

Barrel cortex and whisker-mediated behaviors

Michael Brecht

Neural networks of the rodent barrel cortex are particularly tractable for developing a quantitative understanding of response transformations in a cortical column.

A column in barrel cortex consists of ~ 10 compartments. Two thalamic input pathways, a sensory lemniscal one and sensorimotor paralemniscal one, are transformed to ~ 7 population outputs, each with distinct spatiotemporal response characteristics. Granular and supragranular layers are sites of segregated processing in lemniscal and paralemniscal pathways, whereas infragranular layers are sites of intracolumnar, lemniscal/paralemniscal integration. Individual thalamocortical connections are relatively weak, and a considerable fraction of thalamocortical afferents contributes to each sensory response. Intracortically, relatively few but strong synaptic connections contribute to sensory responses, and responses are rapidly terminated by inhibition. Overall cortical population activity is very low. Whiskers mediate a wide range of behaviors and many natural tactile behaviors occur very rapidly. Vibrissal object recognition can be size invariant and motion invariant and is based on the tactile 'Gestaltwahrnehmung' of shape.

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The input layer of the whisker somatosensory cortex of rodents contains discrete cytoarchitectonic units, called barrels, which have captured widespread attention; a Pubmed search for 'barrel cortex' leads to ~ 1000 references, about 20% of which were published in the past two and a half years. Given this rush of publications, one wonders if the barrel field is a goldmine or simply a mousetrap? This review summarizes recent efforts to disentangle the neural networks of barrel cortex with a particular focus on (1) the barrel cortex microcircuit, (2) barrel cortex response dynamics, and (3) analysis of whisker-mediated behaviors. Other issues like the development and plasticity of the barrel cortex or sensor-

imotor interactions in this system will not be covered here, but these have recently been reviewed [1,2].

The barrel cortex microcircuit

A quantitative description of the barrel cortex microcircuit is emerging

In the past 10 years, a huge amount of detailed analysis of barrel cortex microcircuitry has been performed. A breakthrough in this field came about by aligning anatomical, synaptic, photostimulation/uncaging, and *in vivo* recording data using the layer 4 barrel as a reference [3]. This alignment led to close collaboration and agreement between cellular and systems neuroscientists.

Input–output transformations by the barrel column

A classic way to analyze cortical processing is to compare thalamic afferent input with cortical output. In visual cortex, non-orientation selective thalamic input is transformed into orientation-selective cortical responses. In barrel cortex, however, no single response transformation describes processing. Instead, it appears that barrel cortex generates multiple outputs that are not only different from the thalamic input but also distinct from one another.

Two major thalamic inputs

Acquisition of sensory information is an active process in the vibrissal system, in which not only the whisker deflections by obstacles but also the active positioning of whiskers – whisker movement – play an important role. These two signals, sensory ones about whisker deflections and sensorimotor ones about whisker movements, reach barrel cortex via two major thalamic pathways. The so-called lemniscal input arrives from the ventral posterior medial (VPM) nucleus of the thalamus, yellow Figure 1a), and paralemniscal input arrives from the posteromedial (POM) nucleus of the thalamus, blue Figure 1a) [4]. Lemniscal inputs have relatively small receptive fields and short response latencies [5] and carry largely or exclusively sensory information about whisker deflections; this input innervates strongly L4 barrel neurons and weakly L5B, L6, and barrel-related L3 neurons. Lemniscal input is ideally suited to represent whisker deflections with high-spatiotemporal resolution. The so-called paralemniscal inputs have relatively large receptive fields and long response latencies [5] and are thought to carry sensory as well as motor information about whisker movements [6]; this input innervates strongly L5A neurons and L4 septum neurons, as well as septum-related L3 and L2 neurons. Paralemniscal input is not suited for signaling sensory detail but rather represents sensory and motor signals as they arise from the collective movement of whiskers during active exploration (whisking). It should be noted that

further subdivisions of thalamic input (into up to four subdivisions [7]) have been suggested, but the significance of the further subdivisions for cortical processing is not clear yet.

Multiple output transformations

Our elaborate knowledge of the wiring scheme and the physiology of the barrel column has clarified how the sensory lemniscal/VPM and the sensorimotor paralemniscal/POM inputs are transformed by the barrel cortex. Accordingly, the barrel cortex generates five to seven distinct population outputs (Figure 1a). Corticocortical outputs originate from the supragranular layers and show lemniscal/paralemniscal segregation but intercolumnar integration. Subcortical outputs originate from the infragranular layers and show lemniscal/paralemniscal integration and – to varying extents – intercolumnar integration (Figure 1a). The information carried by corticothalamic outputs from layer 6 is poorly understood.

Layout of the microcircuit

The neural architecture that leads to these response transformations is shown in Figure 1b–e, which summarizes a host of anatomical as well as *in vitro* and *in vivo* physiological data. The column consists of ~10 major processing compartments (Figure 1b). It has been suggested that some of these compartments are not entirely homogeneous [8] and may be organized in subdomains of differing directional selectivity [9,10]. In most instances these subdomains are difficult to demonstrate, perhaps indicating that subdomain organization is weak. Lemniscal VPM thalamic input (yellow Figure 1a) and paralemniscal POM inputs (blue Figure 1a) are processed separately in the granular and supragranular layers (Figure 1c [11–13]), an arrangement that is enforced by the vertical/columnar alignment of L4 axons [14]. There is massive intercolumnar integration in layers 2, 3, and 5B, while such intercolumnar interactions are weak in layers 4 and 5A (Figure 1d). This pattern of intercolumnar interactions is dictated largely by the architecture of axonal arborizations.

Analysis of L5A circuitry: a case study

One of the surprising developments of the past few years has been the re-evaluation of the role layer 5A neurons. On the basis of their massive paralemniscal/POM input, layer 5A neurons were originally conceptualized as a paralemniscal cortical relay station [15]. However, analysis of the response properties of identified layer 5A cells *in vivo* [16] and the analysis of intracortical connections of layer 5A did not support this view (Figure 1b and e). *In vivo* analysis showed that layer 5A neurons have small receptive fields [16]. In the input maps of layer 5A cells derived by photostimulation (glutamate uncaging) (Figure 2 [17•, 18•]), a strong direct input from L4 barrels to L5A was identified, and this direct L4 barrels to L5A input was characterized on the synaptic level by a dual intracellular recording study [19].

Thus, it is now clear that lemniscal and paralemniscal pathways converge on L5A neurons. This convergence can be attributed to the dendritic architecture of L5A neurons: L5A basal dendrites are not aligned with and do not respect barrel borders, and L5 apical dendrites bend such that they preferentially pass through the borders of L4 barrels [16,20]. Both of these features foster a convergence of paralemniscal and lemniscal pathways. Taken together, these results suggest that L5A barrel cortex cells serve intracolumnar integration by combining inputs from different pathways and laminae [16].

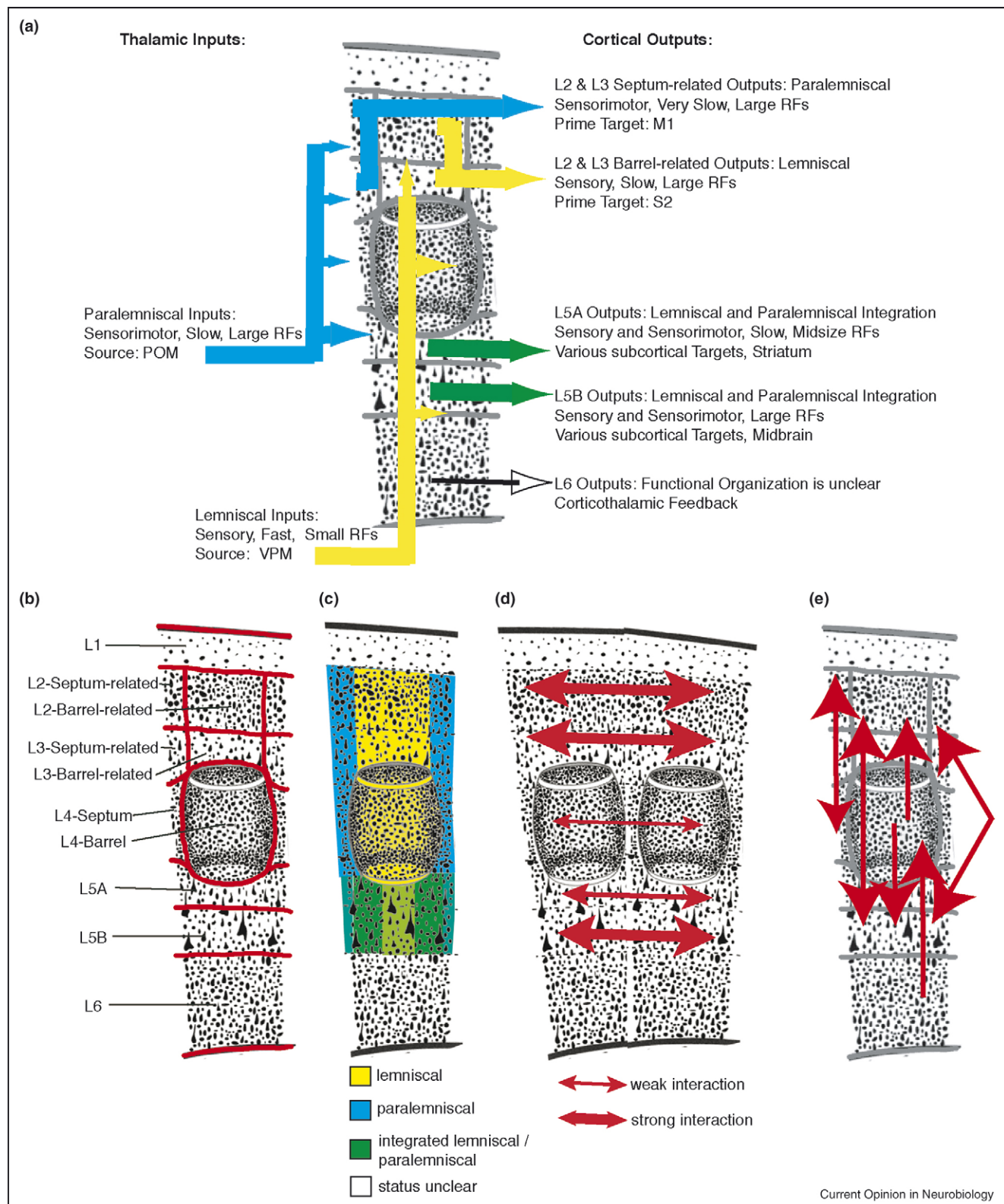
Quantitative analysis of synaptic transmission

One of the most fascinating features of barrel cortex research is the fact that this circuit has now been analyzed in much detail at the synaptic level. From such work it has become clear that most of the local intralaminar unitary excitatory connections are formed by two to six terminals and have a postsynaptic potential (PSP) amplitude of ~1 mV [21–23]; it should be noted that most but not all authors agree on these values [24]. Interlaminar connections seem to be weaker than intralaminar connections with PSP amplitudes ~0.6 mV. Recently, the thalamic input from VPM to layer 4 barrel neurons was characterized under *in vivo* conditions by combined intracellular and extracellular recordings [25•]. Much like cortical interlaminar connections, thalamocortical unitary PSP amplitudes were small—in this case ~0.5 mV. Altogether, it appears that individual cortical synaptic connections are considerably weaker than in subcortical structures, where unitary PSPs can be several millivolts and even fire postsynaptic cells [26,27].

Synaptic transmission and sparse network activity

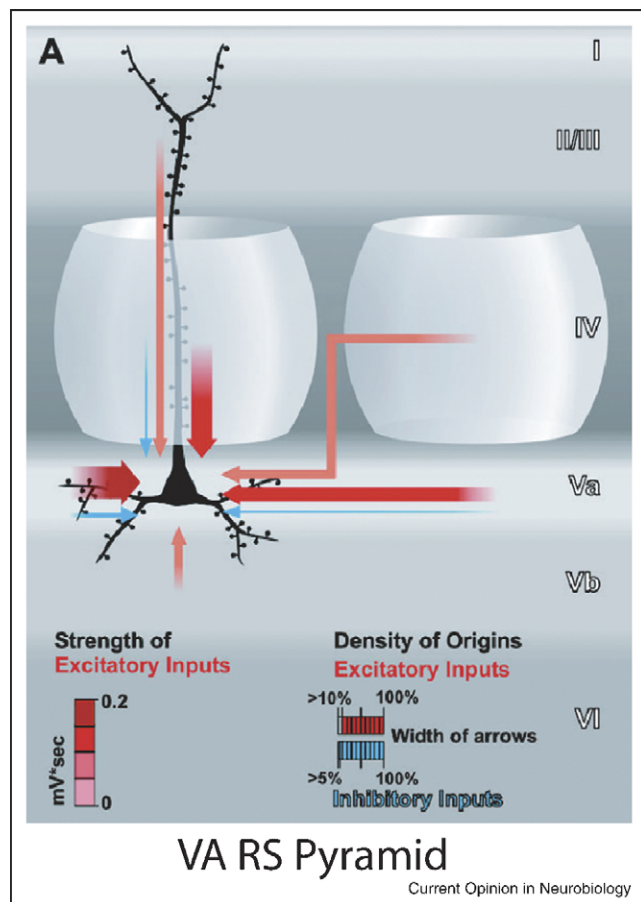
Even though weaker than subcortical connections, the average PSP of cortical synapses of 0.5–1 mV is remarkable when compared with the average amplitude sensory responses. Population averages of sensory responses vary between 5 and 15 mV in various cortical layers, and even large-scale variations of background activity (the so-called Up and Down states) that one sees in anesthetized animals usually do not exceed 10–15 mV. Since barrel cortex neuron responses are tightly locked to stimulus onset, a small number (say 5–50) of excitatory unitary connections might account for the entire average sensory response or the initiation of an Up state. Alternatively, one might speculate that a much larger number of excitatory synapses contribute to a sensory response or an Up state but that their effect is cancelled out by concomitant inhibition. Given our detailed knowledge of synaptic transmission in the barrel cortex, the quantitative composition of ongoing and sensory-evoked activity in the barrel cortex can be experimentally determined by a combination of *in vivo* intracellular recordings and compartmental single cell simulations. Such biophysical analysis supports the idea that both ongoing [28•] and evoked activities [29] are generated from a small number

Figure 1



The microcircuit of the barrel cortex. **(a)** Left, thalamic inputs. Thickness of arrows indicates the relative strength of thalamic inputs. Right, outputs from barrel cortex. Depending on whether one distinguishes between layer 2 and layer 3 outputs, five or seven population outputs can be recognized. *Abbreviations:* L, layer; RF, receptive field; M1, primary (vibrissa) motor cortex; S2, secondary somatosensory cortex; VPM, Ventral Posterior Medial

Figure 2



Excitatory and inhibitory intra-columnar and inter-columnar synaptic inputs onto layer 5A pyramidal neurons in rodent barrel cortex based on caged glutamate photolysis. The thickness of the arrows represents, in percent, the layer-specific density of origins for excitatory (red) and inhibitory inputs (blue). For simplification, densities of origins <10% for excitatory and <5% for inhibitory inputs are not shown. The average strength of the excitatory inputs are represented by the arrows' color intensity. The position of the arrowheads is not meant to indicate any specific localization of synaptic contacts. Note the massive input from layer 4 to layer 5A. Modified from Schubert *et al.* [17**].

of synaptic inputs and that usually only a fraction of a given excitatory postsynaptic response in the barrel cortex is cancelled out by inhibition. Thus, the quantitative analysis of postsynaptic activity in barrel cortex supports the findings from *in vivo* whole-cell recordings [13,30–32], which indicate that action potential activity in barrel cortex is very sparse.

Barrel cortex response dynamics

Layer 4 dynamics

The analysis of response dynamics is a classic area of interest in barrel cortex research. Pioneered by Simons and colleagues it became clear early on that responses within layer 4 are brief and very transient [33,34]. Subsequent analysis showed that the recruitment of local inhibition within layer 4 by thalamocortical afferents defines 'a brief window of opportunity' in which cortical layer 4 cells can actually respond to thalamic excitation [35]. Recent work has confirmed and considerably refined this picture. Such studies have identified and quantitatively characterized the inhibitory cell types and synaptic connections that define the window of opportunity at the cellular level. The time course of excitatory and inhibitory conductances in putative layer 4 neurons is consistent with the original claims of the Simons group [30,31]. Moreover, it was found that certain subclasses of fast-spiking interneurons receive massive thalamic input. The resulting fast-rising inhibitory activity will short-circuit responses in a feed-forward manner shortly after the arrival of the thalamic volley [36–38*]. The exact timing of excitation relative to inhibition seems also to play a crucial role in determining the direction selectivity of barrel cortex neurons [39**].

Adaptation

A number of recent studies addressed the role of adaptation in barrel cortex responses. The work of Castro-Alamancos and colleagues demonstrated that the strength of thalamocortical transmission is crucially determined by the adaptation state of thalamocortical synapses, which tend to be depressed in the awake, aroused state, when ongoing thalamic activity is high in the barrel system [40]. Analysis on the level of unitary thalamic connections is in line with this view [25**]. These and other studies [41,42] give a detailed picture of the role of the thalamocortical transmission in the adaptation of cortical responses. Recently, Diamond and colleagues demonstrated sophisticated forms of adaptation in barrel cortex neurons showing that neurons rapidly adapt to changes in the stimulus statistics [43*].

Patterned activity

The presence and significance of patterned activity in the cortical networks is a further focus of interest. Previous computational/experimental studies suggested that within single neurons the timing of responses relative to the stimulus provides important information about the

nucleus of the thalamus; POM, posteromedial nucleus of the thalamus. **(b)** Compartments. Red lines divide compartments for which both physiological and anatomical/synaptic differences have been demonstrated. Further subcompartments may exist, but the functional differences among such subdomains are likely to be weaker than the ones between the compartments indicated here. **(c)** Lemniscal versus paralemniscal processing. **(d)** Intercolumnar interactions. For simplicity in layers 2–4 only barrel and barrel-related interactions are considered. Interactions in layer 6 are poorly characterized and not shown. **(e)** Intracolumnar interactions. Only the most important interlaminar connections are shown and local recurrent connections are not indicated. Arrowheads pointing to borders of two compartments refer to both compartments. Intracortical input to layer 6 is poorly characterized and not shown. Note the convergence of intracortical inputs on layer 5 neurons.

stimulus properties [44,45]. By contrast, response patterns across neurons provide little or no extra information. A recent analysis of patterned neural discharge in ongoing barrel cortex activity came to the conclusion that such activity is largely stochastic in nature [46^{••}]. This result is in sharp contrast to conclusions from *in vitro* and *in vivo* preparations, where it was concluded that ongoing cortical activity contains complex patterns such as ‘synfire chains’ and ‘cortical songs’ [47].

Microcircuit dynamics

Although good progress has been made in unraveling thalamic and L4 dynamics, we still lack an understanding of the mechanisms that determine the overall dynamics of the barrel cortex microcircuit. It is clear that afferent information reaches barrel cortex extremely fast. Thus, sensory-evoked PSPs have latencies as short as 5–6 ms and the PSP in L4 peaks at around 15 ms [13]. This short delay is remarkable, since it involves the transduction process as well as brain stem, thalamic, and thalamocortical transmissions. While afferent transmission to L4 is probably as fast as physically possible, intracortical transmission of information is slow. The sensory-evoked PSP reaches its peak only at 33 ms in barrel-related cells of the supragranular layers and at 35 ms L5A [12,16], whereby most of the action potential output from these layers is, however, generated before the PSP reaches its peak. Given the monosynaptic connections from L4 to L2/3 and L5A, it is not clear, why intracortical transmission takes so much time. It appears that L2/3 and L5 process information in parallel rather than sequentially, and they seem to do so in recurrent circuits that go through many synaptic steps.

Behavioral analysis of active touch

Behavioral physiology

One of the biggest challenges in barrel cortex research is to derive a functional understanding of barrel cortex circuitry based on electrophysiological recordings in awake behaving animals. Much early work of this type has focused on active touch and has been recently reviewed [2]. An increasing number of labs perform recordings in awake behaving animals, and there is much very promising work in progress. Such research faces two major difficulties. First, quantitative stimulus control, which is superb in anesthetized animals, is very difficult to achieve in awake behaving animals. Second, histological identification of recording sites – which contributed crucially to our understanding of barrel cortex circuitry – is also often difficult to obtain in awake behaving preparations. In the long run novel methodologies might help to tackle such issues [48,49].

Probing whisker function in staged tests

Most of what we know about whisker function comes from staged tests, in which investigators trained rats to solve a task of choice with their whiskers. Most of these

tests were focused on the long macrovibrissae [50], and one of the first paradigms tested this way was roughness discrimination [51]. Rats show superb behavioral performance in texture discrimination tasks [52], and their discrimination capacities seem to depend to some extent on the integration of information from multiple whiskers [52]. Data on whisker movements during texture discrimination are available [53], and research on vibrissal texture discrimination is currently a very active research topic [54]. Evidence from psychophysical tests, where head-fixed rats reported whisker deflections of varying velocity and amplitude, indicates the existence of distinct psychophysical channels for sensing whisker deflections. These channels might correspond to slowly adapting and rapidly adapting afferents [55[•]]. Rats have been trained to estimate the width of an aperture with their whiskers, and also in this task discrimination capacities seem to depend on the integration of information from multiple whiskers [56]. Similarly, rats can also be trained to report the horizontal position of an obstacle from vibrissal touch [57[•]]. A particularly interesting study recently demonstrated the ability of rats to report the presence of horizontal object position with a single intact whisker [58^{••}]. This observation may suggest that rats can use an internal reference (for example, an efference copy signal) to deduce whisker position. In summary, staged tests have elucidated a wide range of whisker discrimination abilities. So far, most of these tests targeted simple psychophysical parameters. It is likely that many of such tests can easily be extended to neurophysiological studies because most of them were conducted *a priori* under rather restrained conditions.

Biological assays of active touch

An alternative approach to assess whisker function is the analysis of freely ranging animals that engage in biologically relevant behaviors. Such studies are not designed to test the animal's performance on a psychophysical parameter of the experimenter's choice. Instead experimental control is sacrificed in order to allow the animal to solve a problem of its choice. Along this line Prescott and colleagues recently analyzed whisker movements of freely ranging rats as they navigated around obstacles [59^{••}]. In this rather minimal experimental setting the authors made a host of interesting observations about whisking under natural conditions. A major one of these was the minimal impingement observation, namely that rats showed a pronounced tendency to minimize the impingement of whiskers in obstacle collisions. Prescott and colleagues also observed that unilateral object contacts triggered extremely fast (13 ms latency) contralateral protraction and ipsilateral retraction (Figure 3; [59^{••}]). The mere speed with which these behaviors occur suggests that they might be mediated by short and direct sensorimotor loops in the brain stem [60]. Whisker movements do not only interact with obstacles, but are also modulated in a complex way by the animal's head move-

Figure 3

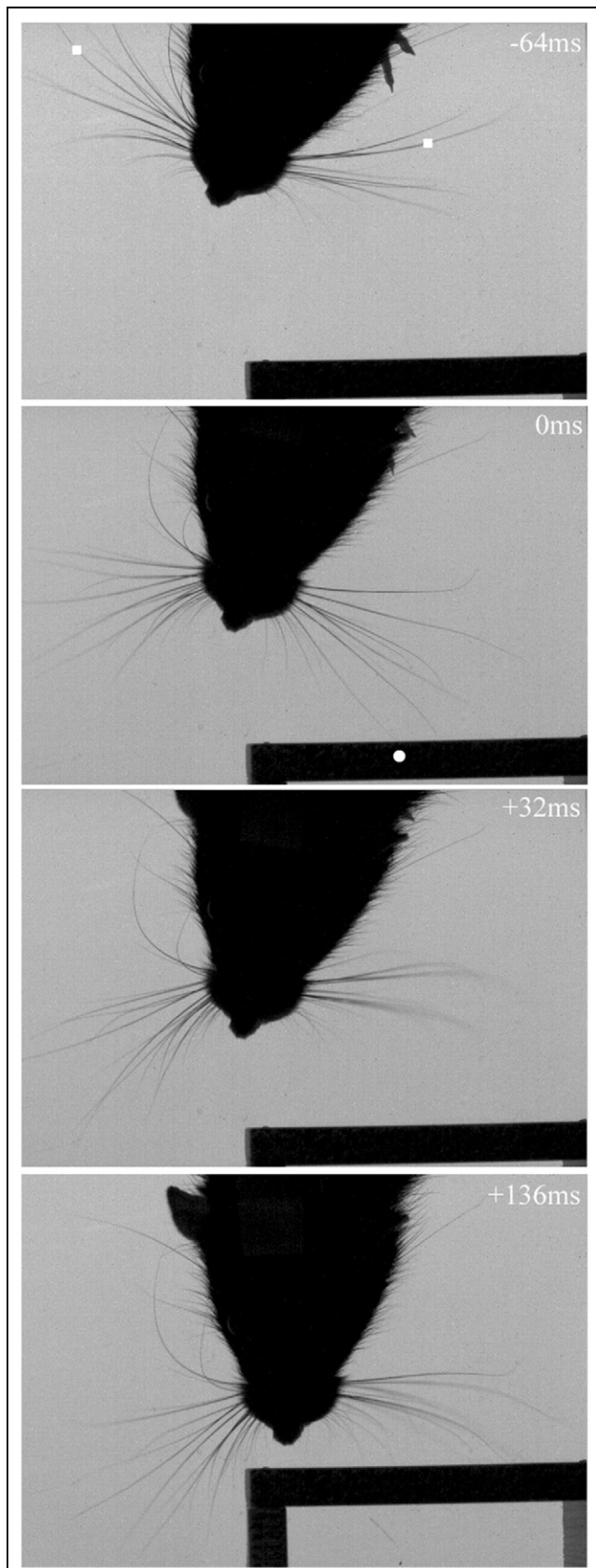
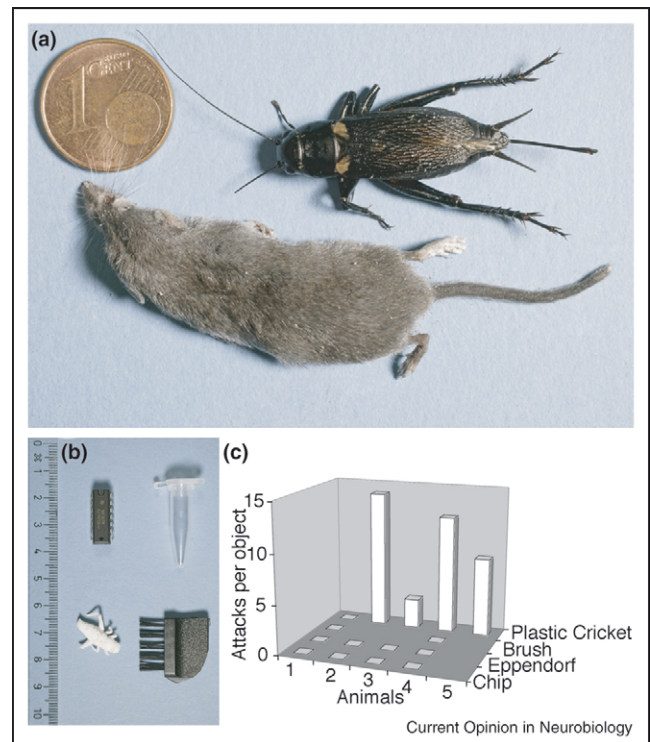


Figure 4



Tactile prey capture in Etruscan shrews. **(a)** Etruscan shrews and their cricket prey. The €-cent is 16.25 mm in diameter. **(b)** Control objects and plastic cricket. **(c)** Attack behavior toward the various objects. Attacks are selective for the plastic cricket, even though the potential olfactory, gustatory, auditory, and movement cues do not match with the real cricket. Accordingly, tactile shape cues are necessary and sufficient to trigger attacks. Modified from reference Anjum *et al.* [63**].

ments [61]. Another tactile behavior that was recently studied in detail was food acquisition in the star-nosed mole [62**]. The authors found that the mole's tactile (but in this case not vibrissal) behaviors mediate extremely fast acquisition and handling of prey [62**]. Whisker-mediated prey capture was studied in the Etruscan shrew, one of the smallest mammals [63**]. This animal

Contact triggered asymmetric whisker movements in a free ranging rat. High-speed video frames showing the effect of unilateral object contact (at $t = 0$) on bilateral whisker protraction. From the top down: ($t = -64$ ms). Protraction commences approximately synchronously on both sides of the snout; the filled white squares show the tracked rear column whiskers ($t = 0$ ms). A deflection occurs on a forward whisker; the filled white circle indicates the point of contact with the vertical surface ($t = +32$ ms). Protraction ends on the side contralateral to the contact; note that whiskers on the ipsilateral side are already partially retracted having ceased protraction at $t = +12$ ms ($t = +136$ ms). Contralateral whiskers reach maximum protraction in the whisk cycle subsequent to the initial contact. Note that the movement asymmetry occurs with a very short latency and minimizes the impingement of whiskers on the obstacle. From Mitchinson *et al.* [59**].

attacks crickets almost as big as itself (Figure 4a) and prey capture behavior relies completely on tactile shape cues. Thus, shrews attack plastic dummy crickets up to 15 times (Figure 4b and c). Attacks proceed very fast. Shrew behavior appears to be based on the 'Gestaltwahrnehmung' of crickets, that is, shrews do not only recognize local elements but also form a global construct of the cricket: (i) complex shape cues are recognized, (ii) local contact information can be used in a global way, namely to guide attacks toward distant cricket body parts, (iii) local shape manipulations of crickets lead to global behavioral effects. In summary, the analysis of unrestrained animals in biologically relevant tasks has provided rich insight into whisker function. In all cases whisker-mediated behaviors proceeded very fast, and with respect to object recognition there are perceptual similarities between primate vision and vibrissal active touch.

Conclusion

Research on barrel cortex has been dramatically advanced by a remarkable convergence of results from cellular and systems neuroscience. Processing in a column appears to be more heterogeneous than anticipated. With respect to thalamic input, cortical layers 4, 3, and 2 operate as functionally segregated compartments, and consequently the corticocortical output from these layers contributes to separate lemniscal and paralemniscal processing streams. Layer 5 neurons, on the contrary, integrate lemniscal and paralemniscal inputs as well as inputs from most or all cortical layers. Subcortical output from these neurons therefore signals an overall result of columnar computation rather than representing a specific processing stream. The response dynamics of cortical layers are strikingly different, and the intracolumnar differences in response timing by far exceed the difference in response timing between barrel cortex and secondary somatosensory cortex [64]. Thus, processing in cortical layers occurs asynchronously. A substantial fraction of thalamic afferents is required to initiate a cortical response, whereas a small fraction of cortical neurons is active in intracortical processing. While our knowledge about barrel cortex microcircuits is impressive, our understanding of the functional implications of this architecture lags behind. We know more about barrel cortex than we understand about it. Microcircuit analysis in the brains of awake behaving animals might provide answers here, but is technically still very difficult to do. A range of simple whisker-mediated behaviors has now been systematically tested. In addition, the analysis of freely ranging animals that engage in biologically relevant tactile behaviors has allowed fascinating insights into the sensory world generated by vibrissal touch.

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