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EXPOSURE TO A NOVEL STIMULUS ENVIRONMENT ALTERS PATTERNS OF LATERALIZATION IN AVIAN AUDITORY CORTEX

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Abstract—Perceptual filters formed early in development provide an initial means of parsing the incoming auditory stream. However, these filters may not remain fixed, and may be updated by subsequent auditory input, such that, even in an adult organism, the auditory system undergoes plastic changes to achieve a more efficient representation of the recent auditory environment. Songbirds are an excellent model system for experimental studies of auditory phenomena due to many parallels between song learning in birds and language acquisition in humans. In the present study, we explored the effects of passive immersion in a novel heterospecific auditory environment on neural responses in caudo-medial neostriatum (NCM), a songbird auditory area similar to the secondary auditory cortex in mammals. In zebra finches, a well-studied species of songbirds, NCM responds selectively to conspecific songs and contains a neuronal memory for tutor and other familiar conspecific songs. Adult male zebra finches were randomly assigned to either a conspecific or heterospecific auditory environment. After 2, 4 or 9 days of exposure, subjects were presented with heterospecific and conspecific songs during awake electrophysiological recording. The neural response strength and rate of adaptation to the testing stimuli were recorded bilaterally. Controls exposed to conspecific environment sounds exhibited the normal pattern of hemispheric lateralization with higher absolute response strength and faster adaptation in the right hemisphere. The pattern of lateralization was fully reversed in birds exposed to heterospecific environment for 4 or 9 days and partially reversed in birds exposed to heterospecific environment for 2 days. Our results show that brief passive exposure to a novel category of sounds was sufficient to induce a gradual reorganization of the left and right secondary auditory cortices. These changes may reflect modification of perceptual filters to form a more efficient representation of auditory space.

Key words: auditory, birdsong, plasticity, lateralization, forebrain.

INTRODUCTION

Over the course of a lifetime, an individual is exposed to a wide and varying range of acoustic stimuli. Although the peripheral auditory system initially parses sounds into their constituent frequencies and phase, evidence is increasing that the auditory cortex, and perhaps earlier stations, can represent more complex sound features (Schreiner, 1995; Woolley and Casseday, 2004; Woolley et al., 2009; O'Connor et al., 2010). These representations are established during development (Miller and Knudsen, 2001; Bao et al., 2013; Amin et al., 2013), but they are not fixed (Edeline et al., 1993; Gentner and Margoliash, 2003; Gentner et al., 2004; Cheung et al., 2005; Fritz et al., 2007; Meliza, 2011; David et al., 2012). As new sounds are experienced, the cortex may adapt dynamically in order to represent the statistics of the current acoustic environment in an efficient manner (Scheich et al., 2007; Nelken, 2008; Sharpee et al., 2011). In many vertebrates, early exposure to a set of species-specific sounds shapes perceptual filters to respond preferentially to these highly relevant communication signals (Maier and Scheich, 1987; Ehret, 1987; Suga et al., 1997; Belin et al., 2000; Portfors et al., 2009; Amin et al., 2013). In some species that are capable of learning a complex set of vocal communication signals, both auditory perception and vocal production of these salient sounds have been shown to be lateralized, e.g. for native language in humans and song in songbirds (Nottebohm et al., 1976; Floody and Arnold, 1997; Springer et al., 1999; Wild et al., 2000; Dronkers et al., 2007; Voss et al., 2007; Poirier et al., 2009; Phan and Vicario, 2010; Moorman et al., 2012; Ocklenburg et al., 2013). This raises the question of how adaptive changes in acoustic representations induced by experience with new sounds in adulthood interact with pre-existing patterns of lateralized processing.

In humans, the acoustic categories of native vs. non-native language are established by the first year of age and, in adulthood, robust lateralization is seen only for the native language (Doupe and Kuhl, 1999; Hickok and Poeppel, 2007; Kovelman et al., 2011). Similarly, in songbirds, lateralized processing is dependent on normal auditory exposure during an early period, and is not seen for simple sounds (Phan and Vicario, 2010). Although this groundwork for recognition and categorization of sounds is laid down during the juvenile period, the auditory cortex retains a level of plasticity into adulthood (Recanzone et al., 1993; Bao et al., 2004); this could contribute to the ability to master a new language or to refine pitch

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Abbreviations: ARM, Absolute Response Magnitude; NCM, caudo-medial neostriatum; rms, root mean square.

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perception in musicians. When the acoustic environment changes, e.g., when an English-speaking adult is immersed in a foreign language environment containing new contrasts and categories not encountered in the native language, the auditory cortex may change to represent the new auditory information. The challenge of changing acoustic statistics could drive a process of neural reorganization that affects the existing pattern of lateralization if the modification of perceptual filters to represent new sound categories occurs separately in the left and right hemispheres. In the present study, we tested this scenario by immersing adult songbirds in a novel acoustic environment (the vocalizations of a different species) and then assessing changes in auditory responses in the two brain hemispheres.

The many parallels between songbird vocal learning and human speech acquisition (Doupe and Kuhl, 1999), including, most importantly, hemispheric lateralization for both motor and auditory processing (Nottebohm et al., 1976; Williams et al., 1992; Cynx et al., 1992; Floody and Arnold, 1997; Wild et al., 2000; Voss et al., 2007; Poirier et al., 2009; Phan and Vicario, 2010), make the songbird the best model system for addressing this question with invasive physiological techniques. In addition, recent anatomical evidence suggests close analogies, if not homologies, between the thalamo-cortical auditory system of birds and mammals (Haesler et al., 2004; Wang et al., 2010; Bolhuis et al., 2010; Dugas-Ford et al., 2012; Karten, 2013; Jarvis et al., 2013), though the homology hypothesis is not undisputed (Montiel and Molnár, 2013). This study focuses on neural responses in the caudo-medial neostriatum (NCM) of the

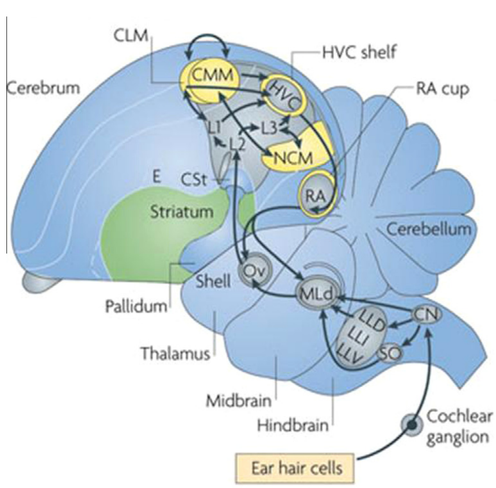

Fig. 1. Avian auditory system. Ascending auditory inputs travel from hair cells to nucleus mesencephalicus lateralis pars dorsalis (MLD; avian homolog of mammalian central nucleus of the inferior colliculus), through auditory thalamus, nucleus Ovoidalis (Ov; avian homolog of mammalian medial geniculate nucleus). Ov then projects to forebrain region Field L2, thought to be homologous to thalamo-recipient layers III–IV of the mammalian cortex (Wang et al., 2010; Dugas-Ford et al., 2012). Field L2 sends projections to adjacent areas, Field L1 and L3, which in turn project to the caudo-medial nidopallium (NCM) and caudal mesopallium (CLM and CMM). Reprinted by permission from Macmillan Publishers Ltd: Nature Reviews Neuroscience (Bolhuis et al., 2010).

zebra finch, a forebrain area that is analogous to superficial layers of mammalian A1 or perhaps a secondary auditory cortex (Theunissen et al., 2000; Wang et al., 2010). Fig. 1 illustrates the circuitry of the birdsong auditory system used in sound perception (Bolhuis et al., 2012). NCM neurons respond selectively to vocalizations with acoustic features typical of their own species and undergo stimulus-specific adaptation to the unique songs of individual conspecifics, which represents a form of long-lasting neuronal memory (Chew et al., 1995; Stripling et al., 2001; Phan et al., 2006). Lateralization of auditory processing in NCM has been demonstrated in both electrophysiological and IEG studies (Phan and Vicario, 2010; Bolhuis et al., 2012). Neural responses to song are stronger and adapt faster in the right NCM hemisphere than in the left; this lateralization depends on early auditory experience (Phan and Vicario, 2010). These properties make songbird NCM an excellent place to study the interaction of novel auditory experience with lateralization for complex vocal sounds.

EXPERIMENTAL PROCEDURES

Animals

Adult male zebra finches (> 120 days of age) were obtained from the zebra finch breeding aviary at Rutgers University, New Brunswick, NJ or purchased from a local supplier. At the start of the experiment, subjects were removed from the general aviary and individually housed in soundproof isolation boxes for 9, 4, or 2 consecutive days. A separate group of birds housed in the general aviary served as aviary controls (AV), with exposure to the general acoustics of the aviary. All subjects were maintained on a 12/12 light cycle with *ad libitum* access to food and water.

Environment

Subjects were randomly assigned to groups and exposed to either a control conspecific environment (9-d and 4-d CONENV) or an experimental heterospecific environment (2-d, 4-d, and 9-d HETENV). During lights-on, individually housed birds received continuous 12-h playback of either zebra finch (CONENV) or canary (HETENV) aviary sounds. Playback environments were recorded from zebra finch and canary aviaries at Rockefeller University, Millbrook, NY to ensure that all acoustic environments were novel at the start of the experiment. Exposure to canary songs and calls in the HETENV group, simulated a ‘foreign’ acoustic environment, to replicate acoustic experience of zebra finches in the “cross housed” condition described in Terleph et al. (2008). Exposure of the CONENV group to zebra finch songs and calls represented the ‘native’ acoustic environment. HETENV stimuli contain relatively more energy at higher frequencies and longer durations than CONENV stimuli (Fig. 2A). The sounds presented in HETENV contained acoustic features typical of canary vocalizations such as rapid trills and high-pitched whistles with long durations and many repetitions. In contrast,