Behavioural Processes xxx (xxxx) xxx–xxx

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Social interaction with a tutor modulates responsiveness of specific auditory neurons in juvenile zebra finches

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ARTICLE INFO

Keywords:
Social interaction
Auditory response
Song bird

ABSTRACT

Behavioral states of animals, such as observing the behavior of a conspecific, modify signal perception and/or sensations that influence state-dependent higher cognitive behavior, such as learning. Recent studies have shown that neuronal responsiveness to sensory signals is modified when animals are engaged in social interactions with others or in locomotor activities. However, how these changes produce state-dependent differences in higher cognitive function is still largely unknown. Zebra finches, which have served as the premier songbird model, learn to sing from early auditory experiences with tutors. They also learn from playback of recorded songs however, learning can be greatly improved when song models are provided through social communication with tutors (Eales, 1989; Chen et al., 2016). Recently we found a subset of neurons in the higher-level auditory cortex of juvenile zebra finches that exhibit highly selective auditory responses to the tutor song after song learning, suggesting an auditory memory trace of the tutor song (Yanagihara and Yazaki-Sugiyama, 2016). Here we show that auditory responses of these selective neurons became greater when juveniles were paired with their tutors, while responses of non-selective neurons did not change. These results suggest that social interaction modulates cortical activity and might function in state-dependent song learning.

1. Introduction

Perception, and even sensation, can vary from moment to moment depending on an animal's behavioral state or context. The same acoustical signals can be sensed differently when attention is focused on them. Interestingly, focused attention modulates sensing or recognition of a specific signal, rather than shifting overall sensitivity. This suggests that behavioral states can filter sensory signals to target them for further processing. Recent studies have shown that the behavioral state directly modifies cortical sensory responsiveness via top-down cortico-cortical input, rather than through thalamic feedforward inputs. Neuronal responses to visual stimulation in V1 neurons of awake mice, but not in neurons of the lateral geniculate nucleus (LGN), increased during locomotion (Niell and Stryker, 2010). Locomotor activity also decreased auditory responses in A1 by top-down M1 input through local inhibitory circuits (Schneider et al., 2014). Sensory responses are not just increased or decreased, rather response tuning can also be modified when animals are engaged in a task (Fritz et al., 2003).

Songbirds learn to sing through vocal communications during early development. In zebra finches, which are highly social and less territorial, and have long-lasting pair bonds, juvenile song learning is greatly improved through social vocal communications, although juveniles can learn from playback of recorded tutor songs (Bolhuis et al., 2000), much as human infants do not learn phonetic detection in speech via audio-visual aids (Eales, 1989; Kuhl 2010; Chen et al., 2016). Interestingly, juvenile zebra finches do better at learning from song playback when they are engaged in juvenile task performance (Tchernichovski et al., 2001). They also learn more from conspecific adults with which they interact intensely when they have multiple choices (Williams, 1990). Those studies suggest that juvenile behavioral states, such as focused attention during social interaction, filter out background auditory signals, so that tutor song forms exclusive memories.

Various studies have shown that auditory memories of tutor song are stored in the zebra finch caudomedial nidopallium (NCM), homologous to the mammalian higher auditory cortex. Greater numbers of neurons in the NCM manifest immediate early gene expression in birds exposed to tutor songs, than in birds exposed to novel conspecific songs (Gobes et al., 2010). The expression level of immediate early genes in birds that are exposed to a tutor song is proportional to the amount of

Abbreviations: NCM, caudomedial nidopallium; TUT, tutor song; BOS, bird's own song; CON, conspecific song; HET, heterospecific Bengalese finch song; Mcall, adult male zebra finch call; Fcall, adult female zebra finch call; WN, white noise

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https://doi.org/10.1016/j.beproc.2018.04.003
Received 24 March 2017; Received in revised form 23 March 2018; Accepted 9 April 2018

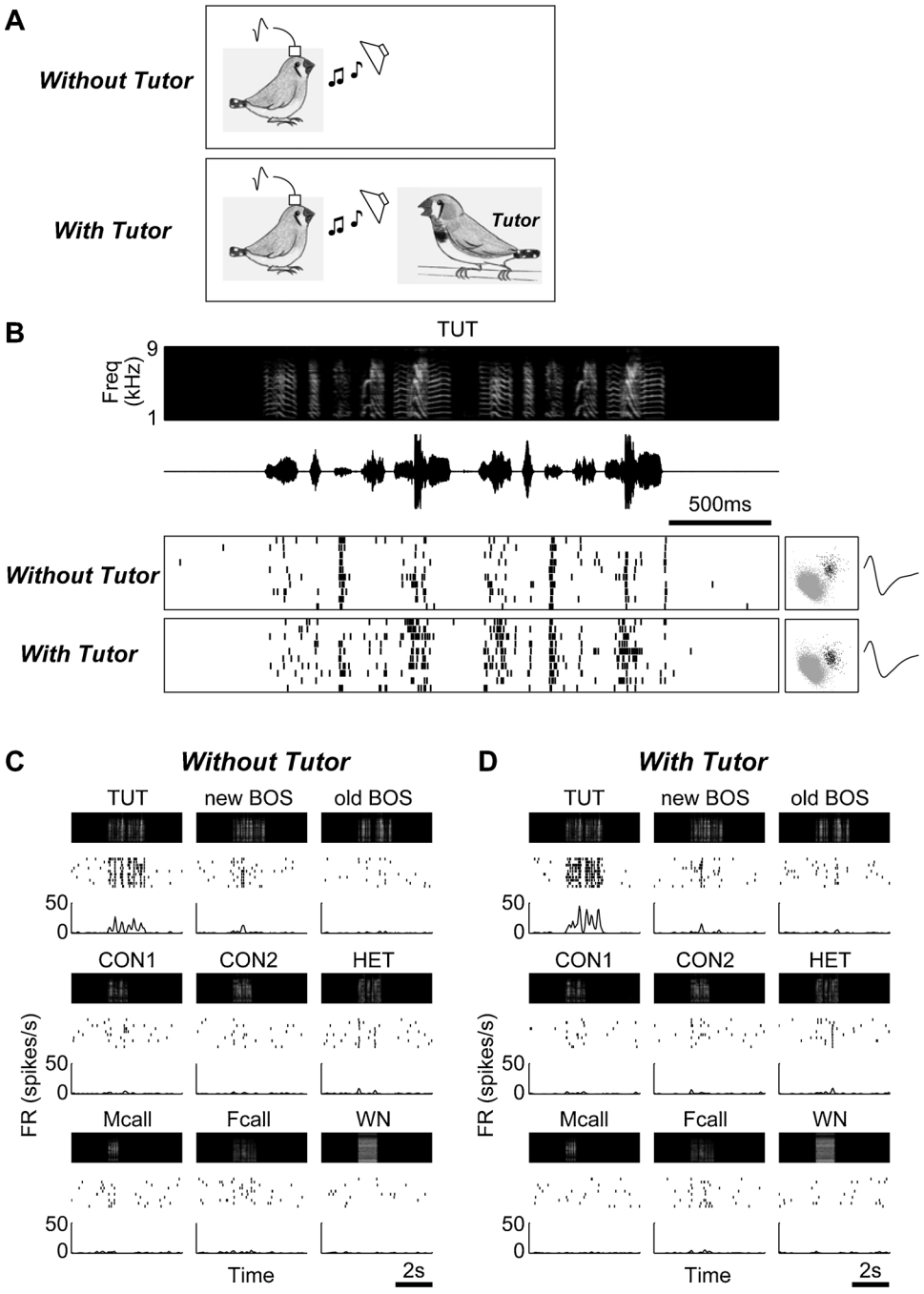

Fig. 1. Tutor presence modifies auditory responses in the zebra finch auditory cortex.
A: Diagram of the experimental design. Neuronal responses to various song stimuli were recorded in juvenile zebra finch higher auditory cortex in freely behaving conditions, with or without a tutor present. B–D: With the tutor present, neurons in the higher auditory cortex, the NCM, show greater responses to song stimuli. B: Representative responses to a tutor song (TUT)-selective neuron with and without the tutor. Sonogram (top), oscillogram (middle), and raster plots (bottom) are shown. Spike clusters and spike waveforms with or without the tutor are shown on the right. C–D: Auditory responses of the same TUT-selective neuron without (C) and with (D) a tutor. Sonogram (top), raster plots (middle), and firing rate histogram (bottom) for each sound stimulus are shown.

tutor song learning (Bolhuis et al., 2000). Electrophysiological recording shows faster habituation with repeated tutor song presentation than with repeated novel songs (Phan et al., 2006). Pharmacological blockade of ERK activation during tutor song exposure prevents juveniles from learning these songs (London & Clayton, 2008). Recently we suggested that early tutor auditory experiences shape cortical neuronal circuits to form memories of tutor songs (Yanagihara and Yazaki-Sugiyama, 2016). As a neurophysiological representation of tutor song memory, a specific type of neuron responds selectively to tutor songs after experiencing those songs, and selectivity changes depending on the bird's arousal state. Here we show that these selective neurons, but not non-selective neurons, exhibit greater auditory responses in the presence of a live tutor.

2. Methods

2.1. Subjects and experimental design

Experiments were performed in accordance with experimental protocols approved by the Animal Care Committee at Okinawa Institute of Science and Technology (OIST) Graduate University. Five male juvenile zebra finches, born and reared in our colony, were used in experiments. Birds were raised in cages with their parents and siblings. Then, at 53–62 days post hatch (DPH), male juveniles underwent surgery for electrode implantation under isoflurane anesthesia. After electrode implantation, juveniles were caged singly in sound attenuation chambers, and were occasionally moved to an experimental chamber for electrophysiological recordings. Single-unit activity was recorded from juveniles while they were isolated in the recording