

EMERGENT CATEGORICAL REPRESENTATION OF NATURAL, COMPLEX SOUNDS RESULTING FROM THE EARLY POST-NATAL SOUND ENVIRONMENT

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Abstract—Cortical sensory representations can be reorganized by sensory exposure in an epoch of early development. The adaptive role of this type of plasticity for natural sounds in sensory development is, however, unclear. We have reared rats in a naturalistic, complex acoustic environment and examined their auditory representations. We found that cortical neurons became more selective to spectrotemporal features in the experienced sounds. At the neuronal population level, more neurons were involved in representing the whole set of complex sounds, but fewer neurons actually responded to each individual sound, but with greater magnitudes. A comparison of population-temporal responses to the experienced complex sounds revealed that cortical responses to different renderings of the same song motif were more similar, indicating that the cortical neurons became less sensitive to natural acoustic variations associated with stimulus context and sound renderings. By contrast, cortical responses to sounds of different motifs became more distinctive, suggesting that cortical neurons were tuned to the defining features of the experienced sounds. These effects lead to emergent “categorical” representations of the experienced sounds, which presumably facilitate their recognition. © 2013 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: natural sound, spectrotemporal receptive field, neurogram, sparse coding, unsupervised learning.

INTRODUCTION

The cerebral cortex is highly adaptive to its sensory environment both during development and in adulthood. During an epoch of early life known as the “critical period”, cortical sound representations can be profoundly shaped by the acoustic environment (Zhang et al., 2001; Insanally et al., 2009). Previous studies, using tone pips or noise bursts, demonstrated that the specific effects of the early environment on auditory

neurons depend on the spectrotemporal properties of the sensory stimuli (Zhang et al., 2002; Chang and Merzenich, 2003; Nakahara et al., 2004; de Villers-Sidani et al., 2008; Kim and Bao, 2009; Insanally et al., 2010). Notably, auditory cortex over-represents experienced sounds. In stark contrast to exposure to tone pips and noise bursts in experimental conditions, humans and animals in normal acoustic environment experience natural and complex sounds that are highly structured during sensory development. Such enriched experience is necessary for the proper development of language/vocalization and other cognitive skills. In this report, we investigate how a rich and structurally complex auditory environment reorganizes acoustic representations by auditory cortical neurons, and its potential impact for categorical sound perception.

Auditory stimuli in the natural environment are rich, complex and highly structured. Animal vocalizations are an important class of natural sounds. Many animal species show stronger neural responses and better perceptual sensitivity to vocal sounds of their own species (Margoliash, 1983; Doupe and Konishi, 1991; Esser et al., 1997). For instance, neurons in the primary auditory cortex (AI) of marmoset monkeys responded more strongly to their conspecific calls than their time-reversed version (Wang and Kadia, 2001). In cats, both the normal and the reversed marmoset calls activated AI neurons equally weakly (Wang and Kadia, 2001). However, in most plasticity studies, experimental animals were given extensive experience of a single, often simple stimulus, such as a single-frequency tone (Zhang et al., 2001; Han et al., 2007). Those experimental stimuli were impoverished in terms of variability, complexity and structures, which are presumably important for normal sensory development. Thus, it is unclear how those results are applicable in understanding normal sensory development. For instance, it has been shown that animals that had experienced single-frequency tone pips exhibit enlarged cortical representations of the experienced sounds (Zhang et al., 2001), which presumably leads to refined cortical sensory processing (Recanzone et al., 1993; Godde et al., 2000; Bao et al., 2004; Polley et al., 2004a; Tegenthoff et al., 2005). However, recent studies failed to correlate enlarged cortical representations with refined perceptual performance (Talwar and Gerstein, 2001; Brown et al., 2004; Han et al., 2007; Reed et al., 2011), questioning the implication and generality of

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Abbreviations: AI, primary auditory cortex; CC, correlation coefficient; FM, frequency-modulated; STRF, spectrotemporal receptive field.

findings in animals with impoverished sensory experience.

Animal vocalizations exhibit complex statistical structure (Holy and Guo, 2005; Takahashi et al. 2010). For example, rodent pup and adult calls are repeated in bouts with repetition rates in a range near 6 Hz (Liu et al., 2003; Holy and Guo, 2005; Kim and Bao, 2009). Calls of the same type are more likely to occur in the same sequences than do calls of different types (Holy and Guo, 2005). This higher-order statistical structure may provide information for classifying the calls into distinct, categorically perceived groups of sounds (Ehret and Haack, 1981). Indeed, a recent study showed that auditory cortex was shaped to represent sounds in the same sequences more similarly, and represent sounds that never occurred in the same sequences more distinctively, forming a representational boundary (Köver et al., 2013). In addition, perceptual sensitivity was also elevated across the representational boundary, establishing a perceptual boundary (Köver et al., 2013). Such representational and perceptual changes could contribute to categorical perception of the experienced sounds.

Categorical perception of conspecific animal vocalizations has been reported in a wide range of non-human animals (May et al., 1989; Nelson and Marler, 1989; Wyttenbach et al., 1996; Baugh et al., 2008), including rodents (Ehret and Haack, 1981). Although the existence of language-specific differences in speech sound perception (Fox et al., 1995; Iverson and Kuhl, 1996) has long pointed to a role for early experience in shaping human speech perception, the contribution of early experience to categorical perception in non-human animals is still unclear (Kuhl and Miller, 1978; Mesgarani et al., 2008; Prather et al., 2009). In the present study, we examine effects of early experience of a set of animal vocalizations recorded in a natural environment—referred to here as “jungle sounds”—on primary cortical acoustic representations. Our results reveal emergent categorical representation of the experienced heterospecific vocalizations, suggesting a role of early experience in categorical perception of natural complex sounds.

EXPERIMENTAL PROCEDURES

Animals and experimental design

All procedures were approved under University of California San Francisco Animal Care Facility protocols. Four groups of rat pups were used in this study, including three sound exposure groups and one naïve control group. The naïve control group was housed in regular animal room. The three sound exposure groups were exposed to natural animal vocalizations, noises with separately modulated power spectrum and envelope, or pitch-shifted human speech sounds. After sound exposure, responses to natural animal vocalizations were recorded from AI neurons to determine how experience shapes cortical representation of complex sound. The noise group was used to determine effects of simple sound features such as separate spectral and

temporal modulations. Speech group was used to determine if effects of complex sounds were specific to the stimuli. Naïve control animals were also mapped at the same age.

Sound stimuli

A set of natural animal vocal sounds (referred to hereafter as “jungle sounds”, 1-h long, continuously recorded from a natural forest at a sampling rate of 44.2 kHz) was used as the experimental stimuli. In this sound record, there were at least 40 repeated vocalization or communication sounds generated by different mammalian, avian or insect species.

We filtered the jungle sound stimuli with 109 Gaussian filters with center frequency separation and bandwidth (SD) of the filters equal to 0.05 octave. Analytical signal decomposition was performed on the signal in each frequency band to obtain its instantaneous amplitude. To construct the spectrogram, the instantaneous amplitude was plotted on a logarithmic scale in frequency and time. Two-dimensional Fourier transforms of the stimulus spectrograms were computed to obtain spectrotemporal modulation spectra of the stimuli. Noises with overall frequency spectra and temporal envelope modulation similar to those of the jungle sounds were used as control stimuli. To make these noise stimuli, white noise was first filtered with the 109 Gaussian filters. The amplitude of the signal in each frequency band was adjusted to match the mean amplitude of the jungle sound stimuli in that frequency band. Signals were then added together and amplitude-modulated to match the overall amplitude of the jungle sound stimuli. Speech stimuli used for acoustic rearing were 5 min of sentences of Western American English naturally spoken by different male and female speakers, which were obtained from Linguistic Data Consortium at University of Pennsylvania. To match the rat's hearing, spectra of the speech stimuli were shifted 1.46 octaves higher.

Acoustic exposure

Litters of rat pups were placed (with their mothers) in a sound-shielded chamber with a 12/12-h light/dark cycle from postnatal day 13 (P13) to P30. The jungle sounds, noises and speech stimuli were continuously played. The sound pressure level was rarely above 65 dB and never higher than 80 dB. After sound exposure, the rats were placed back in the animal room.

Physiological recording

Under anesthesia (ketamine and xylazine), frequency-intensity receptive fields were recorded from multiunits sampled across the right temporal cortex to outline AI (Bao et al., 2001). Multiunits were then recorded from layer 4/5 in AI. Auditory stimuli were delivered through a calibrated earphone to the right ear. Frequency/intensity response areas were reconstructed in detail by presenting 60 pure-tone frequencies (0.5–30 kHz, 25-ms duration, 5-ms ramps) at each of eight sound intensities.

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