



Research Paper

Developmental hearing loss impedes auditory task learning and performance in gerbils

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ABSTRACT

The consequences of developmental hearing loss have been reported to include both sensory and cognitive deficits. To investigate these issues in a non-human model, auditory learning and asymptotic psychometric performance were compared between normal hearing (NH) adult gerbils and those reared with conductive hearing loss (CHL). At postnatal day 10, before ear canal opening, gerbil pups underwent bilateral malleus removal to induce a permanent CHL. Both CHL and control animals were trained to approach a water spout upon presentation of a target (Go stimuli), and withhold for foils (Nogo stimuli). To assess the rate of task acquisition and asymptotic performance, animals were tested on an amplitude modulation (AM) rate discrimination task. Behavioral performance was calculated using a signal detection theory framework. Animals reared with developmental CHL displayed a slower rate of task acquisition for AM discrimination task. Slower acquisition was explained by an impaired ability to generalize to newly introduced stimuli, as compared to controls. Measurement of discrimination thresholds across consecutive testing blocks revealed that CHL animals required a greater number of testing sessions to reach asymptotic threshold values, as compared to controls. However, with sufficient training, CHL animals approached control performance. These results indicate that a sensory impediment can delay auditory learning, and increase the risk of poor performance on a temporal task.

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1. Introduction

Developmental hearing loss studies often postulate a causal relationship between impaired sensory encoding and degraded perceptual abilities. There is good reason for this. Both peripheral and central auditory function are vulnerable to auditory trauma or deprivation during development; for the peripheral nervous system (Bock and Saunders, 1977; Henry, 1973; Kujawa and Liberman, 2006; Lenoir and Pujol, 1980; Saunders and Hirsch, 1976; Saunders and Chen, 1982; Stanek et al., 1977); for the central nervous system (Aizawa and Eggermont, 2006, 2007; DeBello et al., 2001; Fallon et al., 2008; Knudsen et al., 1984a; Mogdans and Knudsen, 1993,

1994; Moore et al., 2002; Popescu and Polley, 2010; Raggio and Schreiner, 1999; Razak et al., 2008; Rosen et al., 2012; Salvi et al., 2000; Snyder et al., 2000; Takahashi et al., 2006; Wang et al., 2002; Yu et al., 2005). Even a transient period of monaural hearing loss causes persistent encoding deficits in auditory cortex after normal audibility is restored (Polley et al., 2013). Although a sensory framework likely explains many behavioral deficits that attend hearing loss, there is also compelling clinical evidence suggesting that cognitive skills may also be delayed or impaired (Bennett and Furukawa, 1984; Feagans et al., 1987; Manders and Tyberghein, 1984; Mody et al., 1999; Psarommatis et al., 2001; Reichman and Healey, 1983; Schlieper et al., 1985; Teele et al., 1990). For example, slight to mild childhood hearing loss is associated with a decline in phonological short-term memory (Briscoe et al., 2001; Park and Lombardino, 2012; Wake et al., 2006), suggesting that non-sensory mechanisms are vulnerable to early deprivation. Therefore, this study was designed to determine whether adult animals reared with conductive hearing loss (CHL) display deficits

Abbreviations: AM, amplitude modulation; CHL, conductive hearing loss; CNS, central nervous system; NH, normal hearing

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both in their initial performance on an auditory task, and in their asymptotic performance following a period of practice.

A primary motivation for studying mild to moderate developmental hearing loss is that long-lasting auditory-processing deficits can be induced by the kind of mild, transient hearing loss that is prevalent in childhood. In general, studies on childhood otitis media with effusion that confirm impaired hearing also demonstrate subsequent deficits in perception, speech, and language processing that can persist for months to years, long after normal audibility is restored (Whitton and Polley, 2011). Moreover, the childhood population with mild to moderate loss is estimated to be relatively large (Niskar et al., 1998) NIDCD Statistical Report 2005, as compared to those with severe or profound loss, and newborn hearing screens typically do not identify infants who have a loss of less than 30–40 dB (Johnson et al., 2005; Morton and Nance, 2006; Prieve et al., 2013). Since well-controlled clinical studies of childhood hearing loss are challenging, the use of non-human models can provide a valuable assessment of the inherent risk for diminished perceptual development.

The non-human studies that have explored the effects of CHL on auditory perception primarily focus on the impact of unilateral hearing loss on sound localization, and neural encoding properties that support binaural processing (Clements and Kelly, 1978; Keating and King, 2013; Keating et al., 2013; Kelly et al., 1987; Knudsen et al., 1984a,b; Moore et al., 1999). However, since otitis media with effusion is more commonly bilateral in humans (Engel et al., 1999), it is important to study the consequences of mild to moderate binaural hearing loss on the perception of spectral or temporal cues that support speech comprehension. In fact, a transient period of mild binaural hearing loss does lead to a perceptual deficit on an amplitude modulation (AM) detection task (Caras and Sanes, 2015b; Rosen et al., 2012). This perceptual deficit is most severe when transient hearing loss occurs during a well-defined developmental critical period, and closely correlates with a critical period during which auditory cortex synaptic and membrane properties are vulnerable to the same manipulation (Mowery et al., 2015).

To evaluate the behavioral impact of bilateral CHL, animals were subjected to bilateral malleus removal during juvenile development, and reared to adulthood. Using an appetitive reinforcement operant conditioning procedure (Buran et al., 2014a), adult CHL and control animals were trained on an AM rate discrimination task. AM is a favorable acoustic feature to examine because it is an important component of most vocalizations, including speech (Elliott and Theunissen, 2009; Rosen, 1992; Singh and Theunissen, 2003). The testing procedure allowed us to characterize task acquisition (i.e., learning rate), as well as perceptual sensitivity (i.e., psychometric performance) at the earliest stage of testing and when animals reached asymptotic performance. The results show that CHL animals display a slower rate of task acquisition for AM discrimination, and poorer performance at the outset of testing, although some animals reached control-like performance after sufficient training.

2. Experimental approaches

2.1. Animals and groups

Data were obtained from adult Mongolian gerbils (*Meriones unguiculatus*) with normal hearing (NH, $n = 12$, 7 male) and developmental conductive hearing loss (CHL, $n = 8$, 5 male). Animals were assigned to one of two behavioral tasks: amplitude modulation (AM) rate discrimination at 4 Hz ($n = 5$ NH; $n = 5$ CHL) or 32 Hz ($n = 7$ NH; $n = 3$ CHL). All animals were trained and tested on AM discrimination as juvenile-adults (>P70) and were weaned

from commercial breeding pairs (Charles River). All procedures related to the maintenance and uses of animals were in accordance with the Institutional Animal & Use Committee Handbook and approved by the University Animal Welfare Committee at New York University.

2.2. Hearing loss surgery

For the CHL group, bilateral conductive hearing loss was induced at postnatal day 10, just before the ear canals would open naturally, as described previously (Xu et al., 2007). A surgical level of anesthesia was induced (methoxyflurane, Medical Developments International), and the malleus was removed through a perforation in the tympanic membrane. After recovery, animals were reared to adulthood with a permanent bilateral conductive loss of approximately 40 dB (Buran et al., 2014a; Rosen et al., 2012; Tucci et al., 1999). Normal hearing (NH) animals did not undergo a sham surgery. However, previous work from our lab indicates that similar neural effects of CHL are observed whether compared to sham controls or non-sham controls (Kotak et al., 2013; Takesian et al., 2012). As an additional control to assure that poorer task performance was not due to a CHL-related impairment of motor function, we compared behavioral response times between NH and CHL animals. During the discrimination task we found that CHL animal response times for a “Yes” (made contact with the water spout) response (mean \pm SEM; 2.16 ± 0.05 s) and a “No” (initiated a new trial) response (1.30 ± 0.04 s) were not significantly slower than NH “Yes” (2.2 ± 0.04 s) and “No” (1.36 ± 0.04 s) responses animals in any of the training phases.

2.3. Auditory psychophysics

2.3.1. Testing conditions

Gerbils were placed in a plastic cage in a sound-isolation booth (Gretch-Ken Industries) and observed via closed-circuit monitor. A personal computer, connected to a digital input/output interface (TDT RZ6, Tucker-Davis Technologies), controlled acoustic stimuli, reward delivery timing, as well as the acquisition of behavioral data. AM stimuli generated by the Tucker-Davis Technologies system (RZ6) were delivered via calibrated tweeter (DX25TG05-04; Vifa) positioned 1 m above the test cage. Sound levels were measured with a spectrum analyzer (3550, Bruel & Kjaer) via one-quarter inch free-field condenser microphone positioned at the location where animals head aligned with the nose port during a trial. For NH animals, sound level was constant (50 dB equivalent SPL) for all AM stimuli to exclude the use of energy cues. The carrier was broadband noise, with a 25 dB roll-off at 3.5 kHz and a 25 dB roll-off at 20 kHz. All stimuli began with a 200 ms ramp, followed by an unmodulated period of 200 ms, and then transitioned to an amplitude modulation (AM). The delay period prevented animals from making a decision at stimulus onset. For CHL animals, identical stimuli were used however they were presented at 95 dB SPL (i.e., 45 dB louder than that used for NH animals), to compensate for the induced loss. Except for the sound level used for CHL animals, all general training and testing procedures were similar to those described previously for NH animals (Buran et al., 2014b; Sarro et al., 2015).

The difference in sound levels was implemented so as to present stimuli to CHL and NH animals at equivalent sensation levels. The adjustment in sound pressure level for CHL animals was based on physiological measurements (cochlear microphonics and auditory brainstem responses) that show audiometric thresholds for this manipulation produce an attenuation of ≈ 40 – 45 dB (Rosen et al., 2012; Tucci et al., 1999; Xu et al., 2007). In addition, behavioral data indicates that the threshold at which a 100% AM stimulus can

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