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Somatosensory and Motor Research

Publication details, including instructions for authors and subscription information: http://www.informaworld.com/smpp/title~content=t713393866

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First Published on: 01 September 2007 To cite this Article: Ramos, Raddy L. and Brumberg, Joshua C. (2007) 'Barrels XIX Meeting Report', Somatosensory and Motor Research, 24:3, 135 - 138 To link to this article: DOI: 10.1080/08990220701538562 URL: http://dx.doi.org/10.1080/08990220701538562

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Barrels XIX Meeting Report

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The 19th annual Barrels Meeting (Barrels XIX) was hosted by the Neuroscience Institute at the Morehouse School of Medicine in Atlanta, Georgia on 12th and 13th of 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.

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 Peter Land's 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 multiwhisker 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 Howeling and Michael Brecht (Erasmus, the

Correspondence: J. C. Brumberg, Department of Psychology, Queens College, CUNNY, 65–30 Kissena Boulevard, Flushing, NY, 11367, USA. Tel: +1 718 997 3541. Fax: +1 718 997 3257. E-mail: joshua.brumberg@qc.cuny.edu ISSN 0899–0220 print/ISSN 1369–1651 online © 2007 Informa UK Ltd. Netherlands) used a head-fixed awake-behaving preparation to show that in vivo juxtacellular microstimulation of individual barrel neurons could elicit a sensation measure via tongue lick responses. 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 Chakrabarti (Pennsylvania State University College of Medicine) demonstrated that primary motor cortex neurons, especially those in the deeper layer, demonstrate short-latency responses to whisker stimulation. Inactivation of S1 and S2 led to a decrease in the 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 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 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 damped regime, respectively. Jason Ritt vs. (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 "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 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. 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 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 face continue to move. Using their videographic/

behavioral results, they were able to construct a robotic rodent (whiskerbot) that could whisk Carl and orientate to objects. Peterson Polytechnique Federale de Lausanne, (Ecole Switzerland) using a combination of in vivo wholecell 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 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 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 a poster session whose abstracts follow this report.

The second day of Barrels XIX began with a talk by Steve Hsiao (Johns Hopkins University) providing data from single unit recording studies in awake, 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 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 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 from single unit recordings from the lateral dorsal nucleus (LD) of the thalamus. In urethaneanesthetized rats, it was observed that whisker stimulation resulted in short-latency excitatory responses suggestive of direct input from peripheral afferents. Consistent with this observation, electrical stimulation of nucleus interpolaris resulted in short-latency excitation of LD units. Interestingly, electrical stimulation of barrel cortex resulted in both antidromic and orthodromic responses, suggesting 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 vivo. Whole-cell recordings from barrel in 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 the excitation of barrel has on 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 axons reorganization was restricted to 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.

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, 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.