Journal Club

Editor's Note: These short reviews of recent *JNeurosci* articles, written exclusively by students or postdoctoral fellows, summarize the important findings of the paper and provide additional insight and commentary. If the authors of the highlighted article have written a response to the Journal Club, the response can be found by viewing the Journal Club at www.jneurosci.org. For more information on the format, review process, and purpose of Journal Club articles, please see <https://www.jneurosci.org/content/jneurosci-journal-club>.

Sense and Action across the Layers of the Rat Posterior Parietal Cortex

Maximiliano José Nigro

Centre for Neural Computation, Egil and Pauline Braathen and Fred Kavli Centre for Cortical Microcircuits, Kavli Institute for Systems Neuroscience, Norwegian University of Science and Technology, NO-7491 Trondheim, Norway
Review of Mohan et al.

The integration of sensory stimuli and ongoing motor outputs is called sensorimotor integration, and it occurs in motor as well as sensory cortices, where it helps to guide motor output (Petersen, 2019). The rodent whisker system is an excellent system in which to study the interaction of sensory inputs and motor outputs in behaving animals with tight control of the stimulus timing and intensity. Rodents explore their environment through a stereotyped movement of their whiskers, and the information from the whiskers enters the cortex mainly through the primary somatosensory cortex, specifically, the barrel cortex (Feldmeyer et al., 2013). Whisker-guided behavior has been shown to depend on a broad cortical network that includes barrel cortex, secondary somatosensory cortex, and frontal motor areas (anterior lateral motor cortex and vibrissal motor cortex; Petersen, 2019). The posterior parietal cortex (PPC) is extensively interconnected with sensory cortices (including barrel cortex), and frontal motor areas. The multisensory proper-

ties of PPC and its connections with motor areas suggests that it might play an important role in the integration of sensory and motor signals and in guiding motor output (Mohan et al., 2018; Hwang et al., 2019). However, whisker representation in PPC as well as how PPC neurons encode information about whisker movement and touch are still poorly understood.

To fill this gap, Mohan et al. (2019) performed *in vivo* recordings in anesthetized and awake head-fixed rats to measure spontaneous and evoked activity of PPC neurons throughout the cortical depth. A loose topographic representation of the whisker pad has previously been described in the mouse extrastriate rostromedial area (RL), which is part of PPC (Wang and Burkhalter, 2007; Olcese et al., 2013). The area of PPC explored by Mohan et al. (2019) includes RL, anterior area (A), and part of anteromedial area, thus extending previous findings in the mouse (Olcese et al., 2013). The authors measured responses to whisker deflection from the local field potential (LFP) and confirmed that PPC contains a coarse topographic representation of the whisker pad. By using loose-patch recordings, the authors found that all PPC neurons across layers responded to the stimulation of multiple whiskers, thus matching the loose somatotopy at the input stage obtained from the LFP with the output of PPC neurons. Recently, a coarse somatotopic representation of the trunk and head was reported in the rat PPC (Mimica et al., 2018). The re-

cordings of Mohan et al. (2019) seem to target more lateral sites of PPC compared with Mimica et al. (2018), and thus it will be interesting to address whether and how these two representations interact and whether body posture has any impact on sensory processing in PPC.

The cortex is constituted of distinct cortical layers that contain different neuronal populations, receive different input and likely have different functions (Harris and Shepherd, 2015). For instance, layer 4 is considered an input layer for sensory information, layer 5 is the main output of the cortex, layer 2/3 is an integrative layer projecting to other cortical areas, and layer 6 provides feedback to the thalamus. Mohan et al. (2019) used the following two main approaches to monitor the activity of PPC neurons across layers: (1) loose-patch recordings from single neurons in anesthetized rats, which allowed them to histologically confirm the location of the recorded cells and their morphology by filling them with biocytin; and (2) high-density recordings with silicon probes in the awake head-fixed preparation, which allowed a high yield of simultaneous recordings throughout layers during whisking and nonwhisking periods.

The loose-patch recordings showed that layer 5 neurons had a higher spontaneous firing rate and responded more strongly to whisker stimulation compared with layer 2/3 neurons in the anesthetized preparation. In awake rats, excitatory

Received Sept. 23, 2019; revised Dec. 11, 2019; accepted Dec. 21, 2019.

This work was supported by the Centre of Excellence scheme of the Research Council of Norway—Centre for Neural Computation, Grant 223262; the National Infrastructure scheme of the Research Council of Norway—NORBRIN, Grant 197467; and The Kavli Foundation. I thank Dr. Menno Witter, Dr. Jonathan Whitlock, and Dr. Giulia Quattrocchi for comments on the manuscript.

The authors declare no competing financial interests.

Correspondence should be addressed to Maximiliano José Nigro at maximiliano.nigro@gmail.com.

<https://doi.org/10.1523/JNEUROSCI.2289-19.2019>

Copyright © 2020 the authors

neurons in layers 2–4 and 6 showed sparse activity during quiescent behavior (i.e., not whisking) but were significantly activated by spontaneous whisking.

To measure how PPC neurons encode movements of the whiskers while reaching for an object, the authors used principal component analysis to compute the dynamics of the population activity during whisking onset while the rats explored the object. Mohan et al. (2019) were able to decode movement goals in PPC neurons and found that the activity in layers 2–4 and 6 predicted movement goals in awake rats reaching for an object with their whiskers. The layer-specific population activity during exploration was in line with responses during free whisking (i.e., without object touch). These findings suggest that in PPC information on whisker movements flows across cortico-cortical and corticothalamic networks, through the projections of layer 2/3 and 6, respectively. Interestingly, layer 2/3 neurons in PPC project to the secondary motor cortex (M2) and control movement trajectory in a visual sensory detection task (Hwang et al., 2019). The data from Mohan et al. (2019) are in line with observations that the activity in PPC precedes that in secondary motor cortex, strengthening the argument that PPC might be involved in the selection of motor outputs (Mimica et al., 2018).

Intriguingly, the activity of layer 5 neurons was not modulated by whisker movements or touch in the awake rats. The majority of layer 5 neurons in PPC in mice and ferrets respond preferentially to the combination of visual and tactile stimuli, suggesting that this layer is mainly involved in processing multisensory information (Foxworthy et al., 2013; Olcese et al., 2013). Moreover, layer 5 in PPC contains neurons projecting to the striatum that have been shown to encode task history necessary for the selection of motor output (Hwang et al., 2019). This evidence suggests that layer 5 neurons might be preferentially engaged by tasks that require multisensory integration or the selection of a motor output based on the history of the task (Hwang et al., 2019).

An input to PPC that deserves more attention is the posteromedial thalamic nucleus (PoM), which is reciprocally connected with PPC (Olsen and Witter, 2016). Neuronal activity in PoM has been shown to be modulated by layer 5B corticothalamic feedback (Mease et al., 2016).

Pyramidal cells in layer 5B of the barrel cortex have broad receptive fields and might transfer this property to PoM and PPC (Manns et al., 2004). The activity of neurons in PoM increases during whisking behavior and exert powerful activation of the barrel cortex through a colliculo-thalamo-cortical pathway (Gharai et al., 2019). Collicular neurons respond stronger to multiwhisker deflection and movement (Cohen et al., 2008), and this property might underlie the loose somatotopy in PPC through its inputs from PoM and the septal columns of the barrel cortex. Sensorimotor information from layer 6 of PPC (Lee et al., 2011; Olsen and Witter, 2016) might be feedback to PoM, enhancing the transmission between PPC and motor cortex via cortico-thalamo-cortical loops (Jaramillo et al., 2019). Previous work has pointed out the correlation of neuronal activity in PPC with behavioral output in tasks involving visual or auditory processing. However, optogenetic inactivation of PPC during a whisker-dependent task concluded that PPC is not involved in performance in well trained mice (Guo et al., 2014). PPC might have a more prominent role during learning, as suggested by Mohan et al. (2019). Indeed, synaptic transmission at PoM terminals in barrel cortex is also enhanced during learning, suggesting that this thalamic pathway might be relevant during motor learning in PPC as well (Audette et al., 2019).

Further experiments exploring responses of PPC neurons in tasks involving the integration of inputs from multiple sensory modalities in decision-making will be needed to reach a more complete picture of the layer-specific computational properties of PPC. These tasks might also recruit a broader cortical network, and the thalamo-cortical connectivity of PPC puts it in the perfect position to act as a cortical hub integrating multisensory and motor inputs and connecting several cortical areas.

The study of Mohan et al. (2019) provides valuable information about layer-specific somatomotor processing in PPC that will constitute solid ground for future studies addressing sensorimotor integration in PPC during complex naturalistic behaviors with cell-type specificity.

References

- Audette NJ, Bernhardt SM, Ray A, Stewart LT, Barth AL (2019) Rapid plasticity of higher-order thalamocortical inputs during sensory learning. *Neuron* 103:277–291.e4.
- Cohen JD, Hirata A, Castro-Alamancos M (2008) Vibrissa sensation in superior colliculus: wide-field sensitivity and state-dependent cortical feedback. *J Neurosci* 26:11205–11220.

- Feldmeyer D, Brecht M, Helmchen F, Petersen CC, Poulet JF, Staiger JF, Luhmann HJ, Schwarz C (2013) Barrel cortex function. *Prog Neurobiol* 103:3–27.
- Foxworthy WA, Clemo HR, Meredith MA (2013) Laminar and connective organization of a multisensory cortex. *J Comp Neurol* 521:1867–1890.
- Gharai S, Honnuraiah S, Arabzadeh E, Stuart GJ (2019) Superior colliculus modulates cortical coding of somatosensory information. *bioRxiv*. Advance online publication. Retrieved January 8, 2020. doi:10.1101/715847.
- Guo ZV, Li N, Huber D, Ophir E, Gutnisky D, Ting JT, Feng G, Svoboda K (2014) Flow of cortical activity underlying a tactile decision in mice. *Neuron* 81:179–194.
- Harris KD, Shepherd GM (2015) The neocortical circuit: themes and variations. *Nat Neurosci* 18:170–181.
- Hwang EJ, Link TD, Hu YY, Lu S, Wang EH, Lilascharoen V, Aronson S, O'Neil K, Lim BK, Komiyama T (2019) Corticostriatal flow of action selection bias. *Neuron* 104:1126–1140.e6.
- Jaramillo J, Mejias JF, Wang XJ (2019) Engagement of pulvino-cortical feedforward and feedback pathways in cognitive computations. *Neuron* 101:321–336.e9.
- Lee T, Alloway KD, Kim U (2011) Interconnected cortical networks between primary somatosensory cortex septal columns and posterior parietal cortex in rat. *J Comp Neurol* 519:405–419.
- Manns ID, Sakmann B, Brecht M (2004) Sub- and suprathreshold receptive field properties of pyramidal neurons in layer 5A and 5B of the rat somatosensory barrel cortex. *J Physiol* 556:601–622.
- Mease RA, Sumner A, Sakmann B, Groh A (2016) Corticothalamic spike transfer via the L5B-pom pathway in vivo. *Cereb Cortex* 26:3461–3475.
- Mimica B, Dunn BA, Tombaz T, Bojja VPTNCS, Whitlock JR (2018) Efficient cortical coding of 3D posture in freely behaving rats. *Science* 362:584–589.
- Mohan H, de Haan R, Mansvelder HD, de Kock CPJ (2018) The posterior parietal cortex as an integrative hub for whisker sensorimotor information. *Neuroscience* 368:240–245.
- Mohan H, de Haan R, Broersen R, Pieneman AW, Helmchen F, Staiger JF, Mansvelder HD, de Kock CPJ (2019) Functional architecture and encoding of tactile sensorimotor behavior in rat posterior parietal cortex. *J Neurosci* 39:7332–7343.
- Olcese U, Iurilli G, Medini P (2013) Cellular and synaptic architecture of multisensory integration in the mouse neocortex. *Neuron* 79:579–593.
- Olsen GM, Witter MP (2016) Posterior parietal cortex of the rat: architectural delineation and thalamic differentiation. *J Comp Neurol* 524:3774–3809.
- Petersen CCH (2019) Sensorimotor processing in the rodent barrel cortex. *Nat Rev Neurosci* 20:533–546.
- Wang Q, Burkhalter A (2007) Area map of mouse visual cortex. *J Comp Neurol* 502:339–357.