Two-Dimensional Coincidence Detection in the Vibrissa/Barrel Field

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Rodgers, Krista M., Alexander M. Benison, and Daniel S. Barth. Two-dimensional coincidence detection in the vibrissa/barrel field. J Neurophysiol 96: 1981–1990, 2006. First published June 21, 2006; doi:10.1152/jn.00404.2006. Coincidence detection in visual and auditory cortex may also be critical for feature analysis in somatosensory cortex. We examined its role in the rat posteromedial barrel subfield (PMBSF) using high-resolution arrays of epipial electrodes. Five vibrissae, forming an arc, row, or diagonal, were simultaneously or asynchronously stimulated to simulate contact with a straight edge of different angles at natural whisking velocities. Results indicated supralinear responses for both slow-wave and fast oscillations (FOs, about 350 Hz) at intervibrissae delays <2 ms. FO represented the earliest and most precisely tuned response to coincident vibrissa displacement. There was little difference in the spatiotemporal pattern of slow-wave or FO responses in the row, arc, or diagonal. This equivalence of function suggests that the PMBSF may be capable of working as a two-dimensional integrative array, processing spatial features based on coincidence detection despite the direction that the vibrissae pass across an object.

INTRODUCTION

Spatiotemporally structured stimuli, such as a figure moving across the retina or a low-frequency sound arriving at the left and right cochlea at slightly different times, provide essential information about object presence, location, and in the case of vision, information about form, based solely on the timing with which subsections of the receptive surface are coincidentally excited (Carr 1993; Lee and Blake 1999; Usher and Donnelly 1998). In the visual system, temporal synchronization of neuronal responses between regions of retinotopically organized sensory cortex has been postulated as a fundamental mechanism by which salient stimulus features may be dynamically bound together (Engel et al. 1992; Singer 1993; Singer and Gray 1995) and has been demonstrated to occur with millisecond accuracy in the CNS (Konig et al. 1996; Singer et al. 1996). Temporal coincidence detection on a much finer time scale of microseconds occurs in the auditory cortex and is essential for coding intraaural time differences required for sound localization (Carr 1993).

Coincidence detection may also be critical for feature analysis in the somatosensory system (Roy and Alloway 2001). Perhaps the most attractive candidate for exploring this possibility is the rodent vibrissa system. The somatosensory system of rodents is dominated by afferent input from the vibrissae, which serve as a primary means of close range environmental exploration. Approximately half of the primary somatosensory cortex consists of an orderly array of cellular columns, or “barrels” (usually referred to as the posteromedial barrel subfield or PMBSF), in register with the macrorhynchosae on the contralateral face. As rats examine an object in the environment, they repeatedly whisk the vibrissae forward as a unified array, establishing rapid spatiotemporal patterns of contact (Sachdev et al. 2001) that presumably result in similarly rapid spatiotemporal patterns of neuronal activity within and between the barrels of the PMBSF. Although the rodent vibrissa system is thought to perform a number of complementary tasks, including texture discrimination (Andermann et al. 2004; Arabzadeh et al. 2004, 2005; Carvell and Simons 1990; GuImage-Robles et al. 1989; Neimark et al. 2003) and spatial sampling such as gap detection, distance discrimination, and head-centered orientation (Harris et al. 1999; Hutson and Masterson 1986; Krupa et al. 2001; Sachdev et al. 2000; Schiffman et al. 1970; Shuler et al. 2002; Vincent 1912), behavioral and physiological studies suggest that the macrorhynchosae may also provide information about object features such as edge orientation and shape (Benison et al. 2006; Carvell and Simons 1990; Harvey et al. 2001; Simons 1995).

Features extracted by whisking might be uniquely identified by coincident contact of multiple whiskers with an object as it sweeps across the two-dimensional vibrissa array. Such coincidence detection in the PMBSF would require a highly accurate temporal relationship between vibrissa displacement and cortical response, which has been clearly indicated by single-unit studies of single and multiple vibrissa stimulation (Ego-Stengel et al. 2005; Sachdev et al. 2001; Shimigi et al. 1999, 2000; Simons 1985; Simons and Carvell 1989). In addition, we recently demonstrated temporal fidelity in field potentials recorded with epipial electrode arrays placed on the surface of the PMBSF (Barth 2003; Benison et al. 2006). The precise timing of field potentials across the PMBSF permits classification and reconstruction of object orientation and shape based solely on submillisecond timing patterns in the barrels (Benison et al. 2006). Of particular interest are very fast oscillations (FOs, about 350 Hz) that accompany the classic field potential slow wave in somatosensory cortex (Barth 2003; Jones and Barth 1999a; Jones et al. 2000; Kandel and Buszaki 1997; Staba et al. 2003, 2004, 2005) because these have been shown to exhibit phase-sensitive interactions between barrels with submillisecond precision and exert a strong influence on the probability of cell firing (Barth 2003).

However, there were several limitations of our previous study of multivibrissa interactions (Benison et al. 2006) based mainly on the stimulus paradigm used. First, only five vibrissae aligned dorsosventrally (“arc”) were stimulated, providing no insight into how spatiotemporal information may be integrated between arcs. Second, the stimulus consisted of a straight edge rotating on a smooth drum. The vibrissae could not be placed...
individually on the drum to record their separate responses and then replaced in the same location as a group to examine multivibrissa responses. Thus we could not estimate supralinear and sublinear responses in this study because we could not obtain an accurate linear model for comparison (i.e., a model constructed from the linear combination of single vibrissa responses). Finally, slight misalignment of the vibrissae on the x-axis (axis of rotation) resulted in asynchronous contact even for upright edges (which should simultaneously strike an arc of vibrissae). This misalignment may have had the effect of obscuring the potential impact of simultaneous stimuli (coincidence detection) while at the same time potentially masking distinct phase-sensitive interactions of FO.

The purpose of the present study was to examine the possible role of coincidence detection in identifying stimulus features in the PMBSF. Stimuli consisted of precisely timed displacement of groups of five vibrissae aligned in an arc, rostrocaudally ("row"), or along a diagonal. The timing of vibrissa stimulation was under independent computer control and set to stimulate the vibrissae moving at a physiologically realistic speed and contacting a straight edge of various angular orientations, producing either simultaneous or varying degrees of asynchronous displacements. To identify preferred stimuli, we recorded population field potentials from the entire PMBSF with high-resolution arrays of epipially placed electrodes and examined possible supra- and sublinear responses as a function of simulated stimulus angle. FO and slow-wave responses were analyzed separately to obtain information about their potentially unique contribution to coincidence detection.

METHODS

Animals and surgery

All procedures were conducted within the guidelines established by the University of Colorado Institutional Animal Care and Use Committee. Adult male Sprague-Dawley rats (n = 4, 250–400 g) were anesthetized to surgical levels using an intraperitoneal injection of urethane (1.25 g/kg body weight) and a mixture of xylazine (14 mg/kg) and acepromazine (2.3 mg/kg). Animals were placed on a regulated heating pad to maintain normal body temperature (37°C). Anesthesia levels were maintained throughout the experiment so that the corneal and flexor withdrawal reflexes could barely be elicited. A unilateral craniotomy was performed over the right hemisphere extending from bregma to lambda and from the midsagittal suture to the lateral aspect of the temporal bone, exposing a wide region of the contralateral frontal bone, amplified (1,000), analog filtered (band-pass) or fast oscillatory (FO; 250- to 1,000-Hz digital band-pass) potentials were referenced to a silver ball electrode secured over the contralateral frontal bone, amplified (>1,000), analog filtered (band-pass cutoff = –6 dB at 1 to 3,000 Hz, rolloff = 5 dB/octave), and digitized at 10 kHz.

Stimulation

Vibrissae on the left mystacial pad were trimmed to 2 cm and displaced about 300 μm (0.1 ms in duration, 1-s interstimulus interval) by inserting them into the ends of 6-cm stainless steel hypodermic tubes attached to laboratory-built solenoids (Barth 2003; Jones and Barth 1999b). Prior calibration of vibrissa displacement produced by these solenoids revealed no notable afteroscillations at the latency or frequency of fast or slow evoked potential components reported here (Barth 2003). Three groups of five vibrissae were studied (Fig. 2), forming a single arc (A3–E3), diagonal (A1–E5), or row (C1–C5). Within each group, the timing of sequential pulses delivered to the five solenoids simulated a straight edge moving at 0.2 mm/ms, to approximate natural whisking velocities observed in behaving animals (Sachdev et al. 2001). Simulated angles for each group were referenced to 0°, which represented a straight edge simultaneously striking the five vibrissae in a direction perpendicular to their axis of orientation (i.e., moving in the caudal, dorsocaudal, or dorsal direction for the arc, diagonal, or row, respectively). The timing of sequential vibrissa displacement was computed to simulate angles of ±45, 30, 20, 10, 5, 1, and 0° in one experimental condition and angles of ±6, 5, 4, 3, 2, 1, and 0° in a second condition, to obtain finer spatial and temporal resolution. Because the velocity of the simulated straight edge was 0.2 mm/ms, this resulted in delays between adjacent vibrissae of 25, 14.4, 9.1, 4.4, 2.18, and 0.44 ms in the first condition and 2.63, 2.18, 1.75, 1.31, 0.87, and 0.44 ms in the second condition. For example, a +45° straight edge moving caudally through the arc of vibrissae was simulated by displacing vibrissa E3 first, followed at 25-ms intervals by D3, C3, B3, and A3. An opposite A3–E3 sequence simulated –45°. Lead vibrissae for positive angles in the diagonal and row were E5 and C5, respectively.

Evoked potential recording

Epipial maps of the vibrissa-evoked SEP (somatosensory-evoked potential) complex were recorded using a flat multichannel electrode array consisting of 64 silver wires arranged in a 8 × 8 grid (tip diameter: 100 μm; interelectrode spacing: 500 μm) covering a 3.5 × 3.5-mm area of the cortical surface in a single placement. Surface field potentials were referenced to a silver ball electrode secured over the contralateral frontal bone, amplified (>1,000), analog filtered (band-pass cutoff = –6 dB at 1 to 3,000 Hz, rolloff = 5 dB/octave), and digitized at 10 kHz.

Data collection and analysis

At the outset of each experiment, SEPs evoked by individually stimulating each of 25 macrovibrissae (arcs 1–5 and rows A–E) were averaged (n = 100; duration = 500 ms). Bicubic spline interpolated maps of the initial positive SEP deflection (Fig. 1C), representing the most focal response before icraptopical spread (Fig. 1B, inset), were computed for all 25 single vibrissa responses and the array positioned across animals. Average loci were used to construct a template of the PMBSF for subsequent illustration (Fig. 1, D and E).

For each vibrissa group (arc, diagonal, or row) and condition (±45 or ±6° angle ranges), 100 trials (500 ms) were randomly sampled at each of the 13 simulated angles and later sorted and averaged. Data were analyzed separately for the slow-wave (1- to 100-Hz digital band-pass) or fast oscillatory (FO; 250- to 1,000-Hz digital band-pass) components. Digital filtering was performed forward and backward in time to eliminate phase shifts using a second-order Butterworth response to minimize the possibility of ringing that could contaminate FO. Interpolated maps of root-mean-squared (RMS) power in the slow-wave or FO frequency bands were plotted as a function of simulated stimulus angle. A linear model of SEPs for each angle was also computed by summing the appropriately time-shifted SEPs (based on the sequential interval between delays used for simulation) obtained from the separate principal vibrissa for a given group (i.e., single vibrissa SEPs for A3–E3 during the arc condition). RMS power at each electrode was compared with the linear model and tested for significant supra- or sublinear responses using paired t-tests with significance set to P ≤ 0.05. RMS power within the slow-wave and FO frequency bands was also averaged across the electrode array and plotted as a function of stimulus angle. Because power consistently declined with deviations from 0° (simultaneous) stimulation, the angles at which power dropped to half-amplitude were determined for each condition and frequency band and tested for significant
RESULTS

The 25 macrovibrissae form a 5 × 5 array, with arcs typically labeled 1–5 on the caudorostral axis and rows labeled A–E on the dorsoventral axis (Fig. 1A). The somatotopic representation of these vibrissae in the contralateral PMBSF consists of a similar array of distinct cellular aggregates with a similar caudorostral organization of the vibrissa arcs but an inverted dorsoventral organization of the rows. The 8 × 8 epipial electrode array was consistently aligned to the PMBSF across animals using SEPs evoked by stimulating each of the 25 vibrissae separately. For example, stimulation of the C3 vibrissa (Fig. 1A, blue dot) evoked a typical positive/negative/positive slow wave of maximum amplitude at its corresponding barrel (Fig. 1B, labeled P1/N1/P2 in the inset to reflect the polarity and sequence of the temporal components). The earliest visually identifiable positive deflection at the rising phase of the P1 (Fig. 1B, inset) yielded the most focal interpolated amplitude maps (Fig. 1C) preceding intracortical spread. These maps were used to locate each barrel in the PMBSF based on position of maximum response. Loci of barrels within the PMBSF, determined from single-vibrissa SEPs, were averaged across animals (SE = 0.19 mm; n = 4) and used as a template for further illustration (Fig. 1, D and E).

Sequential stimulation of a vibrissa arc (A3–E3), starting with vibrissa A3 and an intervibrissa delay of 25 ms (simulating a straight edge at 45° from vertical and moving caudally at 0.2 mm/ms with a 5-mm intervibrissa separation on the rostrocaudal and dorsoventral axis), produced multiple slow waves in the SEP (Fig. 1D, blue traces). The earliest response recorded from an electrode near barrel A3 (Fig. 1Da, arrow) was followed by several additional lower-amplitude slow waves separated by the 25-ms intervibrissa stimulus interval. The SEP slow waves recorded near vibrissa D3 were largest in amplitude at the latency of D3 stimulation (Fig. 1Db, arrow).
but were also present in lower amplitude during preceding and subsequent vibrissa stimulation in the sequence. A notable feature of the asynchronous SEP was marked attenuation of sharp wave amplitude following response to the first (A3) vibrissa deflection (Fig. 1D, a and b). To quantify this attenuation, a linear model (Fig. 1D, red traces) was computed for comparison. The linear model consisted of the sum of appropriately time-shifted single-vibrissa SEPs (recorded separately for isolated deflections of vibrissae A3–E3). Only the initial slow wave produced by A3 matched the linear model (Fig. 1Da, "="). Subsequent slow waves throughout the array were attenuated to roughly 50% of the linear model (Fig. 1D, a and b, "—"). Simultaneous stimulation of vibrissae A3–E3, simulating an upright straight edge at 0° to the orientation of the arc, produced a simpler SEP morphology that was similar to the P1/N1/P2 slow wave evoked by single-vibrissa stimulation but
spread across the principal vibrissa barrels (Fig. 1E, blue traces). However, the evoked response still differed from the linear model (Fig. 1E, red traces). The initial P1 was typically sublinear (Fig. 1E, a and b, “−”), whereas the N1 and subsequent P2 were typically supralinear (Fig. 1E, a and b, “+”). Supralinear responses were particularly evident at electrode sites surrounding the principal vibrissae (Fig. 1E, c and d). Maps of slow-wave power, averaged across animals at all electrode sites during arc stimulation, indicated maximum responses with simultaneous (0°) or near-simultaneous (±1°) vibrissa deflections (Fig. 2A, top row). Significant supralinear responses (Fig. 2A, top row, white dots; P ≤ 0.05) occurred at electrode sites immediately surrounding areas of maximum response during simultaneous 0° stimulation and with 0.44-ms interbarrel delays simulating ±1°. Several electrodes near barrel E3 showed supralinear responses at interbarrel delays as long as 4.4 ms (+10°), although, at this and longer interbarrel delays extending to 25 ms (±45°), the predominant response was attenuated and typically sublinear (Fig. 2A, top row: black dots; P ≤ 0.05). Stimulation of the A1–E5 diagonal (Fig. 2A, middle row) and C1–C5 row (Fig. 2A, bottom row) yielded similar results, with a window of about ±0.4-ms interbarrel delay (±1°) where simultaneous and near-simultaneous stimulation produced maximum and usually supralinear responses at electrode sites on and flanking the principal barrels. Outside this window (±5–45° or ±2.18–25 ms), responses were considerably attenuated and sublinear at most sites. Stimulation simulating a straight edge ranging from −6 to +6° in 1° increments (±2.63-ms interbarrel delays in 0.44-ms increments) provided a more precise view of changes in sharp wave power with small changes in interbarrel delays (Fig. 2B). In all three stimulation conditions (arc, diagonal, and row), the largest slow-wave responses occurred during simultaneous stimulation (0°) and were supralinear in electrodes adjacent to the maximum response. Arc and diagonal stimulation (Fig. 2B, top and middle rows, respectively) also produced large and often supralinear responses at interbarrel delays of ±1.75 ms (diagonal) and 2.63 ms (arc) that corresponded to 4 and 6°, respectively. Responses during row stimulation differed in that supralinear responses were confined almost entirely to simultaneous (0°) stimulation with attenuation and sublinear responses becoming apparent at interbarrel delays of ±0.87–1.31 ms (±2–3°).

As depicted in the example of Fig. 1E, when supralinear responses were evoked, they were confined to the N1 and P2. In all animals, the P1 was either linear or sublinear. This effect is depicted again in Fig. 3A, displaying wideband (1–10,000 Hz) SEPs from an electrode site near barrel C3 during ±6° stimulation of the arc in one animal. In this example, the P1 was sublinear and the N1 was slightly supralinear at all angles. However, close examination of the P1 during simultaneous stimulation (0°) revealed small, high-frequency FOs superimposed on this component and on the falling limb of the N1 (Fig. 3C). In this example, FOs in the wideband trace consisted of slight rises and dips just preceding and following the crest of the P1 that were aligned with successive FO waves in the 250- to 1,000-Hz filtered trace (Fig. 3C, Composite). FO bursts of similar latency relative to the P1 were recorded in all animals, with an average period of 2.9 ± 0.3 ms (or 345 ± 38 Hz). Interverbarrel delays in the range of ±2.63 ms produced by ±6° stimulation in this example would be expected to bring FO out and then almost back into phase because the half-period (180° out of phase) was 1.45 ms. FOs did indeed demonstrate a marked phase sensitivity (Fig. 3B), with the largest and supralinear responses at 0° and +1° (0.44 ms), minimum responses at ±3–4° (±1.31–1.75 ms), and partial recovery of amplitude at ±6° (±2.63 ms). Full in-phase recovery would not be expected until a delay of 2.9 ms, which was not examined here.

Compared with the slow wave, averaged power maps of FOs indicated that they were consistently more confined to the principal barrels in all stimulation conditions (Fig. 2, C and D). During asynchronous stimulation at ±45° (Fig. 2C), FO amplitude dropped rapidly at angles of ±1° (interbarrel delays of ±0.44 ms) with supralinear responses (Fig. 2C, white dots; P ≤ 0.05) largely confined to this temporal window. As with the slow-wave, attenuated and sublinear responses predominated at angles > ±5° (2.18 ms; Fig. 2C; black dots; P ≤ 0.05). Similar to the example of Fig. 3, submillisecond phase sensitivity was apparent in the power maps when smaller 1° (0.44-ms) angular increments were simulated (Fig. 2D). The largest FO responses were evoked by 0° (simultaneous) and ±1° angles (±0.44 ms), reached a minimum at ±3–4° (±1.31–1.75 ms), and appeared to be recovering amplitude at ±6° (±2.63 ms). Supralinear responses were most prevalent during simultaneous or near-simultaneous stimulation (however, note +2 to +5° conditions during both arc and row stimulation, where supralinear responses appear to cluster around the earliest vibrissa contacted).

Power was averaged across all 64 electrodes in the array to simplify direct comparison of changes in FO and slow-wave amplitude as a function of simulated stimulus angle and interbarrel delay (Fig. 4). With a range of ±45° stimulation, FO displayed the steepest decline in power with increasing angle.
The total angular window widths (symmetrical about 0°) at which FO amplitude had dropped to half-peak amplitude were 5.59 ± 0.25, 6.91 ± 0.94, and 3.5 ± 0.1° for arc, diagonal, and row stimulation, respectively (Fig. 4A, light red traces). Half-amplitude angular windows for FO were significantly narrower for the row versus arc stimulation conditions (P = 0.011), and the grand average across conditions was 5.3 ± 0.2° (Fig. 4A, dark red trace). The half-amplitude angular window computed for the sharp wave was 19.3 ± 1, 17.45 ± 2, and 11.18 ± 0.71° for arc, diagonal, and row stimulation, respectively. Again, row stimulation produced a significantly smaller angular window than the arc (P = 0.002). The more rapid decline of FO with stimulation angle compared with the slow wave was significant across conditions (P < 0.00003) as it was for the separate arc, diagonal, and row conditions (P values of 0.005, 0.019, and 0.006, respectively).

Similar differences between FO and slow-wave amplitude were observed when finer 1° changes in stimulus angle were examined (Fig. 4B). Here, the half-amplitude angular width of FO (Fig. 4B, dark red trace) averaged 2.69 ± 0.06°, which was significantly smaller (P = 0.000015) than 6.33 ± 0.15° for the slow wave (Fig. 4B, dark blue trace). Angular widths of FO and slow wave for the arc, diagonal, and row stimulation conditions were 2.8 ± 0.12, 3.1 ± 0.22, 2.1 ± 0.19, and 6.5 ± 0.45, 7.3 ± 0.61, 5.1 ± 0.35, respectively, with FO (Fig. 4B, light red traces) significantly smaller than the slow wave (Fig. 4B, light blue traces) in each condition (P values of 0.007, 0.009, and 0.031, respectively). No significant differences in half-amplitude angle widths were observed between conditions within the FO or slow-wave frequency bands when examined separately. As in the example of Fig. 3, FO power appeared to reach a minimum in all animals at ±3–4° and begin to recover at ±6°. The spacing of interbarrel delays between the FO minima was close to the average FO period of 2.9 ms.

**DISCUSSION**

Sublinear responses, feedforward inhibition, and temporal integration

Temporal responses in somatosensory cortex is shaped largely by inhibition. Slow- or long-latency inhibition (Connors et al. 1988) corresponds to a long period (50–100 ms) of maximum response suppression in somatosensory cortex noted in paired stimulus paradigms (Gardner and Costanzo 1980;
The rapid decline of both FO and slow-wave power in the present study. Feedforward inhibition is also typically more widely distributed than excitation, consistent with the widespread suppression and significant sublinear responses observed for simulated stimulus angles $>\pm 10^\circ$ in the present results. Finally, recent evidence combining direct cortical responses to electrical stimulation with subsequent vibrissa stimulation suggests that intracortical inhibitory pathways play a minimal role in interbarrel-suppressive effects, and that either widespread thalamocortical feedforward inhibition or intrahalamic inhibition may be involved (Civillico and Contreras 2005, 2006). There is compelling evidence that rapid feedforward inhibition results from monosynaptic thalamocortical input to inhibitory interneurons, in tandem with excitatory input to the pyramidal cells, establishing a brief window of excitability before inhibitory suppression (Gabernet et al. 2005; Sun et al. 2006; Swadlow 2003, 2002). Such a narrow window of excitability would suggest that pyramidal cells are maximally responsive to closely timed excitatory inputs in that only these stimuli would be given a chance to bring cells to threshold. Supporting this conclusion are unit recordings indicating that regular spiking units (RSUs, probably pyramidal cells) show peak facilitation with simultaneous multivibrissa stimulation (Shimegi et al. 1999) and drop off rapidly in response amplitude with increases in intervibrissa delays greater than a couple of milliseconds, similar to the rapid decline of both FO and slow-wave power in the present study.

**Supralinear responses, excitation, and temporal integration**

Within the brief window of excitation imposed by feedforward inhibition, our data indicate that short intervibrissa delays ($<2$ ms) produce significant supralinear responses in wide areas of the PMBSF for both slow-wave and FO power measurements. These results are in agreement with a number of unit studies demonstrating response facilitation with closely timed stimuli (Ego-Stengel et al. 2005; Erchova et al. 2003; Ghazanfar and Nicolelis 1997; Shimegi et al. 1999, 2000). It is thus puzzling why several unit studies of the spatiotemporal dynamics of multivibrissa stimulation report a predominance of suppressive interactions even with short (0–5 ms) intervibrissa delays (Mirabella et al. 2001; Simons 1985; Simons and Carvell 1989). As noted by Simons and coworkers (Simons 1985), one explanation may be that the failure to find supralinear responses to simultaneous vibrissa deflections reflects a ceiling effect produced by occlusion of multiple inputs to maximally activated neural pools. In studies where multivibrissa stimulation at short intervals do not produce supralinear responses, there is usually a dramatic recovery from sublinearity with decreasing delay, approaching a linear or barely sublinear response with simultaneous stimuli (Mirabella et al. 2001; Simons 1985; Simons and Carvell 1989). This finding is consistent with increased excitation or less inhibition resulting from closely timed stimuli, even if the net effect is not a supralinear response.

We also reported a ceiling effect arising from maximum depolarization in field potential measurements of excitability cycles in the PMBSF (Barth and Di 1991). This may explain why the supralinear responses of the present data are almost exclusively recorded from electrodes surrounding the principal...
vibrissa barrels for a given stimulation condition (i.e., 0°; Fig. 2A). Responses from sites corresponding to the principal vibrissa barrels typically sum linearly (except, note Fig. 2C; 0°). Similar results, obtained from mapping studies of spatially distributed unit responses in the PMBSF, indicate supralinear summation only in the far surround of a neuron’s receptive field and rarely in the center (Ghazanfar and Nicolelis 1997). The largest supralinear responses are usually observed in cells that respond weakly or not at all to individual vibrissae but are robustly driven by combined stimulation, suggesting minimum single-vibrissa response levels are most effective for revealing supralinear multivibrissa effects (Ego-Stengel et al. 2005; Ghazanfar and Nicolelis 1997; Shimegi et al. 1999, 2000).

Interestingly, recent examination of intervibrissa interactions using voltage-sensitive dyes failed to find supralinear responses in the PMBSF to simultaneous vibrissa deflection, except rarely and in the extreme periphery of the principal barrels (Civitillo and Contreras 2006). One possible explanation for this difference with the present data is that these investigators used paired vibrissa stimulation as opposed to five-vibrissa stimulation of the present study. Facilitative interactions between multiple barrels may be better suited to production of reliable supralinear responses.

**Fast oscillations versus slow waves in coincidence detection**

Although the brief window of responsiveness in our results is probably shaped in large part by fast inhibition, the angular tuning of FO is significantly narrower than the slow wave, suggesting involvement of an additional mechanism. Unlike the slow wave, angular sensitivity of FOs reveals a periodicity that corresponds to the average frequency of 345 Hz in these animals, suggesting submillisecond phase sensitivity in addition to the inhibitory damping evident for both FO and the slow wave. Because FOs represent the earliest and the most precisely tuned response to simultaneous or near-simultaneous vibrissa displacement, they may serve a primary role in coincidence detection in the PMBSF. The angular tuning of slow waves is roughly threefold wider than that of FO, suggesting a heightened sensitivity to coincident stimuli, yet one that is not further narrowed by the phase sensitivity apparent in FO. It is notable that only the N1 and P2 produce supralinear responses to coincident stimuli; the P1 is typically linear or sublinear, suggesting different functional roles for these temporal components. Laminar field potential studies have demonstrated that the P1 reflects depolarization of the proximal apical dendrites of supragranular (Di et al. 1990) and, to a lesser extent, infragranular (Staba et al. 2004) pyramidal cells in the PMBSF. Although not registering supralinear responses to simultaneous stimuli, the P1 may reflect establishment of an essential background of common excitation among subgroups of activated barrels, bringing select populations of cells near threshold and facilitating phase-sensitive interbarrel interactions of concurrently recorded FOs. Recent computational models suggest that, under conditions of near-threshold depolarization, even weakly correlated synaptic inputs can dramatically increase discharge probability (Salinas and Sejnowski 2000), possibly improving coincidence detection between pyramidal cells of mutually depolarized barrels. Laminar recording of the subsequent N1 in PMBSF indicates depolarization of distal apical dendrites of both supra- and infragranular pyramidal cells (Di et al. 1990). Supralinear responses recorded for the N1 and P2 during closely timed stimuli suggest a late phase of coincidence detection distinct from FOs. It cannot be determined from our data whether this is conducted independently of FO or is in fact boosted by preceding discharge of FO-generating neurons. However, the long poststimulus latency and wider spatial distribution of these late components suggest the involvement of multisynaptic pathways for their generation, perhaps serving to distribute the results of coincidence detection performed locally in the principal barrels to wider areas of the PMBSF.

**Homogeneity of multivibrissa integration: two-dimensional processing in the barrel field**

Anatomical studies show a bias toward interconnectivity between barrels within rows versus arcs in the PMBSF (Bernardo et al. 1990; Hoeflinger et al. 1995) that may be reflected in elongation of vibrissa-evoked activity patterns along the rows (Armstrong-James and Fox 1987; Kleinfeld and Delaney 1996; Simons 1978). Perhaps for this reason, a number of studies concerned with multivibrissa stimulation have examined integration within barrel rows as opposed to arcs (Goldreich et al. 1998; Kleinfeld and Delaney 1996; Simons 1985). Investigations that have compared multivibrissa stimulation within an arc versus row at short interstimulus intervals variously suggest a tendency toward supralinear responses in arcs and rows, respectively (Ego-Stengel et al. 2005; Ghazanfar and Nicolelis 1997), or sublinear responses in both (Mirabella et al. 2001).

A surprising finding of the present experiment is that there is little difference in the spatiotemporal pattern of sub- or supralinear responsiveness in the rows versus arcs, and neither differs from the diagonal group of vibrissa. To our knowledge intradiagonal integration within the PMBSF has not been previously examined. For all three conditions (arc, diagonal, and row), course range (±45°) stimulation yields half-amplitude angular windows averaging 5.3° for FO and 15.9° for the slow wave. Closer examination, with a finer range of stimulation angles (±6°), yields half-amplitude angular windows averaging 2.7 and 6.3° for FO and slow wave, respectively. Whereas the angular windows in both frequency bands are significantly smaller in the rows (FO = 2.1°, slow wave = 5.1°) than in the arcs (FO = 2.8°, slow wave = 6.5°), suggesting a slight improvement of angular tuning in the rows (neither significantly differing from the diagonal), this difference is quite small. Indeed, the most striking result is the similarity in all response characteristics between stimulus conditions. These characteristics include the spatial distribution of responses (relative to the principal barrels), sublinear and supralinear responsiveness with large and small stimulus angles, respectively (intervibrissa delay), and correlated changes in both FO and slow-wave power, suggesting an appreciable absence of direction specificity within the PMBSF. Furthermore, in all experimental conditions, the decline of both FO and slow-wave power with stimulus angle is nearly symmetrical about 0°, indicating that intervibrissa interactions are insensitive to the order in which the vibrissae are stimulated. Field potential mapping was used in the present study to examine the central tendency of population interactions in the entire PMBSF. This central tendency suggests a predominant
spatial and temporal homogeneity underlying multivibrissal integration. However, unlike unit recording, field potential recordings may be relatively insensitive to selective activation of subpopulations of cells within or between barrels. Thus our results ignore the potential contributions to spatiotemporal integration of somatotopically organized motion direction maps, recently demonstrated in single- and multiple-unit recordings (Andermann and Moore 2006). Proper examination of possible contributions from directionally tuned subpopulations at the subcolumnar level to the present field potential records would require multivibrissae stimulation at a variety of orientations instead of the consistently orthogonal orientation used here.

Coincidence detection and spatial feature analysis

The present experiments were performed in anesthetized rats with passive stimulation. As such, they may be assumed to provide a simplified view of mechanisms underlying spatial feature analysis in the awake behaving animal, where attentional states, whisking strategies, head position, and accompanying interactions between motor and somatosensory cortex all must come into play. However, the sharp angular tuning of population responses recorded here suggests that simultaneous or near-simultaneous displacement of multiple vibrissae may constitute a preferred stimulus in the PMBSF. Responses to asynchronous vibrissa contact, with delays more than a couple of milliseconds, are considerably suppressed. Inhibition has long been thought to enhance both spatial contrast (Laaris et al. 2000; London et al. 1989; Mountcastle and Powell 1959; Petersen et al. 2001; Simons 1995; Simons and Carvell 1989) and temporal contrast (Gabernet et al. 2005; Gardner and Costanzo 1980; Pinto et al. 2000, 2003) in somatosensory cortex. Temporal contrast enhancement could serve to improve resolution of asynchronous input by briefly suppressing responses to an initial stimulus in preparation for response to a subsequent one (Gardner and Costanzo 1980). In the PMBSF, this would result in an improved resolution of sequentially activated vibrissae within a row when brought in contact with an object during forward extension (Simons 1985).

However, our results support an alternative role for temporal contrast enhancement, one in which asynchronous vibrissa contact outside a short time window of several milliseconds is powerfully suppressed in favor of simultaneous or nearly simultaneous contact, producing sharply tuned supralinear responses particularly notable in high-frequency oscillations arising from additional phase sensitivity. In this way, intra- and interbarrel circuitry may serve the function of coincidence detection (Berger and Luscher 2003; Gabernet et al. 2005; Ghazanfar and Nicolesis 1997; Pinto et al. 2000, 2003; Roy and Alloway 2001; Schaefer et al. 2003; Shimigi et al. 1999, 2000; Stuart and Hausser 2001; Swadlow 2003), favoring inputs with low temporal contrast, and identifying common object features on the basis of simultaneous contact with subgroups of vibrissae (Pinto et al. 2000, 2003; Shimigi et al. 2000). The equivalence of function apparent during arc, diagonal, and row stimulation suggests that the PMBSF may be capable of working as a two-dimensional integrative array, processing spatial features according to common mechanisms despite the direction with which the vibrissae pass across an object. Spatial features, extracted from coincident contacts within two-dimen-

sional vibrissa space, include orientation of straight edges or planes (Shimigi et al. 2000), with a potential resolution of 1° as suggested here. However, the same mechanism of coincidence detection should also provide information about object curvature or shape (Benison et al. 2006) indicated by behavioral studies of object discrimination in rats (Harvey et al. 2001; Polley et al. 2005).

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