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Journal id: CSMR_A_253717

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Title: Barrels XIX Meeting Report

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Barrels XIX Meeting Report

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(Received ■ ■ ■ ■ ■; accepted ■ ■ ■ ■ ■)

10 The 19th annual Barrels Meeting (Barrels XIX) was hosted by the Neuroscience Institute at the Morehouse School of Medicine in Atlanta, Georgia on 12 and 13 October 2006. The meeting brought together over 125 researchers from ten different countries to discuss the anatomy, physiology, and behavior of the rodent whisker-to-barrel pathway as well as its associated neuronal structures.

15 The meeting began with a session focused on the neuronal activity patterns evoked by whisker deflections. Dr Mathew Diamond (SISSA, Trieste, Italy) focused on the effect that temporal noise had on action potential discharges in the barrel cortex. Noise was defined in the temporal domain such that the overall stimulation rate was fixed at a specific rate, for example, 10 or 20 Hz but the interval between stimuli was varied accordingly. It was found that as the noise increased there was less adaptation to the stimulus presentation and the magnitude and temporal precision of the cortical response increased. It was suggested that the noise in the stimulus may play an adaptive role in setting the gain of the whisker-to-barrel system with low frequency noise resulting in low velocity sensitivity whereas high frequency noise makes the system more sensitive to high velocity stimuli. Dr Daniel Barth (University of Colorado) followed with a talk that demonstrated the existence of fast oscillations within the barrel system and that they served as coincident detectors for inputs from multiple whiskers. Similar to classic single unit studies conducted by Daniel Simons and colleagues, field potential recordings show suppressive effects between adjacent whiskers which act to sharpen the temporal window in which coincidence detection can occur. Interestingly,

there were no differences in summation between within arc vs. within row interactions suggesting that the barrel cortex may function as a two-dimensional integrative array. The session was concluded by Dr Mitra Hartmann (Northwestern University) who asked the question, what aspect(s) of tactile stimuli is/are encoded by the whisker? Using a combination of robotic, computational, and neurophysiological approaches Dr Hartmann argues that moment (often called torque) and the rate of change of moment are crucial for three-dimensional feature extraction of an object by a rodent's whiskers.

The past year saw the passing of Peter Land (University of Pittsburgh) a respected member of the Barrels community. Daniel Simons (University of Pittsburgh) a longtime friend and collaborator reminded the community of his research accomplishments with special emphasis on his work in studying the development of the barrel system. Peter will be remembered fondly for his enthusiasm not only for scientific research but for experiencing life to its fullest extent.

A series of short talks highlighted the diversity of responses seen within the barrel system *in vivo* following whisker deflections. Vincent Jacob (CNRS, Gif-sur-Yvette, France) presented results from intracellular *in vivo* recordings from barrel cortex while simultaneously stimulating up to 25 whiskers on the contralateral mystacial pad. Using a sparse noise stimuli, Jacob and his colleagues were able to construct spatiotemporal receptive fields for each neuron and found that most neurons had multi-whisker receptive fields and were sensitive to the temporal ordering of whisker contacts. Does a single neuron's firing have an effect on sensory processing? To address this question, Arthur

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80 Howeling and Michael Brecht (Erasmus, the
Netherlands) used a head-fixed awake-behaving
preparation to show that *in vivo* juxtacellular micro-
stimulation of individual barrel neurons could elicit
a sensation measure via tongue lick responses.
85 Soo-Hyun Lee (University of Pittsburgh) showed
that activation of primary motor cortex (M1) can
result in expression of sensory-evoked receptive
fields in antidromically activated corticothalamic
neurons that under control conditions did not
display suprathreshold responses. Finally, Shubo
90 Chakrabarti (Pennsylvania State University College
of Medicine) demonstrated that primary motor
cortex neurons, especially those in the deeper
layers, short-latency respond to whisker stimulation.
Inactivation of S1 and S2 led to a decrease in the
95 magnitude of the M1 response suggesting that these
areas provide feedforward inputs to M1.

In another series of short talks, the growing
emphasis on the intrinsic biomechanics of the
vibrissae was highlighted. Jason Wolfe (University
100 of California San Diego) showed that during active
whisking in air, whiskers demonstrate different
resonances that are not due to air currents or head
motion. Furthermore, during active whisking
of textured surfaces (sandpaper) it was seen that
105 stick-slip whisker events were observed, though the
nature of the frequency of the whisker responses did
not vary as a function of the roughness of the texture.
These results suggest that during whisking in air vs.
contact with stimuli, the whisker is in an undamped
110 vs. damped regime, respectively. Jason Ritt
(Massachusetts Institute of Technology) using
high speed videography, further demonstrated
the existence of stick-slip events when whiskers
contacted a surface. The result of such events was a
115 “ringing” of the whisker whose frequency was
proportional to the reciprocal of the whisker length
squared. These observations suggested that the
conventional stimuli used to probe receptive fields
in anesthetized preparations have significantly lower
120 velocities than is observed during active whisking
epochs. Dan Hill (University of California
San Diego) showed that a sequence of extrinsic and
then intrinsic muscles govern the whisking cycle and
that there are three distinct phases of muscle activity.
125 The first phase is characterized by retraction and is
mediated by the extrinsic muscles (*M. nasolabialis*
and *M. maxillolabialis*). The second and third phases
are characterized by protractions and are governed
by the extrinsic muscle *M. nasalis* followed by
130 the intrinsic muscles. Tony Prescott (University
of Sheffield, UK) showed that rats can perform
asymmetric whisking in cases where one mystacial
pad contacts an object and remains relatively still
while the whiskers on the opposite side of the
135 face continue to move. Using their videographic/

behavioral results, they were able to construct
a robotic rodent (whiskerbot) that could whisk
and orientate to objects. Carl Peterson
(Ecole Polytechnique Federale de Lausanne,
Switzerland) using a combination of *in vivo* whole-
140 cell recordings and voltage sensitive dye imaging
showed that single whisker deflections can result in
the activation of the large majority of the cortical
plate. Activation was first observed in S1 followed
at short latency by responses in M1 which may
145 drive future whisker movements or head orienting
responses. Finally, Venkatesh Gopal (Northwestern
University) detailed the construction of the
“Whole Rat Catalog”, a complete three-dimensional
150 reconstruction of the rat face including the position,
shapes, and orientations of all whiskers. Such
a database was offered as a way of understanding
the movement and orientation of the whiskers and
head during behaviors involving the whiskers
or olfactory stimuli. The meeting continued with
155 a poster session whose abstracts follow this report.

The second day of Barrels XIX began with a talk
by Steve Hsiao (Johns Hopkins University) provid-
ing data from single unit recording studies in awake,
160 behaving monkeys. Within the periphery, sensory
afferents do not convey any information about
stimulus orientation. In contrast, S1 neurons were
shown to be well tuned for orientation and data from
neural recordings were well matched to identified
165 psychometric thresholds. In S2, three maps exist with
neurons having different receptive field properties
(untuned excitatory RFs, untuned inhibitory
RFs, and orientation tuned RFs). These different
RF types show changes in firing rates in response to
170 changes in hand position which may be important in
object perception.

Following Dr Hsiao’s talk there was another series
of short talks focusing on data derived from *in vivo*
studies. First to present was Tatiana Bezdudnaya
(University of Maryland) who provided new data
175 from single unit recordings from the lateral
dorsal nucleus (LD) of the thalamus. In urethane-
anesthetized rats, it was observed that whisker
stimulation resulted in short-latency excitatory
responses suggestive of direct input from peripheral
180 afferents. Consistent with this observation, electrical
stimulation of nucleus interparialis resulted in
short-latency excitation of LD units. Interestingly,
electrical stimulation of barrel cortex resulted in
185 both antidromic and orthodromic responses, sug-
gesting reciprocal connections from LD to barrel
cortex. Randy Bruno (Max Planck Institute for
Medical Research) presented data from recordings
from pairs of connected thalamic and barrel neurons
190 *in vivo*. Whole-cell recordings from barrel neurons
and cell-attached recordings from thalamic neurons
provided unequivocal confirmation of connected

pairs and revealed that single thalamocortical (TC) impulses result in very weak excitation of barrel neurons (<1mV). These data emphasize the importance that synchronous firing of many TC neurons converging onto individual barrel neurons has on the excitation of barrel cortex. Robert Sachdev (Yale University) presented *in vivo* intracellular recordings from barrel neurons during spontaneous membrane potential fluctuations (up-down states). Interestingly, the up-state was found to be associated with decreased responsiveness to whisker stimulation and appears to be mediated by increased inhibition. Whisker stimulation during down-states often resulted in transitions to up-states suggesting that peripheral inputs can trigger widespread excitation of barrel circuits. Jason Kerr (Max Planck Institute for Medical Research) demonstrated the response properties of networks of barrel neurons to whisker stimulation with 2-photon calcium imaging. Neurons responding to stimulation onset, offset, or both were detected as well as network-level response features. Whisker stimulation resulted in greater spatial correlations in network activity compared to spontaneous firing. With the same imaging preparation, David Greenberg (Max Planck Institute for Medical Research) used reverse correlation and information theory to evaluate the predictive strength of detecting whisker stimulation onset. Near perfect detection of stimuli was achieved when data from 175 to 200 simultaneously imaged neurons were included in analyses. Gaute Einevoll (Norwegian University of the Life Sciences) described novel quantitative methods to extract network-level connections between cortical lamina from data acquired with linear electrode arrays. Extracting low frequency local field potentials representing synaptic inputs and high frequency signals from spiking neurons, this novel method (Laminar Population Analysis) can demonstrate the sequential spread of excitation from granular to supragranular layers and can be used to detect novel connection patterns. Maria Popescu (Vanderbilt University) presented single unit data from rats following unilateral or bilateral whisker trimming. Bilateral deprivation resulted in a decrease in spontaneous and evoked responses in both barrel and septal columns. In contrast, unilateral deprivation (UD) resulted only in changes in and above barrels, while septal neurons remained unchanged.

Moving to anatomical and *in vitro* studies in the afternoon, Julian Broser (Max Planck Institute for Medical Research) demonstrated axonal reorganization made by layer 2/3 barrel neurons following whisker trimming. Whisker trimming of rows A–C was combined with injection of a lentiviral vector encoding GFP into the D2 barrel which revealed a significant reduction in the number of

axons projecting toward C row barrels. Axonal reorganization was restricted to axons of supragranular neurons. Alexis Hattox (Brandies University) identified layer 5 barrel cortex neurons which projected to the striatum, the contralateral cortex, the thalamus, or trigeminal nuclei following retrograde labeling and targeted these neurons for whole-cell recordings *in vitro*. Neurons with callosal and striatal projections were found to display similar intrinsic electrophysiological properties including strong spike frequency adaptation. In contrast, layer 5 neurons with thalamic as well as trigeminal projections showed little adaptation. Microarray analysis of layer 5 neurons revealed differential expression of several genes including potassium channels which may underlie the physiological phenotype of each cell type. Raddy Ramos (Queens College, CUNY) presented data from *in vitro*, whole-cell recordings of identified callosal neurons in layer 2/3. Retrogradely labeled callosal neurons displayed a “regular-spiking” phenotype and had pyramidal cell morphologies including spiny dendrites. In order to reveal the axonal projections of callosal neurons, GFP was expressed in layer 2/3 neurons by electroporation *in utero*. Analysis of labeled axons revealed that layer 2/3 callosal neurons preferentially target layers 1–3 and 5/6 while avoiding layer 4.

The meeting was concluded with two talks which utilized imaging techniques to assay neuronal structure and function. Wen-Biao Gan (New York University) discussed the growth and elimination of dendritic spines as well as the effect of sensory deprivation on these processes. During the first postnatal month, dendritic development in barrel cortex is characterized preferentially by spine elimination rather than growth. Sensory deprivation via whisker trimming during this period results in a reduction in the number of spines eliminated and subsequent regrowth of whiskers accelerates spine elimination. The second talk was by Fritjof Helmchen (University of Zurich), who presented advances in 2-photon microscopy for use in imaging large three-dimensional neuronal networks *in vivo* during the presentation of controlled whisker stimuli. Piezo-electric devices were used to move objectives along predetermined trajectories in order to image from up to 400 cells including neurons and astrocytes. Alternatively, objectives could be moved to image selected cells found along various depths and spatial locations.

Barrels XIX emphasized the inter-disciplinary nature of the field with presentations using a whole host of modern molecular, cellular, physiological, and imaging techniques to probe the structure and function of the barrel model system.

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Acknowledgements

Thanks to Cathy Woodley and Dr Peter MacLeish for their assistance at the Morehouse School of Medicine. Ms Kathy Diekmann was instrumental in putting the meeting together and Drs Randy Bruno,

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Mitra Hartmann, and Jochen Staiger assisted in planning the meeting. The meeting was supported with generous support from the National Science Foundation, Division of Integrative and Organismal Biology.

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