Rodent somatosensory cortex contains an isomorphic map of the mystacial whiskers in which each whisker is represented by neuronal populations, or barrels, that are separated from each other by intervening septa. Separate afferent pathways convey somatosensory information to the barrels and septa that represent the input stages for 2 partially segregated circuits that extend throughout the other layers of barrel cortex. Whereas the barrel-related circuits process spatiotemporal information generated by whisker contact with external objects, the septa-related circuits encode the frequency and other kinetic features of active whisker movements. The projection patterns from barrel cortex indicate that information processed by the septa-related circuits is used both separately and in combination with information from the barrel-related circuits to mediate specific functions. According to this theory, outputs from the septal processing stream modulate the brain regions that regulate whisking behavior, whereas both processing streams cooperate with each other to identify external stimuli encountered by passive or active whisker movements. This theoretical view prompts several testable hypotheses about the coordination of neuronal activity during whisking behavior. Foremost among these, motor brain regions that control whisker movements are more strongly coordinated with the septa-related circuits than with the barrel-related circuits.

*Keywords:* columnar organization, rate coding, sensorimotor integration, spatial coding, temporal coding, whisking behavior

**Introduction**

Rodent barrel cortex has been studied intensively over the past 4 decades because it has a unique structural-functional organization that facilitates the analysis of the neural mechanisms that mediate development, plasticity, and sensory coding. Whether processed for Nissl material or cytochrome oxidase, tangential sections through layer IV of primary somatosensory (SI) cortex reveal a well-defined isomorphic representation of the mystacial whisker pad (Woolsey and Van der Loos 1970; Land and Simons 1985). As shown in Figure 1, each mystacial whisker is represented in layer IV by a “barrel,” and neighboring barrels are separated from each other by narrower zones called “septa.” Because of this grid-like organization, each barrel is identified by its arc position (1–7, caudal to rostral) within a specific row (A–E, ventral to dorsal).

Soon after barrel cortex was first described in 1970, electrophysiology studies indicated that each barrel is selectively activated by the corresponding whisker on the contralateral whisker pad (Welker 1971, 1976; Simons 1978). Consistent with the columnar organization that is ubiquitous throughout neocortex (Mountcastle 1997), extragranular neurons located directly above or below a layer IV barrel are activated best by the same whisker that excites the neurons in the barrel (Welker 1971, 1976; Simons 1978). Because of this one-to-one correspondence, a large body of research on barrel cortex has focused on the circuit mechanisms by which “principal” and “surrounding” whiskers influence the neurons in a barrel column (Simons 1985; Armstrong-James and Fox 1987; Brumberg et al. 1996; Lavallee and Deschenes 2004; Kwegyir-Afful et al. 2005).

Recent work has demonstrated that barrel cortex contains a rich and diverse neuronal organization in which the local circuits are characterized by a high degree of connectional specificity. Single-neuron recordings, often coupled with morphologic reconstructions, have revealed different classes of neurons that have diverse response properties (Porter et al. 2001; Bruno and Simons 2002; Petersen et al. 2003; Schubert et al. 2003; Staiger et al. 2004). Such studies have also shown that neurons within barrel cortex have local connections and interactions that vary systematically with their laminar and columnar locations (Shepard et al. 2005; Shepherd and Sloboda 2005; Schubert et al. 2006).

Although these studies have elucidated many organizing principles that characterize barrel cortex, some structural-functional relationships have been neglected. Compared with the barrels, for example, much less is known about the physiological properties of the neurons that reside in the intervening septa. Few studies have analyzed septal neurons because the septal territory is smaller and septal neurons are not defined by a principal whisker but are equally activated by multiple whiskers. Furthermore, septal territories can vary considerably across species. The septal zones in mouse cortex, for example, are quite narrow, and this has meant that most information about the septal regions has come from the rat.

Despite the lack of detailed knowledge about the septal regions, accumulating evidence indicates that the barrels and septa represent the cortical input stages for 2 circuits that are partially segregated throughout all layers of barrel cortex. When examined from a systems-level perspective, substantial evidence prompts the assertion that the septa and their connected circuits encode the kinetics of whisker movements and send this information to brain regions that regulate whisking behavior. By contrast, the barrels and their connected circuits process spatiotemporal information that encodes whisker contact with external objects. Nonetheless, the information processed by both circuits must be integrated to mediate object recognition and other related behavioral tasks. Hence, in addition to emphasizing evidence indicating that the barrels and septa process different types of information, this review will...
briefly discuss how their circuit connections might cooperate with each other to mediate specific functions.

**Anatomical Evidence for Processing Streams in Barrel Cortex**

Much of the evidence for separate functional circuits in SI barrel cortex comes from anatomical tracing studies that indicate clear distinctions in the connectivity of the barrel and septal compartments. Figures 2 and 3 illustrate the respective afferent and intrinsic connections of the barrel-related and septa-related circuits. As these figures indicate, the terms “barrel column” and “septal column” refer to the collections of neurons that are vertically aligned with their respective layer IV compartments. Whereas “barrel cortex” is meant to indicate the entire SI whisker representation, which contains both barrel and septal columns, the terms “barrel circuits” and “septal circuits” refer to the interconnected collections of barrel columns and septal columns, respectively (see Fig. 3).

**Afferent Projections to the Barrel and Septal Compartments**

Sensory information from the mystacial whiskers is transmitted to the contralateral thalamus by separate lemniscal and paralemniscal pathways (Fig. 2). The lemniscal pathway originates in the principal sensory trigeminal (PrV) nucleus and projects to the ventroposteromedial (VPM) nucleus. By comparison, the paralemniscal pathway originates in the interpolaris division of the spinal trigeminal (SpVi) nucleus and projects to the medial part of the posterior (POm) nucleus and to a slender “tail” region in the ventrolateral part of VPM (Erzurumlu and Killackey 1980; Peschanski 1984; Rhodes et al. 1987; Chiaia et al. 1991; Williams et al. 1994; Pierret et al. 2000; Veinante, Jacquin, and Deschenes 2000).

The thalamocortical projections of the lemniscal and paralemniscal pathways terminate in separate parts of SI barrel cortex. Whereas the layer IV barrels receive dense inputs exclusively from the nucleus VPM (Killackey 1973; Killackey and Leshin 1975; Koralek et al. 1988; Chmielowska et al. 1989; Lu and Lin 1993), the intervening septa receive dense inputs from POm and the slender tail region in VPM (Lu and Lin 1993; Pierret et al. 2000).

The extragranular layers of barrel cortex also receive segregated inputs from the lemniscal and paralemniscal pathways. Thus, VPM sends moderate projections to the adjoining parts of layers VI and Vb, as well as sparse projections to lower layer III (Lu and Lin 1993). By comparison, less-dense secondary projections from POm terminate in layers I, II, III, and Va. In fact, paralemniscal information is transmitted to layers I and Va in both barrel and septal columns, but the projections to layer Va in the barrel columns are less dense than those to neighboring regions below the septa (Lu and Lin 1993). Nonetheless, even though some paralemniscal information is sent to regions vertically aligned with the layer IV barrel compartments, VPM does not innervate layers I or Va, and the thalamocortical

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**Figure 1.** Isomorphic representation of the mystacial whisker pad in the SI cortex of a rat. The photomicrograph on the left depicts a tangential section through the layer IV barrel field after the tissue was processed for cytochrome oxidase. The right diagram, which is based on the photomicrograph, designates each barrel according to its arc position (1-7) within a specific row (A-E). Although many septal zones are no more than 70-80 µm in width, the septal regions indicated by the asterisks are more than 200 µm wide; R, rostral; L, lateral.

**Figure 2.** Laminar location of afferent inputs to SI barrel cortex. The lemniscal pathway (red), which consists of projections from the PrV nucleus to the VPM nucleus of the thalamus, provides dense inputs to the barrel compartments in layer IV. Secondary projections from the lemniscal pathway terminate in layers III, Vb, and VI that are in the same vertical column as the layer IV barrel. The paralemniscal pathway (green), which consists of projections from the interpolaris division of the SpVi to the medial part of the POm nucleus, terminates most densely in the layer IV septa. Secondary projections from the paralemniscal pathway terminate in layers II and III of the septal columns and in layers I and Va of both septal and barrel columns.
projections of the lemniscal and paralemniscal remain segregated from each other.

**Intrinsic Connections within Barrel Cortex**

Most descriptions of intracortical connectivity in barrel cortex indicate that septal projections extend over relatively long horizontal distances (Fig. 3). In the first study that examined this issue, tracer injections into the septa or “perigranular zones” produced extensive “walls” of labeled processes that surrounded the empty barrels in layer IV (Chapin et al. 1987). By comparison, focal tracer deposits in a cortical barrel revealed labeling in the injected barrel, the surrounding septa, and in the supragranular layers overlapping the barrel, but the neighboring barrels in layer IV were completely devoid of labeling (Kim and Ebner 1999). Consistent with these findings, subsequent studies showed that individual neurons in a barrel project to supragranular sites in adjacent barrel columns of the same row, but never to the neighboring barrels in layer IV (Lubke et al. 2000; Petersen et al. 2003). Although many studies emphasize interconnections along the barrel rows (Bernardo, McCasland, and Woolsey 1990; Bernardo, McCasland, Woolsey, and Strominger 1990; Hoeflinger et al. 1995), analysis of individual pyramidal neurons in layer II/III of a barrel column indicate that the axons of these neurons rarely extend further than the neighboring barrel column (Petersen et al. 2003; Feldmeyer et al. 2006).

The possibility that the septa and barrels represent distinct processing units was first proposed in 1995 (Hoeflinger et al. 1995). Noting the “striking” organization of the horizontal connections in the septa, the authors emphasized separate “processing streams” in which the lemniscal pathway conveys information about a single whisker to the corresponding barrel, whereas the paralemniscal pathway conveys multi-whisker information to the septa. The septa were viewed as a “cortical continuation” of the multi-whisker system in the brain stem and thalamus (Hoeflinger et al. 1995), but little evidence indicated whether the lemniscal and paralemniscal processing streams might extend beyond layer IV of barrel cortex.

A subsequent paper in 1999, however, indicates that septal and barrel compartments represent the cortical input stages for separate circuits that extend throughout all layers of barrel cortex (Kim and Ebner 1999). When a focal deposit of biocytin was placed in a barrel or the septa, the projections terminated most densely in the supragranular region lying directly above the injection site. Likewise, focal deposits in the supragranular layers revealed projections to infragranular sites in the same vertical column. Consistent with this columnar pattern, sites located below the septa project to supragranular sites aligned with the septa. The same study also showed that septal columns are selectively interconnected with each other by horizontal intracortical projections. When biocytin was placed at a site above the layer IV septa, the labeled projections had “intense terminal fields” that were “distributed in patches above other septal zones” located at horizontal distances corresponding to the diameter of 1 or 2 barrels (Kim and Ebner 1999).

Recent analysis of local connections and their interactions within barrel cortex indicates that “barrel-related and septal-related columns are associated with distinct functional circuits” (Shepherd and Svoboda 2005). Thus, in brain slices of barrel cortex, photostimulation of caged glutamate at discrete sites spaced systematically throughout the slice revealed septal-related projections from layer V a neurons that were most strongly connected with the layer II/III neurons lying directly above the septa (Shepherd and Svoboda 2005). These and other results prompted the conclusion that interlaminar connections that are vertically aligned with the barrels or the septa “are likely to mediate parallel processing of somatosensory signals” that represent the “intracortical continuations of, respectively, the subcortical lemniscal and paralemniscal systems” (Shepherd and Svoboda 2005). Hence, a growing body of data supports the view that vertical columns of barrel-related and septal-related neurons form interconnected circuits that are partially segregated from each other.

**Efferent Projections from Barrel Cortex**

Barrel cortex projects to multiple cortical areas including primary motor (MI) cortex, the secondary somatosensory (SII) cortex, the parietal ventral region, and the contralateral barrel cortex (White and DeAmicis 1977; Welker et al. 1988; Fabri and Burton 1991; Hoeflinger et al. 1995). Barrel cortex also projects to subcortical motor regions such as the neostriatum, pons, and superior colliculus (Mihaloff et al. 1985; Crandall et al. 1986; Welker et al. 1988; Mercier et al. 1990; Brown et al. 1998; Alloway et al. 1999; Hoffer et al. 2005), as well as to the brain stem and thalamic nuclei in the lemniscal and paralemniscal pathways (Hoogland et al. 1987; Chmielowska et al. 1989; Bourassa et al. 1995; Veinante, Lavalle, and Deschênes 2000; Killackey and Sherman 2003).

Very few of these studies, however, have examined the origin of these projections with respect to the barrel and septal compartments in layer IV. Yet, this is crucial for assessing whether the barrels and septa process different information.
and distribute it to brain regions that have specific computational and behavioral functions. If barrels and septa represent the input components of separate circuits that process specific types of whisker-related information, the projections from these 2 circuits should reveal distinct processing streams.

As shown by Figure 4, retrograde-tracing experiments have revealed 2 distinct projection patterns for barrel cortex (Fig. 4). One pattern is characterized by projection systems that originate predominantly from neurons aligned with the layer IV septa (i.e., septal columns). All these septa-related projection systems terminate in brain regions that are associated with the motor system. The other pattern is characterized by projection systems that originate from populations of neurons that are uniformly distributed throughout barrel cortex and are not preferentially associated with either the barrel or the septal columns. Most notably, there are no projection systems that originate exclusively from the barrel columns.

**Septal and Barrel Processing Streams**

The first indication that some barrel cortex projections originate from the septal circuits came from a study in which lesions of the dysgranular or “agranular” zone revealed degenerating callosal fibers in the corresponding zone of the contralateral hemisphere (Akers and Killackey 1978). Because the dysgranular zone has structural and functional similarities with the septa or “perigranular” regions of barrel cortex (Chapin et al. 1987), this suggests that the septa provide the bulk of the callosal projections between the barrel cortices of the 2 hemispheres. In fact, subsequent work indicated that callosal projections from SI barrel cortex originate exclusively from the septal circuits (Oлаваррия et al. 1984; Hayama and Ogawa 1997).

Other projections also originate predominantly from the septal circuits. In mouse barrel cortex, for example, retrograde tracer injections into the pons, superior colliculus, pyramidal tract, or MI cortex produced labeling of the layer V neurons that reside below the barrel walls and their intervening septa in the layer IV barrel field (Crandall et al. 1986). In rats, we confirmed that the MI whisker representation receives projections predominantly from barrel cortex neurons that are aligned with the layer IV septa (Alloway et al. 2004). Thus, after placing a tracer in MI, the extragranular layers of SI contain dense strips or bands of retrogradely labeled neurons that matched the contours and spatial variations of the layer IV septa.

The compartmental location of corticostriatal projections from barrel cortex varies according to their hemispheric destination. Ipsilateral corticostriatal projections originate from sites that are uniformly distributed with respect to the septal and barrel columns, but the projections to the contralateral neostriatum originate mainly from neurons aligned with the septa (Wright et al. 2001; Alloway et al. 2006). Given that other callosal projections also originate from the septa (Oлаваррия et al. 1984; Hayama and Ogawa 1997), this suggests that septal columns have a role in the bilateral coordination of the whiskers.

Corticostriatal projections from barrel cortex differ according to their laminar distribution. The corticostriatal projections from layer VIa to the nucleus POM originate exclusively from the septal columns (Killackey and Sherman 2003). By contrast, corticostriatal projections to VPM from layer VIa, as well as those to POM from layers Vb and Vlh, originate from both barrel and septal columns (Hoogland et al. 1987; Diamond et al. 1992; Killackey and Sherman 2003). In all sensory systems that have been examined, corticostriatal projections from layer Vb represent a feedforward pathway to higher order thalamocortical circuits (Guillery 1995; Sherman and Guillery 2003). Given that corticostriatal projections from layer VB of barrel cortex terminate exclusively in nucleus POM, the paralemniscal projections from POM to the septa must represent a higher order thalamocortical circuit (Killackey and Sherman 2003). Hence, the thalamocortical projections from POM to the septa support the view that septal circuits represent a distinct functional processing stream.

**Physiologic Evidence for Processing Streams in Barrel Cortex**

The first physiological evidence for processing streams within the same sensory modality came from studies of the visual system (Livingstone and Hubel 1988). Those studies showed that separate populations of neurons responded selectively to visual features such as color, form, stereopsis, and movement. Although the degree of functional segregation is still an issue (Sincich and Horton 2005; Lu and Roe 2007), substantial evidence supports the concept of parallel processing streams in which specific pathways extract selective information and perform distinct computations for a specific function (DeYoe and van Essen 1988; van Essen and Gallant 1994; Roland and...
Zilles 1998; Read et al. 2002; Krauss and Nicol 2005). Similar types of evidence indicate that the barrels and septa differentially process specific types of information related to whisker stimulation. Thus, whereas the barrel-related circuits analyze spatiotemporal information evoked by whisker interactions with external stimuli, the septal-related circuits encode the kinetics (e.g., frequency, velocity) of whisker movements.

**Spatial Coding**

The isomorphic relationship between the peripheral whiskers and the barrel field represents an excellent model for spatial coding. Stimulation of a single whisker activates the corresponding cortical barrel but produces weak neuronal responses in the neighboring barrels (Simons 1985; Armstrong-James and Fox 1987; Diamond 1995; Swadlow et al. 1998; Kwegyir-Afful et al. 2005). Among the factors mediating these spatially tuned responses, the lemniscal pathway has a precise topographic organization that maintains the spatial relationships for neighboring whisker representations. The PrV and VPM nuclei, respectively, contain "barrellettes" and "barreloids" that correspond to the spatial distribution of the cortical barrels (Van der Loos 1976; Jacquin and Rhodes 1983; Killackey and Fleming 1985; Ma 1991). Although neurons in these lemniscal nuclei exhibit multi-whisker responses, a principal whisker can always be identified (Ito 1988; Armstrong-James and Callahan 1991; Diamond et al. 1992; Minnery and Simons 2003). Furthermore, the vast majority of VPM neurons in the same barreloid converge on the corresponding layer IV barrel (Lu and Lin 1993; Land et al. 1995; Arnold et al. 2001). This excitatory input, along with strong activation of a local inhibitory network in each barrel (Kyrizai et al. 1996; Swadlow et al. 1998; Miller et al. 2001; Pinto et al. 2003), sharpens the receptive fields of barrel neurons so that they are dominated by a single, principal whisker (Keller 1995).

Even though barrel cortex is highly specialized and may not represent typical neocortex, it has a well-defined columnar organization that resembles the functional organization found in other mammals. Thus, the extragranular neurons located above and below the barrels have spatially tuned responses in which multiple whiskers may contribute to their receptive fields, but they have the same principal whisker as the neurons in the layer IV barrel (Welker 1976; Simons 1978; Armstrong-James and Fox 1987; Simons et al. 1992). The spatially tuned responses of the barrel columns have prompted the view that spatial coding by the barrel circuitry is used to perceive which whiskers are contacted by an external stimulus (Kleinfield et al. 2006).

Regular-spiking barrel neurons, which are presumed excitatory, respond preferentially to specific directions of whisker deflection (Simons and Carvell 1989; Bruno and Simons 2002; Bruno et al. 2003). Adjacent neurons within a subbarrel domain have similar directional properties, and the directional preferences vary across neighboring domains within a barrel (Bruno et al. 2003; Andermann and Moore 2006). Although the behavioral relevance of directionally tuned neurons in the barrels has not been established, these spatial properties could facilitate the identification of orientation, shape, distance, and other spatial features that rats discriminate with their whiskers (Harvey et al. 2001; Krupa et al. 2001; Shuler et al. 2002).

The importance of barrel columns for analyzing spatial information is consistent with the hypothetical mechanisms by which rats use their whiskers to discriminate surface textures (Guic-Robles et al. 1989, 1992; Carvell and Simons 1990, 1995). According to one hypothesis, texture discrimination is based on a spatial gradient in the mechanical resonance properties of the vibrissae (Neimark et al. 2003; Andermann et al. 2004; Moore and Andermann 2005). Whereas whiskers in the same arc have similar lengths, those in the same row have graded lengths along the anterior-posterior axis. Because the longer posterior whiskers resonate at lower frequencies than the shorter anterior whiskers, a textured surface induces resonance optimally in those whiskers whose resonant properties match the input frequency that is created as the whiskers move across a surface. Hence, differences in the firing rates of the corresponding barrels should produce unique spatial codes for texture.

A competing hypothesis proposes that resonant vibrations are suppressed when the whiskers move across a surface, but vibrations reflecting the surface topology of the whisked object are still present (Arabzadeh et al. 2005; Hipp et al. 2006). By inducing unique temporal spike patterns that reflect textural variations in a surface, vibrissal vibrations may provide sufficient information to mediate texture discrimination. Evidence for this view comes from the temporal discharge patterns of barrel column neurons that are activated by directional fluctuations in the principal whisker (Arabzadeh et al. 2005). Nonetheless, regardless of whether texture discrimination relies on the resonance properties of the whiskers or on the timing of the neuronal spike trains, both hypotheses are based on processing in barrel-related circuits.

Compared with the lemniscal system, POm and its cortical targets do not encode spatial information very precisely. Neurons in POm and in the cortical septa are not characterized by a well-defined principal whisker; instead, they receive similar inputs from multiple whiskers (Armstrong-James and Fox 1987; Diamond 1995). Furthermore, the responses of septal neurons to single-whisker stimulation are much smaller than those evoked in the barrel neurons by a principal whisker (Armstrong-James and Fox 1987; Brecht and Sakmann 2002; Melzer, Champney, et al. 2006).

**Temporal Coding**

In further contrast to the lemniscal system, the paralemniscal system does not encode the precise time of whisker stimulation (Fig. 54). Unlike VPM neurons, which consistently respond 5-7 ms after abrupt whisker deflection, POm neuronal responses are weaker and have variable response latencies that usually range from 11 to 25 ms (Diamond et al. 1992; Trageser and Keller 2004). Furthermore, when barrel cortex is reversibly inactivated, neuronal responses to whisker stimulation are suppressed in POm but not in VPM (Diamond et al. 1992). Initially, this finding prompted the assertion that long-latency responses in POm depend on corticothalamic feedback that reinforces the relatively weak projections from SpVi to POm (Diamond 1995).

This conceptual view was recently revised by data showing that the POm receives powerful inhibition from the zona incerta during whisker stimulation. A narrow nucleus under the ventral portion of the thalamus, the zona incerta, is composed of GABAergic neurons, many of which project to the nucleus POM (Power et al. 1999; Bartho et al. 2002). The zona incerta receives inputs from the SpVi complex (Williams et al. 2003; Zilles et al. 2003).
The phase-locked loop hypothesis states that POm responses depend, in part, on inputs from the corticothalamic feedback (response to a previous stimulus) that arrives in the delays the onset of the POm response to the first stimulus, subsequent corticothalamic activation of the zona incerta eliminates the onset response to the next stimulus cycle. Relative to the other nuclei, the initial response in POm (arrow) is noticeably delayed on the first stimulus and completely absent during subsequent cycles of whisker stimulation. 

Information Processing Streams in Rodent Barrel Cortex

The inhibitory projections of the zona incerta are also likely to influence the timing of responses in the paralemniscal system. The onset and duration of the excitatory response in SpVi does not vary with stimulation frequency (Ahissar et al. 2000), and this indicates that excitatory inputs from SpVi to POm remain constant during each stimulus cycle. Coactivation of inhibitory projections from the zona incerta, however, reduces the initial POm response to the ascending trigeminal input. Furthermore, given that cortical layer V projects to the zona incerta (Mitrofanis and Mikulelic 1999), the corticothalamic feedback response to 1 cycle of whisker stimulation can activate inhibitory projections from the zona incerta and, thereby, delay the POm response to the next cycle of whisker stimulation. Hence, the shift in POm response latency represents an elimination of the onset response by inhibitory inputs from the zona incerta.

Rate Coding

Changes in response latencies during repeated whisker stimulation illustrate how a temporal code can be converted to a rate code (Ahissar et al. 2000, 2001). As the frequency of whisker stimulation increases, paralemniscal responses are delayed, but the time of their offset is not altered. Consequently, the number of spikes evoked by each cycle of whisker deflection is reduced as stimulation frequency increases. Even though the effectiveness of each stimulus is reduced, increases in the frequency of whisker stimulation can produce an increase in the average rate of neuronal activity.

Many studies indicate that repetitive whisker stimulation reduces the effectiveness of each stimulus for evoking responses in barrel cortex (Ahissar et al. 2001; Garabedian et al. 2003; Castro-Alamancos 2004; Khatri et al. 2004; Higley and Contreras 2006), but few have characterized this effect with respect to neurons in the barrels or septa. Recent comparisons of these layer IV compartments indicate that an increase in the frequency of whisker stimulation produces fewer spikes per stimulus in both compartments (Melzer, Champney, et al. 2006; Melzer, Sachdev, et al. 2006). When neuronal responses are expressed as a rate (spikes per second), however, neurons in the layer IV barrels show increases in rate as whisker stimulation increases to 9 stimuli per second, but the spike rate declines at higher frequencies (Melzer, Sachdev, et al. 2006). By contrast, neurons in the septa are less responsive than those in the barrels, but their response rates increase linearly as whisker stimulation rises to 18 stimuli per second. Hence, septal neurons encode the rate of passive whisker movements more effectively than neurons in the barrels (Melzer, Champney, et al. 2006; Melzer, Sachdev, et al. 2006).

Responses to Whisking Movements

Consistent with its responses to passive whisker stimulation, the paralemniscal system monitors the frequency of active whisker movements. This view is based on experiments in which electrical stimulation of the facial nerve in anesthetized
rats causes 5-Hz whisker movements that mimic exploratory whisking (Brown and Waite 1974). This paradigm has revealed different classes of neurons in the trigeminal ganglion, including neurons that respond only to whisking in air, others that respond only when the moving whiskers contact an object, and others that respond both to free-air whisking and to whisker contacts with an external object (Szwed et al. 2003).

The different classes of responses produced by facial nerve stimulation are also relayed to barrel cortex (Ferezou et al. 2006). Thus, POM neurons respond to whisking in air, but do not show any additional response when the whiskers contact an external object (Yu et al. 2006). Lemniscal neurons in the dorsomedial part of VPM respond both to whisking movements and to contacts with external stimuli during free-air whisking, whereas those in the ventrolateral part of VPM (called the extralemniscal pathway) respond only when the whisking motion produces contact with an external stimulus (Yu et al. 2006). Analysis of cortical activity during the electrically evoked whisking motion indicates that layers II, III, and IV of the barrel columns are most responsive when the whiskers contact an external object (Derdikmann et al. 2006). By contrast, neurons in layer Va, which receive paralemniscal inputs (Lu and Lin 1993), respond the same during both no-contact whisking and whisking against an external object (Derdikmann et al. 2006). Hence, in anesthetized animals at least, the lemniscal system and its embedded circuits (i.e., extralemniscal) respond to whisker contacts with external stimuli, whereas the paralemniscal system is activated by whisker motion but not by whisker contacts with external stimuli.

Independent and Cooperative Functions of Barrel and Septal Processing Streams

The anatomical and physiological evidence indicate that the barrel-related and septa-related circuits represent 2 processing streams that differ in their response patterns and computational functions. Whereas the septal circuits encode whisking kinetics (e.g., frequency) and send the processed output to multiple brain regions in the motor system, the spatiotemporal information created by whisker contacts with external objects is processed mainly by the barrel-related circuits. Yet, the neural mechanisms underlying stimulus discrimination and identification are likely to require cooperation and integration of both processing streams.

Regulation of Whisking Behavior

The projections from the septal circuits strongly support the view that this processing stream distributes information about whisking frequency to brain regions that regulate whisking behavior. Projections from the septal columns to the MI whisker representation could regulate specific aspects of whisking behavior (Alloway et al. 2004; Chakrabarti and Alloway 2006). Consistent with MI projections to brain stem regions that control facial nerve activity (Hatton et al. 2002; Grinevich et al. 2005), direct electrical stimulation of MI evokes whisker twitches or sustained oscillations of the whiskers (Hall and Lindholm 1974; Gioanni and Lamarche 1985; Brecht et al. 2004; Haiss and Schwarz 2005). To the extent that the septa encode whisking frequency (Melzer, Champney, et al. 2006; Melzer, Sachdev, et al. 2006), transmission of this information to MI could help maintain whisking at a particular frequency (Kleinfeld et al. 2002).

Barrel cortex also projects densely to the pontocerebellar system (Mihailoff et al. 1985; Crandall et al. 1986; Mercier et al. 1990; Leergaard et al. 2000; Hoffer et al. 2005). In fact, barrel cortex activity is more coherent with the cerebellum than with MI cortex during active whisking (O’Connor et al. 2002; Ahrens and Kleinfeld 2004) and barrel cortex projections to the basal pons are much denser than those to MI cortex (Hoffer et al. 2005). The only study that examined corticopontine projections with respect to the barrels and septa indicates that this pathway originates from neurons aligned with the septa (Crandall et al. 1986). Although this result needs to be confirmed, corticopontine projections that convey frequency-sensitive information are consistent with a long-standing hypothesis that the corticopontocerebellar system modulates motor activity to improve the acquisition of sensory information for stimulus discrimination (Gao et al. 1996; Bower 1997).

Hence, the pontocerebellar system may use whisking frequency information from the septa to refine whisker-related commands sent to MI and other components of the motor system. Consistent with a role in regulating whisking behavior, callosal projections from the septal circuits could coordinate bilateral whisking behavior. Although lateral head movements can initiate asymmetric whisking patterns (Towl and Hartmann 2006), exploratory whisking behavior is characterized by a high amount of bilateral symmetry in which the whisker movements on both sides of the head are synchronized at the same frequency (Gao et al. 2001; Sachdev et al. 2003; Sellien et al. 2005; Mitchinson et al. 2007). Callosal projections from the septal circuits (Olavarria et al. 1984; Hayama and Ogawa 1997) could coordinate or synchronize these circuits in both hemispheres. Given the dense callosal interconnections between the MI whisker representations of each hemisphere (Porter and White 1986), interhemispheric synchronization of the septal columns and their projections to MI could facilitate the symmetric whisker movements that appear bilaterally during free-air whisking.

When whiskers on one side contact a stimulus, however, whisker motion is significantly dampened, while the contralateral whiskers increase their whisking amplitude (Sachdev et al. 2003; Mitchinson et al. 2007). Although the neural basis for this stimulus-induced shift to asymmetric whisking is speculative, corticostrial projections from barrel cortex could play a role. The dorsolateral neostriatum receives dense projections from barrel cortex (Alloway et al. 1999), and this subcortical region controls the temporal sequence of somesthestic-guided behaviors that are repeated in a stereotyped manner (Cromanwell and Berridge 1996; Aldridge and Berridge 1996; Crandall et al. 1986). Furthermore, whereas the septal circuits project bilaterally to the dorsolateral neostriatum, the barrel-related circuits project only to the ipsilateral neostriatum (Wright et al. 2001; Alloway et al. 2006). Hence, to the extent that the basal ganglia are involved in initiating and maintaining bilateral, symmetric whisking movements, bilateral synchronized inputs from the septal circuits could help maintain execution of this motor program. Unilateral whisker contact, however, would activate the ipsilateral corticostrial projections from the barrel circuits and, thereby, produce asymmetric activation of the basal ganglia so that a new motor program emerges.

Stimulus Identification

Despite evidence for differential processing of whisker-related information, certain facts indicate that both processing streams...
must cooperate with each other to identify objects that are detected by passive or active whisker movements. Although the barrel circuits encode the spatial and temporal properties of stimuli at a high resolution, the precise spatiotemporal distribution of neuronal discharges in the barrel circuits is highly dynamic and depends on the velocity and amplitude of the whisker movements. Hence, information obtained by the septal circuits about whisker kinetics must be integrated with the spatiotemporal responses of the barrel-related circuits.

This integration is possible at several sites in barrel cortex and other somatosensory cortical areas. For example, interconnections are present where the barrel and septal compartments adjoin each other in layer IV (Kim and Ebner 1999). In addition, septal neurons project to supragranular sites overlying the barrel compartments and, thereby, provide another substrate for integration (Shepard et al. 2005). Furthermore, the nucleus POM projects to layer Va in both the barrel and septal columns (Lu and Lin 1993). Finally, both the septal and barrel circuits project to SII cortex (Chakrabarti and Alloway 2006).

The exact functional role of SII cortex is not known, but this cortical region receives both lemniscal and paralemniscal information that could be used to analyze objects contacted by passive and active whisker movements. Thus, both POM and VPM project to SII (Carvell and Simons 1987; Spreafico et al. 1987; Chakrabarti and Alloway 2006), although the densest projections from VPM originate from the ventrolateral part, which receives inputs from SpVi (Pierret et al. 2000). The SII whisker region lies adjacent to barrel cortex and it receives dense projections from the septal and barrel circuits (Hoefflinger et al. 1995; Kim and Ebner 1999; Chakrabarti and Alloway 2006).

Consistent with this combined functional input, neuronal responses in the SII whisker region represent a mixture of lemniscal and paralemniscal qualities. Similar to the SI septal neurons, SII neurons have large receptive fields that are not defined by a principal whisker (Kwegyir-Afful and Keller 2004). Furthermore, in response to deflecting a single whisker, SII response magnitudes are smaller than the responses produced in the barrel circuits by principal whisker stimulation (Kwegyir-Afful and Keller 2004). Yet, SII neurons also exhibit directional preferences similar to those observed in the SI barrels (Kwegyir-Afful and Keller 2004). Moreover, changes in the frequency of passive whisker stimulation produce SII responses that resemble those recorded in the SI barrel circuits (Melzer, Champney, et al. 2006). Thus, in contrast to the rate codes observed in the SI septa, neuronal discharges in SII failed to show a monotonic, linear relationship with respect to stimulus frequency (see Fig. 6 in Melzer, Champney, et al. 2006). Collectively, these data indicate that the SII whisker representation extracts information about the sensory attributes of external objects, and we hypothesize that SI and SII work together to discriminate and identify objects contacted by the whiskers.

Conclusions
The connection patterns and responses of the barrel-related and septa-related circuits indicate that these cortical networks represent 2 processing streams that analyze different information. Whereas the septal circuits process information about the rate of whisker movements, the barrel circuits process information related to the temporal and spatial interactions between the whiskers and external objects. Information processed by the septal circuits is sent to a variety of motor brain regions, presumably to regulate whisking behavior. The barrel and septal circuits must work together to discriminate objects detected by passive or active whisker movements, but the exact neural mechanisms for this are not known.

Several testable hypotheses are evident in the thesis that the septal circuits represent a distinct processing stream. Given the extensive horizontal interconnections that characterize septal circuits, simultaneous movements of multiple whiskers should synchronize distant neurons within the septal circuits more strongly than equidistant neurons in the barrel-related circuits. Furthermore, neurons in the septal circuits are functionally linked by virtue of their projections to MI cortex and other regions that regulate motor activity. If these motor regions rely on septal circuits to regulate whisking frequency or other aspects of whisker motion, then the neuronal activity in these motor regions should be much more strongly coordinated with the septal circuits than with the barrel circuits. Finally, in view of the symmetric, bilateral whisker movements that characterize exploratory whisking behavior, the septal circuits in the 2 hemispheres are more likely to be synchronized than the barrel circuits when the whiskers on each side of the face are moved bilaterally at same rate and amplitude.

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