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REPORTS

Barrels XXII meeting report: Barrels blow into the Windy City

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Abstract
The 22nd Annual Barrels Meeting blew into Evanston, near the Windy City, in November 2009 as the meeting was hosted on the Evanston, IL campus of Northwestern University. The longest running satellite meeting to the Society for Neuroscience Meeting annually brings together researchers from around the world focused on the development, function, behavior, and physiology of the rodent whisker-to-barrel system and other associated cortical and subcortical areas. The 2009 edition of the meeting was focused on three central themes: the molecular development and developmental plasticity in barrel cortex, optical analysis of barrel cortex function, and the coding of touch. The main symposia were complemented by short talks, data blitz sessions, and a poster session.

Keywords: *barrel cortex, whisker, vibrissa, sensorimotor*

The 22nd Annual Barrels Meeting was held at the Norris University Center on the campus of Northwestern University in Evanston, Illinois on Thursday and Friday, 15 and 16 October 2009. The meeting brought together over 100 attendees to discuss the latest findings surrounding the development, function, control, and anatomy of the rodent whisker-to-barrel system.

Thursday morning started with a session on the molecular development and developmental plasticity in barrel cortex. The session was introduced and moderated by **Patricia Gaspar** (INSERM, France). She highlighted the necessity for different anatomical sub-circuits to be assembled prior to them being wired together to form the complete pathway from the sensory periphery to the barrel cortex. Dr Gaspar outlined the distinct steps required for the development of the system: path finding, setting up topography, ordering, and finally target reaching.

The morning session was led off by **Tomomi Shimogori** (Riken BSI, Japan) who reminded the audience that specific molecular cues govern the proper formation of barrel cortex. Early manipulation of FGF8 via electroporation shifts the barrel pattern in the thalamus, reducing its overall volume, without impacting the barrel pattern within the cortex. Further work highlighted the existence of specific cellular markers of barrel vs septal neurons. She concluded her presentation with a movie showing how electroporation can be accomplished *in utero*.

The session was followed by **Cathy Leamey** (The University of Sydney, Australia), who characterized the molecular regulators of the development of the visual pathways. Leamey used mice where teneurin_m3 was knocked out (KO). Teneurins are a family of transmembrane glycoproteins that promote neurite outgrowth. Results revealed that the KO mice's non-crossed pathways from the retina to the superior colliculus and the dorsal lateral geniculate nucleus (dLGN) had altered positions but the crossed and non-crossed pathways remained segregated. The changes in topography were related to alterations in behavior, the wild type animals would not cross a visual cliff whereas the KO mice would. The normal behavior of the KO mice was restored

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following TTX injections into one eye. It was proposed that the TTX injections inactivated the KO impacted pathway which restored the normal behavior.

The session was concluded by **Reha Erzurumlu** who investigated thalamocortical (TC) synaptic transmission and barrel formation in mice with genetic disruption of raphe serotonergic (5HT) neurons. Since TC axons use 5HT to regulate the release of glutamate, the first goal was to evaluate if in the absence or reduction of glutamate in 5HT KO mice would still result in barrel formation which they did. Next, Erzurumlu genetically disrupted the NMDA receptors in the barrel cortex in order to detect whether there was an effect on the pattern formation. Both NR1 KO and NR1 knockdown mice were used. Patterning was lost in VPM in a total knockout if the knockout was targeted to thalamic neurons, the Principal sensory nucleus patterning was unaffected by thalamic barreloids, and the cortical barrels did not form. The results demonstrate that glutamatergic activity via NMDA receptors plays a pivotal role in the creation of brain patterns and the disruption of the higher order patterning due to the altered patterning of downstream areas.

A series of short talks moderated by **Daniel Simons** (University of Pittsburgh) concluded the Thursday morning session. The session was initiated by **Qian-Quan Sun** (University of Wyoming) who focused on the role that experience has in the plasticity of interneurons within the layer IV barrels. Mice had their whiskers trimmed from postnatal day (PND) 7 through 29 with whole cell recordings from both fast spiking (FS) and regular spiking non-pyramidal (RSNP) neurons obtained on PND 30. Results demonstrated that there were significant changes in the intrinsic and firing properties of FS but not RSNP cells. The firing threshold, spike frequency, spike adaptation index, and input resistance of FS cells were all significantly altered by sensory deprivation. In general, FS cells became less excitable, due to an upregulation of A-type currents which were used to explain the decrease in strength and increased jitter of TC inputs onto these cells. In contrast, RSNP cells and presumably excitatory cells in the barrel had unchanged thalamic inputs. Taken together this might provide a mechanism to describe the increased activity seen in the barrel following sensory deprivation. **Ayan Ghoshal** (Vanderbilt University) followed with a discussion about how cross-sensory inputs may impact barrel neuron responses. An auditory click was used to test for cross-sensory responsiveness in deprived (whiskers trimmed) and undeprived animals. Across groups neurons did not respond to auditory clicks, but clicks that preceded whisker deflections resulted in shorter latency responses independent of rearing conditions. Animals which were bilaterally trimmed and reared in an environment where they were constantly exposed to the auditory clicks showed the most significant effects. The results demonstrate cross-modality effects in barrel cortex can be shaped by rearing experience. **Chia-Chien Chen** (Queens College and The Graduate Center, CUNY) showed that following sensory deprivation (whisker trimming from birth for 1 month) spine density was increased in layer IV and decreased in layer VI, the two prime TC recipient zones. An independent group of animals were trimmed for a month and then allowed to grow out their whiskers for another month; evaluation after whisker re-growth revealed that spine densities in layer VI were restored, however, in layer IV spine densities were still elevated. Similarly, injection of the NMDA antagonist MK801 for the first post-natal month increased spine densities in layers IV and VI and following 1 month of drug withdrawal layer VI spine densities returned to control levels, but layer IV spine densities remained elevated. Changes in spine density were correlated with changes in several key proteins associated with spine morphology including the extracellular matrix degrading protein tPA (tissue plasminogen activator) and the postsynaptic cytoskeleton-regulating protein spinophilin. Following trimming tPA and spinophilin levels increased; taken together these results suggest that different cortical laminae respond differently to sensory deprivation. The session was concluded by **Hui-Chen Lu** (Baylor College of Medicine) who demonstrated the critical role that endocannabinoids have in axonal path finding and patterning within the barrel system. A knockout of a cannabinoid receptor 1 resulted in aberrant patterning of TC axons in the sub-telencephalic white matter, this however ultimately did not impact barrel cortex patterning. Further analysis showed that the site of the aberrant patterning was within the internal capsule which is the location where the thalamocortical axons identify corticothalamic axons which are then used to guide them to the barrel cortex. The results demonstrated that endocannabinods have an important role in mediating interactions between thalamocortical and corticothalamic axons within the internal capsule during the first postnatal week.

Thursday afternoon started with a data blitz moderated by **Mary Ann Wilson** (Johns Hopkins University). The session was led off by **Tony Prescott** (Sheffield University, UK) describing the whisking patterns of the gray short-tailed possum, noting that whisking was apparent in 5–10 Hz and similar to rats, following contact with an object, asymmetric whisking is initiated, which is likely due to a subcortical mechanism since these animals do not have a corpus collosum. Then **Dan Feldman** (University of California, Berkley) described early results pertaining to the role of inhibition in plasticity, such that when he plucked whiskers in row D for a week and then recorded from the supragranular layers, he found that whisker trimming decreased excitatory and inhibitory synaptic conductances by 50%. **Rhaul Chaudry** (National Brain Research Center, India) showed that following the trimming of rat whisker unilateraly and using a gap cross test to assy changes in behavioral performance there was a 10% reduction in performance and if the somatosensory cortex contralateral to the intact whiskerr was lesioned an even greater decrese in performance was observed. **David Golomb** (Ben Gurion University, Israel) followed by presenting a realistic computational model of the whisker follicle, his simulations showed that intrinsic muscles may be responsible for some degree of whisker retractions. The session was concluded by **Christine Constanitople** (Columbia University) who recorded Up/Down states in isoflurane anesthetized and awake rats. Results demonstrated that these states were not present in the awake animal.

The afternoon session was concluded with a series of short talks moderated by **Daniel Shulz** (CNRS, France). **Brian Hooks** (Northwestern University) started the session with a talk describing results using laser uncaging of glutamate to determine the local inputs onto neurons within first (S1) and second (S2) somatosensory cortex as well as motor cortex (M1). In M1, descending layer II/III to layer Vb was the strongest pathway. Within S1, layer IV to layer II/III projection was the strongest followed by the projection from layers II/III to layer V. Finally, in S2, layer IV projects much stronger to layer II vs layer III which receives predominately local inputs. These data point to laminar and region-specific connectivity patterns within the neocortex. **Joshua Brumberg** (Queens College, CUNY) described results from identified corticothalamic neurons that projected to VPm. Whole cell recording from labeled layer VI CT cells demonstrated that all of them are RS neurons and exhibit with little to no spike frequency adaption. CT-Pairs of electrical stimuli were applied to the VPm and demonstrated the existence of monosynaptic TC inputs onto these neurons with little facilitation over a wide frequency range (2–20 Hz). In contrast, stimulus trains (8 pulses) resulted in significant depression at higher frequencies (10 and 20 Hz). *Post hoc* anatomical analysis revealed that VPm cells were found predominately towards the upper part of layer VI and had pyramidal cell bodies, short basilar dendrites, and predominately either had unbranched apical dendrites that terminated by layer IV or they were much more compact with apical dendrites that did not advance much beyond the layer V–VI border. The session was concluded by **Jason Ritt** (Massachusetts Institute of Technology) who showed that by employing targeted optogenetic techniques fast spiking parvalbumin neurons could be selectively targeted for activation. Activation of these neurons within the barrel induced gamma oscillations. Responses to optical stimulation were dependent on the existing brain state. The day was concluded with a poster session and a dinner in a room overlooking Lake Michigan.

The Friday morning session commenced with a series of long talks moderated by **Randy Bruno** (Columbia University) who gave a comprehensive review on the somatic and dendritic properties in the barrel cortex, as well as the latest advances in optical imaging methods in studying microcircuitry of the cerebral cortex.

Karel Svoboda (Janelia Farms, HHMI) elegantly demonstrated the organizational patterns of synaptic connections in subcellular resolution within the barrel cortex. Using optogenetics approaches such as Channel-rhodopsin2 (ChR2) assisted circuit mapping in combination with multiphoton microscopy, the spatial specificity of interneuronal connectivity within the barrel cortex can be precisely reconstructed. It was found that layer III pyramidal neurons receive most of the thalamocortical VPM inputs via their basilar dendritic arborizations, while the majority of the inputs from M1 are received in the apical dendritic portions. By contrast, the local corticocortical connections within layer III are more evenly distributed throughout the apical as well as basilar dendrites. These results demonstrate that within the barrel cortex inputs from distinct sources may target distinct locations of neuronal dendritic trees. Within layer V Posterior medial thalamic inputs targeted neurons within Va and not Vb. Within M1 it was shown that specific neurons are more responsive to either the correct rejection or correct response during a sensory detection task.

Next, **Carlos Portera-Cailliau** (University of California, Los Angeles) followed with a talk that emphasized the mapping of cortical circuits in postnatal development, with focus on *in vivo* dendritic spine imaging. It was shown that in normal animals, there is a significant increase of dendritic spine density in P21–P24 compared to P10–P12 within the primary visual cortex. In addition, this event coincides with relatively quick dendritic spine turnover, signifying that there is considerable amount of remodeling and refining of synaptic connectivity during this developmentally critical period. However, in a mouse model of Fragile X syndrome of the FRMP-null mice, the overall spine dynamics decreased and the lifetime of dendritic spines increased. It was also found that in these mice with abnormal level of FRMP, the filopodia-like dendritic protrusions have lower chance of morphing into a stable mushroom spine. It was therefore suggested that the protein FRMP is important for maturation of dendritic protrusions and refining of synaptic contact sites. Using *in vivo* calcium imaging it was shown that there was significantly more correlated activity earlier in development (PND 5) than later (>PND 12) and that sensory deprivation due to whisker trimming did not impact this phenomenon.

The session concluded with a talk from **Fritjof Helmchen** (University of Zurich, Switzerland) who uses calcium imaging techniques to investigate the neuronal dynamics in the barrel cortex. Using electroporation to deliver optical calcium reporters such as Oregon Green BAPTA into layer V pyramidal neurons, the calcium activities in these neurons' distal apical dendrites can be readily observed *in vivo*. These calcium-level-induced changes in fluorescent signals are highly correlated with bursts of action potentials rather than in response to a single action potential. By the same token, these changes in dendritic calcium levels are more robustly responsive to multiple whisker stimulation and not well correlated with single whisker stimulation. These findings suggested that the pyramidal neurons in layer V function more as integrative units for processing multiwhisker inputs. Additional calcium optical reporters such as yellow cameleon 3.6 are currently being developed, with preliminary data indicating that this particular optogenetic reporter has extremely high sensitivity and fidelity to the point of single-spike temporal resolution.

Following an insightful discussion, the Friday morning session concluded with two short platform talks moderated by **Adrienne Fairhall** (University of Washington). First to present was **Tony Prescott** (University of Sheffield, UK) who demonstrated the neuro-robotic model for vibrissae system. By taking account of several key aspects of vibrissal signaling processes such as sensory transduction, whisking-pattern generation, orientation to vibrissal stimuli (with respect to head position), and sensory noise cancellation filtering in the cerebellum, this vibrissae-based robotic model can emulate similar whisking behavioral pattern to that of a real rodent. Next, **Neeraj Jain** (National Brain Research Centre, India) concluded the session by providing data on the reorganization of primary motor cortex in adult rodents as a result of chronic lesion of dorsal funiculus in the spinal cord. In control animals it was shown that there were two representations of whisking within M1 one caudal where whisker and neck representations overlap and one rostral which represents just whisker and that in order to observe the two representations low levels of anesthesia have to be used. It was found that in the lesioned animals, the neck representation expands and the threshold for movement for neck muscles is unaffected but it increases for whisker-evoked responses.

After lunch, the conference resumed with another exciting data blitz session moderated by **Dan Feldman** (University of California, Berkeley). **Hilary North** (Georgetown University) showed the relationship between Ephrin A4 and the development of the trigeminal system since Ephrin A4 is expressed in the maxillary region as early as embryonic day 10.5 and KO mice are missing several ventral whiskers. **Michael Bale** (The University of Manchester, UK) focused on the transformation of neural coding from the periphery to the cortex showing that the reliability and the mutual information decrease progressively along the neural axis and it was shown that the first action potential conveyed the most information. Then **Robyn Grant** (University of Sheffield, UK) presented on the effect of neurodegeneration in a mouse model of amyotrophic lateral sclerosis which showed that the number of neurons within the facial nucleus decreased by 50% and there was less coupled whisking. **J. Taigo Goncalves** (University of California, Los Angeles) presented on calcium imaging of Fragile-X mouse model *in vivo* and showed that correlated neuronal activity was higher in a mouse model of Fragile-X when compared to wild type animals. The session was ended by **Jason Middleton** (University of Pittsburgh) using multi-unit recording techniques who showed that fast spiking–regular spiking pairs of neurons showed more correlated activity then fast spiking–fast spiking pairs and that sensory stimulation decreased these correlations.

Following a brief coffee break, the afternoon scientific session was introduced by moderator **Mitra Hartmann** (Northwestern University) who gave a thorough review on the coding of touch, including the multiple axes of the vibrissae positioning system and its relationship to egocentric localization, as well as the object-centered frame approaches to whisker processing.

The initial talk was by **Fan Wang** (Duke University) who presented data on techniques that allowed for the molecular/genetic dissection of the barrelette circuitry. It was demonstrated that in the dorsoventral axis, the trigeminal cell bodies mimic the spatial organizational profiles of whisker patterns on the ipsilateral mystacial pad. However, in the antero-posterior axis, this spatial organization profile is inverted in a mirror image, with considerable amount of areal overlap in the brainstem, specifically within the spinal caudalis nucleus. Furthermore, the formation of this map in the trigeminal system is most likely guided by molecular mechanisms as indicated by markers such as TGFβ and bone-morphogenic proteins (BMPs) that present themselves in a barrelette pattern early in development. Interrupting the TGFβ molecular signaling pathways by deleting a key transducer *Smad4* caused the development of barrelette topography to be delayed, with blurring of the segregation of the clusters that are commonly seen in wild-type barrelettes. In addition, there is some associated loss of peripheral innervation in the conditional KO *Smad4 mice*, as indicated by less dense axonal boutons.

Switching to a more systems level of analysis **David Kleinfeld** (University of California, San Diego) focused on the transformation from body-centered to trajectory-based coordinates. He provided evidence showing that there were reafferent signals being transmitted via brainstem circuits as well as at cortical levels. The information of where a whisker was in space could be used by a single whisker to determine the location of an object in space by comparing the time of spiking relative to the position of the whisker during its whisking cycle. Within M1 approximately 20% of the neurons' spiking responses were found to be phase locked with the whisking cycle and about 60% of the neurons' firing was modulated by the amplitude of the whisk. Similar information about the whisking cycle could also be observed in S1. Thus the responsivity of cortical neurons may depend on the phase of the whisking cycle in which an object is contacted.

Ilan Lampl (Weizmann Institute, Israel) followed by giving a presentation focused on shifts in the balance between excitatory and inhibitory networks in barrel cortex during adaptation as a result of repetitive whisker stimulation. Data revealed that the cells in the supragranular layers exhibited significantly more adaptive firing properties than those within the barrel, and the suggested mechanism of this adaptation was short-term synaptic depression. The findings illustrated that there are differing time constants of synaptic adaptation, in which that inhibitory network adapts more rapidly than its excitatory counterpart. It was also demonstrated that the intensity of sensory stimuli can directly affect the magnitude of adaptation; reduced stimulation strength in the periphery is correlated with decreased synaptic recruitment in the cortex. These phenomena of neuronal adaptation and response to stimulation intensity, however, are surprisingly reversed in the trigeminal barrelette, suggesting a counter-balancing mechanism. Most likely these two gain-control subsystems act in opposing manners in order to maintain the overall homeostatic activity levels in the neural environment.

Finally, **Carl Olson** (Carnegie Mellon University) concluded the session by giving a talk emphasized on the object-centered reference frame. Supplementary eye field (SEF), an area in the primate frontal lobe, is believed to play a critical role in the way that the brain processes abstract spatial localization relative to the oriented object, by interacting with several other neurocognitive processes such as working memory and attentional networks. It was found that neurons in SEF discharge before spontaneous eye movement (saccade) associated with visual attention in the preferred direction. This phenomenon is not influenced by varying the types of cue or object, suggesting that this is an automatic and innate cognitive computational capability. Moreover, following intensive behavioral training, the number of neurons exhibiting object-centered selectivity in SEF increased dramatically, signifying the interplay between hardwired neurocircuitry and recruited neuronal functioning through behavioral reinforcement and feedback. The talk concluded with a proposal that the role of SEF is most likely a general visuospatial sketchpad in the visual system, with interactions with working memory and attentional processes.

The 22nd Annual Barrels Meeting ended with a discussion about how the brain encodes spatial position and the participants headed to the Society for Neuroscience meeting in the Windy City while looking forward to the 23rd annual meeting in San Diego in 2010.

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