Richard Mooney - selected references

1 Schneider, D. M., Nelson, A., & Mooney, R. (2014). A synaptic and circuit basis for corollary discharge in the auditory cortex. *Nature, 513,* 189-194.
Notes: Sensory regions of the brain integrate environmental cues with copies of motor-related signals important for imminent and ongoing movements. In mammals, signals propagating from the motor cortex to the auditory cortex are thought to have a critical role in normal hearing and behaviour, yet the synaptic and circuit mechanisms by which these motor-related signals influence auditory cortical activity remain poorly understood. Using in vivo intracellular recordings in behaving mice, we find that excitatory neurons in the auditory cortex are suppressed before and during movement, owing in part to increased activity of local parvalbumin-positive interneurons. Electrophysiology and optogenetic gain- and loss-of-function experiments reveal that motor-related changes in auditory cortical dynamics are driven by a subset of neurons in the secondary motor cortex that innervate the auditory cortex and are active during movement. These findings provide a synaptic and circuit basis for the motor-related corollary discharge hypothesized to facilitate hearing and auditory-guided behaviours

2 Mooney, R. (2014). Auditory-vocal mirroring in songbirds. *Philos.Trans.R.Soc.Lond B Biol.Sci., 369,* 20130179.
Notes: Mirror neurons are theorized to serve as a neural substrate for spoken language in humans, but the existence and functions of auditory-vocal mirror neurons in the human brain remain largely matters of speculation. Songbirds resemble humans in their capacity for vocal learning and depend on their learned songs to facilitate courtship and individual recognition. Recent neurophysiological studies have detected putative auditory-vocal mirror neurons in a sensorimotor region of the songbird's brain that plays an important role in expressive and receptive aspects of vocal communication. This review discusses the auditory and motor-related properties of these cells, considers their potential role on song learning and communication in relation to classical studies of birdsong, and points to the circuit and developmental mechanisms that may give rise to auditory-vocal mirroring in the songbird's brain

3 Murugan, M., Harward, S., Scharff, C., & Mooney, R. (2013). Diminished FoxP2 levels affect dopaminergic modulation of corticostriatal signaling important to song variability. *Neuron, 80,* 1464-1476.
Notes: Mutations of the FOXP2 gene impair speech and language development in humans and shRNA-mediated suppression of the avian ortholog FoxP2 disrupts song learning in juvenile zebra finches. How diminished FoxP2 levels affect vocal control and alter the function of neural circuits important to learned vocalizations remains unclear. Here we show that FoxP2 knockdown in the songbird striatum disrupts developmental and social modulation of song variability. Recordings in anesthetized birds show that FoxP2 knockdown interferes with D1R-dependent modulation of activity propagation in a

corticostriatal pathway important to song variability, an effect that may be partly attributable to reduced D1R and DARPP-32 protein levels. Furthermore, recordings in singing birds reveal that FoxP2 knockdown prevents social modulation of singing-related activity in this pathway. These findings show that reduced FoxP2 levels interfere with the dopaminergic modulation of vocal variability, which may impede song and speech development by disrupting reinforcement learning mechanisms

4 Tschida, K. & Mooney, R. (2012). The role of auditory feedback in vocal learning and maintenance. *Current Opinion in Neurobiology, 22,* 320-327.
Notes: Auditory experience is critical for the acquisition and maintenance of learned vocalizations in both humans and songbirds. Despite the central role of auditory feedback in vocal learning and maintenance, where and how auditory feedback affects neural circuits important to vocal control remain poorly understood. Recent studies of singing birds have uncovered neural mechanisms by which feedback perturbations affect vocal plasticity and also have identified feedback-sensitive neurons at or near sites of auditory and vocal motor interaction. Additionally, recent studies in marmosets have underscored that even in the absence of vocal learning, vocalization remains flexible in the face of changing acoustical environments, pointing to rapid interactions between auditory and vocal motor systems. Finally, recent studies show that a juvenile songbird's initial auditory experience of a song model has long-lasting effects on sensorimotor neurons important to vocalization, shedding light on how auditory memories and feedback interact to guide vocal learning

5 Roberts, T. F., Gobes, S. M., Murugan, M., Olveczky, B. P., & Mooney, R. (2012). Motor circuits are required to encode a sensory model for imitative learning. *Nature Neuroscience, 15,* 1454-1459.
Notes: Premotor circuits help generate imitative behaviors and can be activated during observation of another animal's behavior, leading to speculation that these circuits participate in sensory learning that is important to imitation. Here we tested this idea by focally manipulating the brain activity of juvenile zebra finches, which learn to sing by memorizing and vocally copying the song of an adult tutor. Tutor song-contingent optogenetic or electrical disruption of neural activity in the pupil's song premotor nucleus HVC prevented song copying, indicating that a premotor structure important to the temporal control of birdsong also helps encode the tutor song. In vivo multiphoton imaging and neural manipulations delineated a pathway and a candidate synaptic mechanism through which tutor song information is encoded by premotor circuits. These findings provide evidence that premotor circuits help encode sensory information about the behavioral model before shaping and executing imitative behaviors

6 Hamaguchi, K. & Mooney, R. (2012). Recurrent interactions between the input and output of a songbird cortico-basal ganglia pathway are implicated in vocal sequence variability. *Journal of Neuroscience, 32,* 11671-11687.
Notes: Complex brain functions, such as the capacity to learn and modulate vocal sequences, depend on activity propagation in highly distributed neural networks. To explore the synaptic basis of activity propagation in such networks, we made dual in vivo intracellular recordings in anesthetized zebra finches from the input (nucleus HVC, used here as a proper name) and output [lateral magnocellular nucleus of the anterior nidopallium (LMAN)] neurons of a songbird cortico-basal ganglia (BG) pathway necessary to the learning and modulation of vocal motor sequences. These recordings reveal evidence of bidirectional interactions, rather than only feedforward propagation of activity from HVC to LMAN, as had been previously supposed. A combination of dual and triple recording configurations and pharmacological manipulations was used to map out circuitry by which activity propagates from LMAN to HVC. These experiments indicate that activity travels to HVC through at least two independent ipsilateral pathways, one of which involves fast signaling through a midbrain dopaminergic cell group, reminiscent of recurrent mesocortical loops described in mammals. We then used in vivo pharmacological manipulations to establish that augmented LMAN activity is sufficient to restore high levels of sequence variability in adult birds, suggesting that recurrent interactions through highly distributed forebrain-midbrain pathways can modulate learned vocal sequences

7 Mooney, R. (2009). Neurobiology of song learning. *Current Opinion in Neurobiology, 19,* 654-660.
Notes: Birdsong is a culturally transmitted behavior that depends on a juvenile songbird's ability to imitate the song of an adult tutor. Neurobiological studies of birdsong can reveal how a complex form of imitative learning, which bears strong parallels to human speech learning, can be understood at the level of underlying circuit, cellular, and synaptic mechanisms. This review focuses on recent studies that illuminate the neurobiological mechanisms for singing and song learning
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