AUDIO-VOCAL MIRROR NEURON IN THE SONGBIRD BASAL GANGLIA

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Speech acquisition in humans is parallel to vocal learning in songbirds (Doupe & Kuhl, 1999; Prather et al., 2017). Both learnings are held by imitating adults' vocalizations and have critical periods that need auditory and motor information (Fromkin et al., 1974; Marler, 1970). In studying vocal learning of humans and songbirds, it is important to understand the neural mechanisms how to integrate auditory and vocal-motor information. Since songbirds have anatomically well-defined brain circuits dedicated to vocal learning, we focused on songbirds to understand the neural mechanisms underlying the audio-vocal integration at the cellular levels that is hard to research on human subjects.

The cortico-basal ganglia circuitry, which includes premotor cortical nucleus (HVC) and a part of the basal ganglia (Area X), is crucial for vocal learning in a songbird (Kao et al., 2005). HVCx neurons, which project to Area X, fire both when the bird is singing and when it is listening to the bird's own song (BOS) (Prather et al., 2008; Hessler & Okanoya, 2018). These neurons are called "audio-vocal mirror neurons". Audio-vocal mirror neurons should have important roles to integrate auditory and vocal motor information. Because HVCx neurons projects to Area X that is important for vocal leaning, there should be audio-vocal mirror neurons not only in HVC but also in Area X. In this study, we used Bengalese finch (*Lonchura striata var. domestica*) and examined whether neurons in Area X shows singing-related and auditory-related activity by recording multiple single-unit activity in freely behaving condition.

We found two types of audio-vocal mirror neurons in Area X that exhibited both singing and auditory-related activity. One type of neurons fired at the

specific syllable timing when a bird was singing and when it was listening to BOS (Fig.1). Based on the firing property and spike waveform (Goldberg & Fee, 2010; Goldberg et al., 2010), these neurons were classified as putative striatum medium spiny neurons (MSNs). The other type of neurons was active when a bird was singing. The same neuron also showed increase in firing rate when a bird was listening to BOS during sleep, while the neuron did not show such auditory responses when a bird was awake. These neurons were classified as internal globus pallidus (GPi) neurons.

MSN is the input stage of Area X from HVC (Farries et al., 2005). Thus, MSN may exhibit similar audio-vocal mirror neuron properties by receiving inputs from HVCx neurons. On the other hand, GPi is the main output in Area X to the thalamic nucleus DLM (Farries et al., 2005). Thus, we assumed that GPi send to DLM both auditory and vocal-motor information necessary for vocal learning. However, GPi neurons did not show any auditory response while MSN showed BOS selective responses when a bird was awake. These results suggest that the neural transmission from MSN to GPi is gated off when a bird is awake.

In conclusion, we found audio-vocal mirror neurons in Area X and these are putative MSN and GPi neurons. We assume that the neurons integrate auditory and vocal-motor information in the cortico-basal ganglia circuitry necessary for vocal learning. We also suggested that the auditory information processing is modulated by arousal levels. Our findings support the idea that audio-vocal mirror neurons in cortico-basal ganglia circuitry are important in vocal learning that needs to integrate sensory and motor information. The mirror neurons that integrate auditory and vocal information may be a common neural substrate not only for vocal learning in birds but also for speech learning in humans, and this study provides new clues for considering the evolution of language.
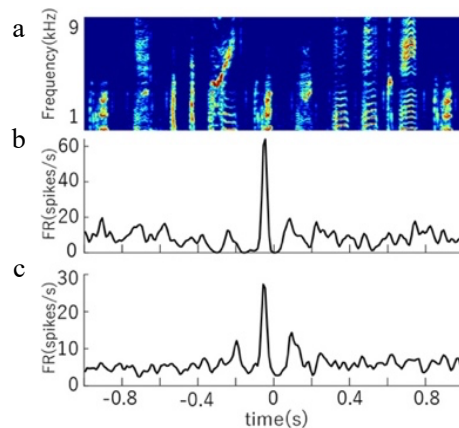

Figure 1. An example of firing pattern of audio-vocal mirror neuron in adult Bengalese finch basal ganglia nucleus Area X. (a) Sonagram. (b) Mean firing rate (FR) when a bird was singing. (c) Mean FR when a bird was listening during wakefulness. Note that the phasic firing occurs at the time of specific syllable during singing and listening to the song.

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