

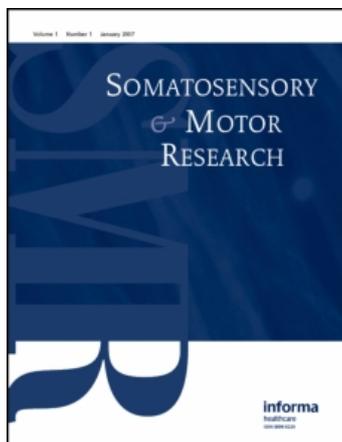
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## Barrels come of age: Barrels XXI meeting report

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### Abstract

The twenty-first annual Barrels meeting, sponsored by NINDS, was held on 12–14 November 2008 on the campus of Johns Hopkins University, near the site of the original discovery of barrels almost 40 years ago. The longest running satellite meeting to the Society for Neuroscience Annual Meeting focuses on the development, physiology, and behavior of the rodent whisker-to-barrel sensorimotor system. This year's event focused on what aspects of the sensory world are encoded by neurons within the system and how specifically the posterior medial nucleus can play a role in information processing. Other highlighted topics included the possible role(s) the cerebellum may have and the cues governing the patterning and development of thalamocortical inputs into the barrel cortex.

**Keywords:** *Barrel cortex, whisker, vibrissae, sensorimotor*

The twenty-first annual Barrels meeting, with the support of NINDS, which focuses on the development, behavior, physiology, and circuitry of the rodent whisker-to-barrel pathway, was hosted in The Charles Commons on the Homewood Campus of the Johns Hopkins University where almost 40 years ago barrels were originally “discovered” by Thomas Woolsey and Hendrik van der Loos.

The meeting commenced with a session emphasizing on how the signals from the external world are encoded by the whiskers and then “translated” into a neural signal within the barrel cortex and other related neural structures. After a brief introduction by **Joshua Brumberg** (Queens College, CUNY), the morning session was led off by **Mathew Diamond** (SISSA, Trieste, Italy) who focused on how texture representation may be transformed into a behavioral category and subsequently recorded into a memory matrix, which was related to hippocampal firing patterns. This is comparable to visually related memory in the case that hippocampal neurons respond to the faces of famous people. It is therefore speculated that there may also be a direct signal

carrier that preferentially transmits information from the whisker system to the hippocampus. In addition, it was presented that there may be coherence in the transmission of the signal from the barrel cortex to hippocampus. It was demonstrated that an onset of response in the barrel cortex elicits subsequent and faithful responses in CA1 place cells. The results of the information analyses further suggested that approximately 40% of the neurons carried significant “event information”, 50% of the neurons carried categorical information (behavioral actions), and 30% of the neurons carried significant “extra texture” information that discriminates subtle textural nuances even within the same category.

Next, **Christine Vahle-Hinz** (University Medical Center, Hamburg, Germany) focused on the relationship between vibrations of the whisker and sensory processing at the barrel cortex. To examine this relationship, recordings from the barrel cortex were taken while the whiskers of a rat were stimulated. Her results indicated that high frequency signals are present in the barrel cortex and that these high frequency signals (>100 Hz) are accompanied

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by an increase in gamma-band activity which may underlie the integration of signals from the whiskers. It was shown that both the local field potentials and single unit activity within the barrel cortex could be entrained by the high frequency whisker stimulations.

**Adrienne Fairhall** (University of Washington) followed with a talk that focused on adaptive coding in the somatosensory cortex. It was proposed that there is a separation of response components at different timescales: short timescales were governed by single spikes, whereas longer timescales were decided by the mean firing rate. Consequently, the multiplexing of the neuronal firing properties is associated with single channel activities. Mathematically, it was suggested that the eigenspectrum of the barrel cortical neurons may play a role as differentiating filter for action potential-inducing stimuli and stimuli that do not induce action potentials. Therefore, the overall change in the amplitude of neuronal firing may be related to the neuronal strategy for differentiating a variety of tactile stimuli in the rodent vibrissae system. The underpinning mechanisms for this adaptive spike coding may be modulated by changes in stimulus statistics (variance and standard deviation of the firing amplitude). For instance, in periodically switched stimulus variance, when the velocity stimulus is low in amplitude, the rate of spiking is also low. Similarly, when the velocity stimulus is high in amplitude, then the rate of spiking is also high. This directly pinpoints that statistical components of the firing amplitude are strongly associated with the spiking train rate. Furthermore, there is also a transfer function when the phase of sine waves is shifted. For instance, when a cortical pyramidal cell is injected with white noise and square wave current, there is a very consistent input and output as a function of the amount of phase shift. Moreover, shifting cell intrinsic properties, such as the characteristics of the afterhyperpolarization, and the sodium current can also generate similar phase shifts. This actually has been suggested to be dependent on the “slow”-acting activities of the ionic channels.

**Daniel Feldman** (University of California, Berkeley) followed with a talk on the responses of barrel neurons in response to active palpation of textured surfaces. It was demonstrated that active whisking of sand paper of different coarseness resulted in the whisker becoming momentarily stuck in a contour followed by it being released and slipping across the surface at a higher velocity than it was going prior to its sticking. It was proposed that when a whisker slips, that is, “lets go” of the contact surface, this creates a highly resonating as well as accelerating event for that whisker, and this may be

related to the coding of the object recognition in the barrels. It was demonstrated that a fast slip event is associated with a weak probability for the firing of the neuron. This peak is temporally very narrow and is approximately 20 ms. Moreover, across the sampled 90 neurons there are about 86.5% that do not elicit action potentials, while the rest have increased firing probability. A further receiver operator curve (ROC) analysis revealed that there is a 97% accuracy rate in predicting the activities of layer IV barrel neurons based on a significant whisker slip event. In addition, slip events also increase firing synchrony in S1.

The session was concluded by **Chris Moore** (MIT) who used high-speed videography to closely observe how whiskers in an awake rat make contact with the environment. His analysis focused on how the texture of an object influenced whisking velocity and amplitude. Similar to Feldman it was shown that whiskers engage in stick-slip events which are followed by a “ringing” as the whisker restarts its motion. Looking at the “stick-slip-ring” movement of the vibrissae, it was found that the “stick-slip” motion was related for rough surface contact, whereas periodic motions were used more for smooth surface contact. Moreover, it was observed that vibrissae length affected frequency timing in both the smooth and rough texture conditions.

Following a spirited discussion, **Laszlo Acsady** (Institute of Experimental Medicine, Hungary) moderated a series of short talks. First to present was **Ayan Ghoshal** (Vanderbilt University) who provided evidence that early sensory deprivation blocked the development of neuronal synchrony within the barrel cortex as well as decreasing the magnitude of the responses and increasing their latency to whisker stimulation. **Randy Bruno** (Columbia University) demonstrated that following sensory deprivation the axons of supragranular pyramidal neurons rearrange such that they tend to avoid barrels whose whisker input has been deprived and target areas over barrels that are still receiving afferent drive from their whiskers. **Qian-Quan Sun** (University of Wyoming) demonstrated that the trophic factor BDNF is expressed in a barrel-related pattern, and following its genetic deletion the clustering of the thalamocortical arbors in a barrel-like pattern was still evident. In animals where BDNF was knocked in to the barrel cortex some effects of sensory deprivation were ameliorated, such as the finding that parvalbumin positive neurons did not show a decline, but paired pulse deprivation was not evident similar to the deprived condition. The session was concluded by **V. Rema** (National Brain Research Centre, India) who demonstrated that a lesion of one barrel cortex resulted in decreased activity in the contralateral barrel cortex, and that side displayed less experience-dependent plasticity.

Following a lesion of motor cortex, the ipsilateral barrel cortex showed increased spontaneous and whisker-evoked activity in layer V and these same animals did not perform as well on a gap crossing task.

Following lunch, **Phil Zeigler** (Hunter College, CUNY) and **Thomas Woolsey** (Washington University) spoke in remembrance of their late mentor and friend, Wally Welker. Wally Welker (1926–2007) was an extremely influential person to the barrels community. Interested in studying behavior and sensorimotor integration, he was one of the first to focus on the importance of understanding the nature of rodent whisking. More than just an influential scientist, he was a kind and sympathetic person who influenced not only the field itself, but the people in it as well. (These presentations are published separately following this meeting report.)

The scientific session then resumed with a series of short talks moderated by **Tony Prescott** (University of Sheffield). **Dan Hill** (UC San Diego) looked at the cortical representation of whisker movements during protraction and retraction. Recording of the vibrissae motor cortex (vM1), it was found that intrinsic muscle groups were responsible for whisker protraction and that intrinsic muscle representations form a vibrissatopic map in vM1. **David Golomb** (Ben-Gurion University, Israel) constructed a computational model of the whisker, mystacial pad, and the intrinsic and extrinsic muscles to examine how spikes from the facial motoneuron control whisker movements. The model suggested that a single intrinsic muscle activated by a single spike is the minimal unit necessary for whisker control. **Todor Gerdjikov** (Hertie Institute for Clinical Brain Research, Germany) examined which physical parameters of a stimulus are encoded in the tactile system and how they are discriminated. Rats had to discriminate between stimuli of varying intensities and amplitudes. It was found that intensity plays a major role in discriminating between stimuli. **Blythe Towal** (Northwestern University) provided data on how rats used their whiskers to explore their environment. A high-speed video camera and a laser light sheet were used to better examine how the whiskers make contact with their environment. It was shown that the whiskers examine their environment in the caudal to rostral plane. It was also found there is a temporal delay when the whisker contacts are distributed along the rostral to caudal plane and this delay may indicate how the flow of information is processed in the cortex. The session was concluded by **Steven Hsiao** (Johns Hopkins University) who focused on the representation of object size in the primate somatosensory cortex. It was observed that finger

position and separation when grasping an object was correlated with the compliance of the material being grasped. Data from the second somatosensory cortex of primates where both cutaneous and proprioceptive inputs are first integrated appear to correlate with the psychophysiological findings.

Following Dr Hsiao's talk, **Peter Strick** (University of Pittsburgh) enlightened the audience with his talk emphasizing the cerebellar–cerebral anatomical loops, and how these intertwining pathways may be related to movement, cognition, and perception. It was found that multiple cortical areas project to the pontine nuclei, which serves as major input into the cerebellum. Utilizing a variety of viral-labeling techniques and sampling at preselected time points, it was found that the majority of the cortical areas in the motor system (M1, premotor area, supplementary motor area) are reciprocally connected to the cerebellum, and these connections are organized in a topographic fashion in the dentate nucleus of the cerebellum. In addition to interconnectivities to the motor system, the dentate also projects diversely to a number of non-motor areas. In general, data indicated that the dorsal part of the dentate gyrus is the motor projecting domain whereas the ventral part of the dentate is the non-motor projecting domain. With respect to the barrel–cerebellar interactions, the barrel cortex projects to pontine nuclei and therefore has indirect connection to the cerebellum. This loop is completed with the cerebellar–thalamic (likely POM) projection. It was posited that due to the interconnections between the cerebellum and barrel cortex, the cerebellum may play an important role in motoric, cognitive, and perceptual integration in general.

Following a brief break, **Zoltan Molnar** (University of Oxford) spoke on early cortical circuit integration of subplate neurons in the developing barrel cortex. The audience was reminded that the cortical plate develops inside-out, and that known laminar-specific transcription factors including *Golli-Z*, *TBR1* (layer 6), and *OTX1* (layers 5 and 6) play important roles. Using the *Golli-eGFP* mouse, there was an interesting “flip” of fluorescence labeling in P6 (labeling predominantly barrels) and P10 (labeling predominantly septa). At P10, the green fluorescent protein (GFP)-labeled neurites aggregate at the layer IV–V boundary, with their somata mostly labeled near septa and their neurites labeled at barrel hollows. Furthermore, results suggest that this septa-to-barrel reorganization is activity dependent, as removal of a whisker row resulted in the absence of GFP reorganization in the corresponding septa/barrel columns.

The first day was concluded with a poster session and a dinner.

The Friday session began with a series of talks moderated by **Ford Ebner** (Vanderbilt University) who reviewed the function of the posterior medial thalamic nucleus (POM) in processing whisker-mediated information.

**Martin Deschênes** (Laval University, Canada) elegantly detailed the circuitry involved in the parallel transmission of sensory information from the sensory periphery to the barrel cortex. The POM was shown to receive a strong input from the SpVir (sensory trigeminal nucleus interpolaris, rostral subdivision) as well as from other structures such as the inferior olive, zona incerta, and para-brachial nucleus. Interestingly, data showed that septal neurons were unaffected by lesions in SpVi, their receptive fields were maintained due to a strong input from the head of the thalamic barreloids within the ventral posterior medial (VPM) nucleus which forms one branch of an important sensorimotor loop which is closed by septal neurons projection to M1 which in turn provide feedback to the head of the barreloids. Although septal neurons were unaffected by SpVi lesions, neurons in the principal sensory nucleus (PrV) showed increased activity, emphasizing the important role of inter-trigeminal nuclei interactions in modulating information headed to higher order centers. Those within trigeminal nuclei interactions are influenced by cortico-fugal inputs originating from both the barrel and motor cortices. Furthermore, it was suggested that these inter-trigeminal nuclei connections can serve as a gate on ascending information. When cholinergic input is low (a sessile rat) there is little activity in the GABAergic neurons within SpVi that target PrV. Conversely, the gate is open when there is high cholinergic input (active states) the PrV gate is closed which may allow for focusing of afferent input onto only behaviorally relevant stimuli.

Next, **Asaf Keller** (University of Maryland Medical School) proposed that the POM plays a more important role in processing pain/nociceptive information than tactile information. One key piece of evidence was the finding that in general POM responses to tactile stimuli are relatively poor, but their responses to noxious stimuli were quite robust. It was shown that under normal basal condition, the zona incerta (ZI) normally inhibits POM neurons, but when the ZI is lesioned, there are larger responses in POM which seem to cause hyperalgesia.

**Ehud Ahissar** (Weizman Institute, Israel) focused on how POM function plays a role in the overall processing of sensory information within the whisker-to-barrel cortex system. It was suggested that passive stimuli activate sensory pathways whereas active stimuli involve motor pathways as well. He found that the POM primarily conveys whisking signals important for object processing and

that the POM might be modifying whisker signals coming from the brainstem before sending the information to the cortex. There are three parallel pathways in which information ascends to the barrel cortex, the lemniscal system which is relayed through the VPM, the paralemniscal system which is relayed through POM, and the extralemniscal system which is relayed through a subdivision of VPM. These three streams are integrated in the cortex within both the barrels and the second somatosensory cortex.

A series of short platform talks moderated by **Rony Azouz** (Ben-Gurion University, Israel) commenced after a brief break.

**Mitra Hartmann** (Northwestern University) led off by focusing on mechanical forces that are experienced by the vibrissae. It was observed that rodents exhibit high diversity in their behavior when it comes to object exploration. Mechanically, the relative motion at the base of the whisker follicles, affected by both intrinsic muscle movement and inertia, play an important role in object exploration. It was suggested that moment is more important than the force in the axial axis of the body. However, force becomes crucial for whisking in regards to the orthogonal axis. Further, it was demonstrated that when the vibrissae's convex side is facing the object, the amount of force is significantly greater than if the concave side is facing the same object. It was therefore postulated that the axial force may be the mechanism for rapid object recognition in the whisker system.

**Laszlo Acsady** (Institute of Experimental Medicine, Hungary) followed by giving a talk on input-specific localizations of A-type  $K^+$  channels in the somatosensory thalamus. It was proposed that these channels are important for dendritic integration of signaling. The clusters of Kv 4.2 and 4.3 are abundant in VPM and sparse in POM. Utilizing the silver particles immunoreactive staining technique, it was found that large presynaptic axonal buttons are associated with silver particles in the VPM thalamus. Furthermore, there is a high probability of Kv 4.3 overlapping with vGLUT2 staining. Since  $K^+$  channels are typically near the membrane of the neurons, the observed silver particles exhibit the highest density amongst the dendritic spine membrane in co-expressed vGLUT2 neurons. By contrast, the overall silver particles are rarely found in PO, suggesting that there are far less Kv 4.2 channels in PO compared with VPM.

**Michael Pesavento** (University of Rochester) presented a talk focusing on barrel neuronal response sensitivity using *in vitro* and computational techniques. It was found that neuronal responses depended on both network interactions and their intrinsic physiological properties. Using computation modeling based on conductance of excitatory and

inhibitory neurons, the firing properties of neurons were simulated. It was found that increasing feedforward inhibition suppressed the slow input. By contrast, if all of the neurons are excitatory, then the network response is enhanced. It was concluded that the interconnectivities between various subtypes of barrel neurons serve as crucial components in terms of the neuronal sensitivities to input.

The session concluded with a talk delivered by **Ariel Agmon** (West Virginia University) using paired recordings between pairs of GABAergic interneurons within the barrel. He showed that in the condition that promoted spontaneous activity (0 mM  $Mg^{2+}$  in the extracellular solution) it was demonstrated that there was a propensity towards synchronous firing of action potentials. The greatest synchrony was displayed by the neuron which co-expressed the  $Ca^{2+}$  binding protein somatostatin.

Following lunch **Mary Ann Wilson** (Johns Hopkins University) moderated another series of short talks.

First to speak was **Rony Azouz** (Ben-Gurion University, Israel) who studied the kinematic responses of whiskers in response to being presented with different gradients of sandpaper on a drum that was rotated such that the whisker of interest could be in constant contact with it. It was found that there was a bi-modal distribution of whisker movement: those at less than 50 Hz and those greater than 50 Hz. It was shown that the whisker served to filter the signal and that there was little spiking response in the trigeminal ganglia following stick-slip-ring events, but that the high frequency perturbations of the whisker faithfully evoked spikes in the trigeminal ganglia neurons.

**Guglielmo Foffani** (Hospital Nacional de Parraplejicos, SESCAM, Spain) followed with a talk highlighting the consideration of more than just the absolute number of action potentials. If consideration of spike timing is also used approximately twice the amount of information can be extracted from the spike train.

**Vivek Khatri** (Vanderbilt University) concluded the session with a talk focused on how VPM and trigeminal ganglia neurons encode kinematic variables measured from the whiskers. Neurons neither in VPM nor the trigeminal ganglia responded robustly to the onset of whisking in air. In general, VPM neurons cannot distinguish between a moving and a stationary whisker.

The meeting was concluded with a session focused on the guidance and patterning of thalamocortical afferents introduced and moderated by **Jochen Staiger** (Albert-Ludwigs Universität, Germany).

**Patricia Gaspar** (INSERM, France) was the first to present a talk focused on development of the cerebral cortex. It was suggested that two crucial

genes, *rim1* and *rim2*, play pivotal roles in priming of synaptic vesicles and functioning of the calcium-dependent rab-GTP in axonal boutons. Utilizing transgenic mouse technology of the floxed animal to preexisting cre-transgenics, it was demonstrated that knocking out *rim1* or *rim2* by themselves does not significantly perturb the development of barrel clusters. However, simultaneous KO of *rim1* and *rim2* significantly disrupts the formation of the barrel pattern in layer IV. Although the extent of this perturbation does not include axonal patterning or gene expression in layer IV, the altered distribution of somal population in barrels is evident. Furthermore, the effect of sensory enrichment in development induced elevated *c-fos* expression in normal animals. This elevated *c-fos* is, however, absent in animals with double KO of *rim1* and *rim2* genes. It is therefore concluded that *rim1* and *rim2* most likely work together in their roles in synaptic transmission and the molecular substrate of axonal pattern development in barrel cortex is independent of synaptic transmission.

**Denis Jabaudon** (University of Geneva, Switzerland) followed by emphasizing in his talk the role of transcriptional control on cortical input and output circuitry. He proposed that two transcriptional factors, *SOX5* and *COUP-TFI*, play important roles in temporal and spatial development of the cerebral cortex. For example, *SOX5*, expressed in early formed cortical layers, has been demonstrated to temporally regulate the cortico-spinal neurons (CSMN) during corticogenesis. Consequently, loss of *SOX5* causes abnormal redistribution of CSMN in layer V pyramidal neurons. *COUP-TFI*, on the other hand, is predominantly expressed in sensory cortices and inhibits subcortical projections. Loss of this transcription factor results in cortical neurons to premature and presents with much more subcortical neuronal features. These data highlight the importance of transcriptional factors in temporal and spatial development of the cerebral cortices.

Finally, two short talks were delivered by **Chia-Chien Chen** (The Graduate Center, CUNY) who examined the morphology of neurons in layer VI of the mouse barrel cortex. Reconstructing over 200 neurons from this layer using the Golgi staining technique and unbiased statistical methodologies revealed six distinct morphological groups within layer VI.

**Moritz Helmstaedter** (Max-Planck Institute for Medical Research, Germany) unveiled a more comprehensive way of constructing neural circuits. Using images obtained by the Serial Block Face Scanning Electron Microscope it is becoming possible to conduct automated electron microscopy with subsequent automated tracing algorithms

which will allow for reconstruction of large cortical circuits.

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