



Research paper

Speech discrimination after early exposure to pulsed-noise or speech

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ABSTRACT

Early experience of structured inputs and complex sound features generate lasting changes in tonotopy and receptive field properties of primary auditory cortex (A1). In this study we tested whether these changes are severe enough to alter neural representations and behavioral discrimination of speech. We exposed two groups of rat pups during the critical period of auditory development to pulsed-noise or speech. Both groups of rats were trained to discriminate speech sounds when they were young adults, and anesthetized neural responses were recorded from A1. The representation of speech in A1 and behavioral discrimination of speech remained robust to altered spectral and temporal characteristics of A1 neurons after pulsed-noise exposure. Exposure to passive speech during early development provided no added advantage in speech sound processing. Speech training increased A1 neuronal firing rate for speech stimuli in naïve rats, but did not increase responses in rats that experienced early exposure to pulsed-noise or speech. Our results suggest that speech sound processing is resistant to changes in simple neural response properties caused by manipulating early acoustic environment.

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1. Introduction

Early auditory experience alters the development of primary auditory cortex (A1). Exposure to structured inputs during critical period of auditory development induces changes of receptive field properties and temporal response dynamics that endure into adulthood (de Villiers-Sidani et al., 2007; Han et al., 2007; Insanally et al., 2010, 2009; Kim and Bao, 2009; Zhang et al., 2001, 2002; Zhou and Merzenich, 2007, 2008, 2009). Exposure to moderate intensity pulsed-noise during development results in deteriorated tonotopicity, broader tone frequency tuning and degraded cortical temporal processing manifested by weaker responses to rapid tone trains (Zhang et al., 2002; Zhou and Merzenich, 2008, 2009). Exposure to pulsed tones during development broadens tone frequency tuning and results in an expansion of the A1 representations of the exposed tone frequency (de Villiers-Sidani et al., 2007; Zhang et al., 2001). Exposure to downward FM sweeps during development gives rise to greater selectivity for the sweep rate and direction of the exposed stimulus (Insanally et al., 2009). It was

suggested that cortical plasticity induced by manipulating early acoustic inputs could impair the processing of complex sounds such as speech (Chang et al., 2005; Zhou and Merzenich, 2007, 2008, 2009). Given the profound effects of native language exposure on speech perception in later life, the early acoustic experience of speech itself is likely to play an important role in shaping the auditory cortex (Kuhl, 2004; Kuhl et al., 2003, 1997a, 1997b). Neural circuits shaped by unique language experience during infancy have been suggested as a primary determinant factor in behavioral ability to discriminate speech (Cheour et al., 1998; Kuhl, 2010; Naatanen et al., 1997). However, the degree of developmental auditory cortex plasticity that is necessary to produce a significant effect on neural representation and behavioral discrimination of speech has not been tested.

Earlier studies have shown that neural activity patterns generated in rat A1 are significantly correlated with behavioral discrimination of speech (Engineer et al., 2008). Rats discriminated easily between consonant pairs that generated distinct spatio-temporal patterns and did poorly between pairs that generated similar patterns. Recent evidence from intraoperative recordings in humans have shown that representation of speech signals in posterior superior temporal gyri significantly predict the psychophysical behavior of speech recognition by humans (Chang et al., 2010). These observations suggest that A1 representations play a key role in speech sound processing and subsequent behavioral outcome of speech perception. In this study we tested the

Abbreviations: A1, primary auditory cortex; BW20, bandwidth at 20 dB threshold; CVC, consonant-vowel-consonant; SPL, sound pressure level.

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hypothesis that, changes of spectral and temporal selectivity of A1 neurons induced by early acoustic environmental patterns are severe enough to influence the behavioral and neural discrimination of speech. We exposed rat pups to two different manipulations of early auditory experience (i.e. exposure to pulsed-noise or speech) and later trained them to discriminate speech sounds. We examined the anesthetized A1 neural activity patterns of pulsed-noise-reared and speech-reared rats before and after speech training.

2. Methods

2.1. Early exposure

We exposed two groups of Sprague–Dawley rat pups during their postnatal development from day 9 (P9) through day 38 (P38) to either a pulsed-noise stimulus or to speech sounds (Fig. 1). The pulsed-noise-rearing consisted of exposure to fifty millisecond noise pulses (5-ms ramps) at 6 pulses per second pps with 1-s intervals in between. The speech rearing consisted of 13 CVC (consonant-vowel-consonant) speech syllables, each 1.5 s long. To match the most ethological rates of presentation, the 13 speech sounds were randomly interleaved with 13 silent wave files of the same duration and a single wave (speech or silent) was presented once every 2 s in random order. These 13 syllables consisted of the same CVC syllables that rats were trained to discriminate in later life (see methods below). Both pulsed-noise and speech sounds contained energy levels below 25 kHz. All sounds were played through an iPod connected to a speaker placed ~15 cm above the rats and with 65-dB sound pressure level. During the exposure period litters of rat pups and their mothers were placed in a sound shielded chamber. A reverse 12-h light/12-h dark cycle was maintained to provide the normal physiological balance during awake and sleep states. Nearly half of the control group of rats was reared in an identical sound shielded chamber that did not play any sounds from P9 to P38. The rest of the control rats were reared (from P9 to P38) in standard housing room environments. The tuning curve properties of the rats reared in the sound shielded chamber without any sounds were not significantly different from the rats reared in the standard housing room condition. For the analysis, therefore, we combined the two sets of control rats into a single control group. Only the female pups were used in the experiments. All experimental procedures were approved by the Animal Care and Use Committee at the University of Texas at Dallas.

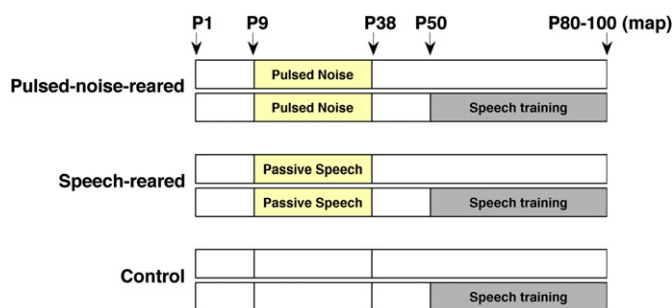


Fig. 1. Experimental timeline. Pulsed-noise-reared and speech-reared rat pups were exposed to a pulsed-noise and speech sounds respectively, from postnatal day 9 (P9) to postnatal day 38 (P38). Control group consisted of rats reared in an identical sound-proof exposure booth without pulsed-noise or speech inputs (nearly half of the control rats) and rats reared in standard housing room conditions. Each group consisted of two subgroups as speech-trained ($n = 12$ in each) and untrained. The trained subgroups started speech training on postnatal day 50 (P50). Physiology recordings from both trained and untrained rats of each group were done during a window of P80 to P100.

2.2. Speech training and analysis

We trained 50 days (P50) old juvenile rats to discriminate 6 consonant pairs and 6 vowel pairs. The 6 consonant pairs included Dad/Bad, Dad/Gad, Dad/Tad, Sad/Shad, Sad/Had, and Sad/Dad. The 6 vowel pairs included Dad/Dud, Dad/Did, Dad/Dayed, Sad/Seed, Sad/Sead, and Sad/Sood. The spectrogram illustrations of these stimuli have been published elsewhere (Engineer et al., 2008; Perez et al., in press). 12 rats from each group of pulsed-noise-reared, speech-reared and control group were trained to discriminate speech in an operant training paradigm. Rats pressed a lever for a food reward for a target stimulus (CS plus) and rejected the lever for non-target stimuli (CS minus). Half the rats in each group (6 rats) were trained on the target 'Dad' (non-targets: Bad, Gad, Tad, Dud, Did, Dayed) and the other half were trained on the target 'Sad' (non-targets: Shad, Had, Dad, Seed, Sead, Sood). Thus each rat performed three consonant discrimination tasks and three vowel discrimination tasks. The speech sounds were spoken by a native female English speaker inside a double walled soundproof booth. To better match the rat hearing range, the fundamental frequency of the spectral envelope of each recorded syllable was shifted up in frequency by a factor of two using the STRAIGHT vocoder (Kawahara, 1997). The intensity of each speech sound was adjusted so that the intensity of the loudest 100 ms of the syllable was at 60 dB sound pressure level (SPL).

The operant training chamber consisted of a double walled, sound shielded booth containing a cage with a lever, a pellet receptacle and a house light. A pellet dispenser mounted outside the booth was connected to the pellet receptacle via a tube. A calibrated speaker was mounted approximately 20 cm from the most common location of the rat's head position while inside the booth (the mid point between the lever and the pellet receptacle). Rats were food deprived during the training days to motivate behavior, but were fed otherwise to maintain between 85% and 100% of their ideal body weight. Each rat was placed in the operant training booth for 1-h session, twice daily for five days per week.

The training began with a brief shaping period to teach the rat to press the lever in order to receive a food pellet reward. Each time the rat was in close proximity to the lever, it heard the target sound, and received a sugar pellet reward. Eventually the rat learned to press the lever without assistance. The shaping continued until the rat was able to earn a minimum of 120 pellets per session, which lasted on average 3–5 days. During the next stage of training the rat began a detection task where it was trained to press the lever when the target sound was presented. Initially the sound was presented every 10 s and the rat received a sugar pellet reward for pressing the lever within 8 s. The sound interval was gradually reduced to 6 s and the lever press window to 3 s. The target sound was randomly interleaved with silent catch trials during each training session to prevent rats pressing the lever habitually. Performance of the rat was monitored using the d' value, which is a measure of discriminability according to signal detection theory (Green and Swets, 1989). The detection training continued until the rats reached a $d' \geq 1.5$ for six sessions. This portion of training lasted for ~15 days (~30 sessions). After completing the detection phase, the rats learned to discriminate the target sound from the non-targets. In a given 1 h session each rat discriminated the target sound against the six non-target sounds that were presented randomly interleaved with silent catch trials. Rats were rewarded with a sugar pellet when they pressed the lever within 3 s following the target stimulus. Pressing the lever for a non-target stimulus resulted in a 6 s time-out in which the training program paused and the house light was turned off. The discrimination training consisted of 20 sessions (10 days). The final percent correct discrimination performance for each task was computed using the number

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