA and RA cells were found in different regions of the Vg. SA cells were found more anterior than the RA cells (P = 0.02), but there was no clear anatomical separation in the mediolateral (P = 0.08) or dorsoventral (P = 0.12) planes (P values from Mann-Whitney U). Because there was no difference in the anteroposterior direction of the distribution of cells with different RFs, it is not clear what the functional significance of this distribution of SA cells is.

Our second result shows that the RA and SA cells were equally distributed across both rows and columns. The ratio of SA to RA cells within each whisker group was compared with the population as a whole to determine if cells within a particular whisker group were more likely to be RA or SA type cells. There was no significant difference between the ratio of SA to RA cells within any whisker row (Fig. 6C) or column group (Fig. 6D) compared with the population ratio (2 proportions test, P > 0.05 for each), although there was some variability in the ratio of SA- to RA-type cells innervating each whisker row or column. Therefore it is unlikely that any computational differences associated with RA and SA cells can be exclusively associated with either caudal or rostral whiskers.

Discussion

There were three major results of this study. First, the Vg has a finer detail of somatotopy than previously reported, and the orientation of cells within the Vg replicates not only the innervation pattern of the trigeminal nerve branches but also the gross arrangement of facial features on the face. Second, there were more cells with caudal whisker receptive fields (RFs) than cells with rostral whisker RFs and a trend of increasing numbers of cells with RFs in the same column along the rostro-caudal axis within the vibrissae-responsive region of the Vg, corresponding to the size of the whisker (which also increases from the smaller, more rostral whiskers to the large more caudal whiskers). Finally, there was a similar distribution of RA and SA cells across every whisker row and column, suggesting that each whisker is represented by a population of cells able to support the information encoded by both RA and SA cells.

Somatotopic organization of Vg

This study demonstrated a dorsoventral somatotopy of cells within the Vg consistent with previous studies (Beaudreau and Jerge 1968; Borsook et al. 2003; Erzurumlu and Jhaveri 1992; Gregg and Dixon 1973; Kerem et al. 2005; Waite and Tracey 1995) and a distinct orientation of cells in the Vg that replicates the arrangement of facial features on face. Cells innervating the more dorsal facial features (eye) were encountered more dorsally, ventral features (lower lip) more ventrally, and midline features (nose, whiskers, and upper lip) in between. Collectively our findings show that the rostral pole of the face is pointing posteromedially and tilted ventrally in the Vg. To illustrate this somatotopy, we provide a figure with an outline of a rat’s face overlaid onto the mean locations of our recorded cells (Fig. 8) and this figure superimposed onto a known grid of the rodent trigeminal ganglion (modified from Schneider et al. 1981).

Our results clarify earlier contradictions regarding the location of eye-responsive cells and cells responding to lower lip and jaw. For example, earlier studies agreed that cells whose RFs are in the eye region of the face are positioned medially, but Jacquin et al. (1986) suggested they were dorsomedially and Waite and Tracey (1995) suggested they were positioned anteromedially. From our results, it is now clear that both are correct, and these cells are positioned dorsally in the anteromedial ganglion. Furthermore, our data are in agreement with Waite and Tracey (1995) regarding cells with RFs that are in the lower lip or jaw region of the face and associated with the mandibular branch of the trigeminal nerve and demonstrate that they are positioned in the posterolateral region of the ganglion. However, we found these cells to be in the most ventral portion of the posterolateral region of the ganglion not dorsolaterally as suggested by Jacquin et al. (1986) and Renehan et al. (1989).

The dorsoventral somatotopy of facial features found in the Vg as a whole extended to the vibrissae-responsive cells the axons of which lie in the maxillary branch of the trigeminal nerve (V2). These vibrissae-responsive cells were found to be clustered in a clearly demarcated region medially within the Vg. Although, it has been suggested that the cells innervating the more dorsal whiskers (i.e., A and B rows) are situated medially in the Vg, whereas cells of ventral whiskers (i.e., D and E rows) lie laterally (Zucker and Welker 1969) and other authors have not disagreed with this statement (Arvidsson 1982; Jacquin et al. 1986; Lichtenstein et al. 1990; Renehan et al. 1989; Rhoades et al. 1990), this pattern was not observed in our study. Animals in our study were equally likely to show the more dorsal rows more medially (2 animals) as they were to show the more dorsal rows more laterally (2 animals). We therefore think the sampling protocol used by Zucker and Welker (1969) may have contributed to their conclusion. Interestingly, however, our data do support the conclusions that caudal whiskers tended to be more dorsal (Jacquin et al. 1986; Renehan et al. 1989; Zucker and Welker 1969). We further show that cells innervating dorsal whiskers were more dorsal than cells innervating ventral whiskers. Therefore somatotopic organization within the vibrissae-responsive region of the Vg mirrors the somatotopic organization of the Vg as a whole and grossly represents the arrangement of RFs on the face.

Our results support developmental theories suggesting that the arrangement of peripheral neurons may be a template for the design of central nuclei (Erzurumlu and Jhaveri 1992; Killackey et al. 1995; Scott and Atkinson 1999). We conclude this for two reasons. First, the dorsal to ventral somatotopic organization of the Vg observed in this study is inverted compared with the somatotopic organization of the trigeminal region of the brain stem, and second, the Vg and the brain stem rotate 180° relative to each other during development (Waite...
FIG. 8. Dorsoventral somatotopy of cells within the Vg. Our findings show a dorsoventral somatotopy of cells within the Vg. Cells innervating the more dorsal facial features (e.g., eye) were encountered more dorsally, ventral features (e.g., lower lip) more ventrally, and midline features (e.g., nose, whiskers, and upper lip) in between. Collectively our findings also show that the rostral pole of the face is pointing posteromedially and tilted ventrally in the Vg. To further illustrate our findings, an outline of a rat's face is overlaid onto the mean locations of our recorded cells. C–E: to relate our findings, we have also superimposed the position of this image onto a known grid of the rodent trigeminal ganglion [C and E, grid of Vg modified from Schneider et al. (1981); D, schematic of rat's face illustrating vibrissal receptive fields used to create image].
and Tracey 1995). During development, the somatotopy in the Vg is established before outgrowing axons have contacted their peripheral or central targets. At this time, the ganglion appears to rest on the brain stem in early head morphogenesis when the distance to travel out to the periphery and centrally to the brain stem is very small. These Vg cells then extend neurites known as pioneers both peripherally and centrally (Scott and Atkinson 1999). Finally, these structures rotate 180° relative to each other, producing, we suggest, the inverted relationship between the periphery and brain stem. Our results show that the somatotopic position of cells in the Vg grouped by trigeminal nerve branch is inverted from that found in the principle trigeminal nucleus (PrV), where cells with RFs that are innervated by the mandibular branch of the trigeminal nerve are situated dorsally, cells with RFs that are innervated by the ophthalmic branch are situated ventrally, and, finally, cells with RF that are innervated by the maxillary branch are situated in between (Waite and Tracey 1995). Given these developmental steps, if the Vg is a template for the organization of central structures, then the ganglion and brain stem should have similar, albeit inverted, somatotopy, which is clearly what we have found.

Receptive field gradient

Our result that there is a trend of increasing number of cells with vibrissal RFs along the rostrocaudal axis of the mystacial pad such that there are more cells with caudal whisker RFs than cells with rostral whisker RFs is consistent with the somatotopic organization of the central nuclei of the brain. This greater representation of cells with caudal whisker RFs compared with cells with rostral whisker RFs has been well-defined in layer IV of the somatosensory cortex (Killackey et al. 1995; Woolsey and Van der Loos 1970), VPM thalamus (Van der Loos 1976), and brain stem trigeminal nuclei (Ma 1991; Ma and Woolsey 1984) and demonstrated previously in the Vg with in a sample of cells (Zucker and Welker 1969). Moreover, the number of cells with RFs for each whisker follows a “pipe-organ” pattern similar to that found for the increasing numbers of axons innervating the caudal versus the rostral whisker follicles (Lee and Woolsey 1975; Welker and Van der Loos 1986). Finally the size of the follicles surrounding caudal whiskers is greater than the size of the follicles around rostral whiskers (Haidarliu and Ahissar 2001). We suggest that because the larger caudal whiskers have a greater follicular size, they have more receptors, and these receptors are supported by more cells, not strictly more axon collaterals per cell.

Structure-function relationship: correlation between RF and physiological response type

Our data suggest that there are more SA cells than RA cells within the Vg. Although many studies have reported the ratio of RA- and SA-type cells in the Vg (Chiaia et al. 1993, 1997; Gibson and Welker 1983a, b; Jacquin et al. 1986; Kyriazi et al. 1994; Lichtenstein et al. 1990; Minnery and Simons 2003; Minnery et al. 2003; Renahan et al. 1989; Shoykhet et al. 2000, 2003; Waite and Jacquin 1992; Waite and Tracey 1995; Zucker and Welker 1969), the proportions of cells identified in those previous studies cannot be taken as the ratio of each type to the total population because of sampling biases in their recording techniques. For example, certain studies have reported relatively low numbers of RA-type cells (Lichtenstein et al. 1990) by excluding cells having large-amplitude, high-velocity thresholds, which are typically RA, or by deliberately recording equal numbers to characterize both populations evenly (Kyriazi et al. 1994). Our goal was to record an unbiased sample from across the extent of the vibrissae-responsive region of the ganglion. Our findings were consistent with studies by Zucker and Welker (1969) and Chiaia et al. (1997) reporting ~60% of the cells as SA and the remaining 40% as RA, despite the differences in rat species.

To date, it is not known if this greater number of SA-type cells compared with the number of RA-type cells has any functional consequences. Cells in the primate associated with the glabrous skin of the hands can also be defined as either RA or SA type cells by their response to tactile stimuli. We suggest it may be possible to extend what is known about the function of these cells in the primate to better understand their function in the rat. In the primate glabrous skin, SA-type cells are likely encoding information about object discrimination (for review, see Johnson 2001). Therefore it may be possible that SA-type cells in the rat whisker follicle also function primarily for object discrimination. Therefore the larger proportion of SA-type cells may be necessary to support the complex array of discrimination tasks performed by the rat’s whiskers. This remains to be tested.

Because it is clear that rats use their mystacial vibrissae to locate and discriminate objects, an interesting question that arises is whether there is a correlation between the cell's vibrissal RF and the cells' response type. Namely could SA-type cells be more likely to have caudal whisker RFs, given that both have been implicated in object discrimination, whereas RA-type cells may be more likely to have rostral whisker RFs because both have been implicated in object localization. This, however, does not appear to be the case. In fact, although there was an increase in cells innervating the more caudal whiskers, the increase was not specific to one cell type (RA or SA) but rather consisted of a similar, proportional increase for both RA- and SA-type cells. Although different whiskers could be specialized for different tasks, this distribution of RA and SA cells across the vibrissal RFs suggests that each whisker has the ability to support a variety of functions, inherent to both RA and SA cells. Recent studies seem to support this idea (Hartmann et al. 2003; Harvey et al. 2001; Jones et al. 2004a, b; Krupa et al. 2001; Neimark et al. 2003; Szwed et al. 2003).

In conclusion, the somatotopic organization of cells within the Vg, including the vibrissae-responsive cells, mirrors the arrangement of features on the face and is reflective of the somatotopic organization in the brain. Because the Vg develops first, it is likely the template for subsequent somatotopic organization throughout the trigeminal somatosensory system. This study provides the most current map of positions of cells within the rodent trigeminal ganglion with respect to their RF and physiological response type, allowing researchers to extend what is known about the function of these cells in the primate to better understand their function in the rat. In the primate glabrous skin, SA-type cells are likely encoding information that both have the ability to support a variety of functions, inherent to both RA and SA cells. Recent studies seem to support this idea (Hartmann et al. 2003; Harvey et al. 2001; Jones et al. 2004a, b; Krupa et al. 2001; Neimark et al. 2003; Szwed et al. 2003).

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