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MIRRORED PATTERNS OF LATERALIZED NEURONAL ACTIVATION REFLECT OLD AND NEW MEMORIES IN THE AVIAN AUDITORY CORTEX

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Abstract—In monolingual humans, language-related brain activation shows a distinct lateralized pattern, in which the left hemisphere is often dominant. Studies are not as conclusive regarding the localization of the underlying neural substrate for language in sequential language learners. Lateralization of the neural substrate for first and second language depends on a number of factors including proficiency and early experience with each language. Similar to humans learning speech, songbirds learn their vocalizations from a conspecific tutor early in development. Here, we show mirrored patterns of lateralization in the avian analog of the mammalian auditory cortex (the caudomedial nidopallium [NCM]) in sequentially tutored zebra finches (*Taeniopygia guttata*) in response to their first tutor song, learned early in development, and their second tutor song, learned later in development. The greater the retention of song from their first tutor, the more right-dominant the birds were when exposed to that song; the more birds learned from their second tutor, the more left-dominant they were when exposed to that song. Thus, the avian auditory cortex may preserve lateralized neuronal traces of old and new tutor song memories, which are dependent on proficiency of song learning. There is striking resemblance in humans: early-formed language representations are maintained in the brain even if exposure to that language is discontinued. The switching of hemispheric dominance related to the acquisition of early auditory memories and subsequent encoding of more recent memories may be an evolutionary adaptation in vocal learners necessary for the behavioral flexibility to acquire novel vocalizations, such as a second language. © 2016 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: songbird, birdsong, speech, memory, sensorimotor, *Taeniopygia guttata*.

INTRODUCTION

Many human behaviors, including speech, are learned during a juvenile ‘sensitive’ or ‘critical’ period and retained throughout life (Knudsen, 2004). Early-formed language representations are maintained in the brain even if exposure to that language is discontinued, supporting the hypothesis that once a memory trace is established for language, it is maintained indefinitely (Bjork and Bjork, 2006; Pierce et al., 2014).

There is considerable variation in lateralization of the neural substrate that supports language, especially when comparing monolinguals with bilinguals. In children and adults who are acquiring language or learning a second language, brain regions activated during speech perception are generally large and right-dominant or bilateral (Dehaene et al., 1997). In monolingual humans, language-related brain activation often shows a distinct lateralized pattern; activity shifts to the left side of the brain or becomes less dispersed with increased language proficiency, and left-dominance is positively correlated with age and more advanced language abilities (Dehaene-Lambertz et al., 2002; Conboy and Mills, 2006; Friederici, 2011). A left-dominant neural substrate for language seems to be advantageous to the individual, as right-dominance has been associated with several speech and language disorders (Sommer et al., 2001; Oertel et al., 2010; de Guibert et al., 2011; Eyler et al., 2012; Johnson et al., 2013; Berl et al., 2014). Studies are not as conclusive regarding the localization of the underlying neural substrate for first and second language in bilinguals (Minagawa-Kawai et al., 2011). Lateralization of the neural substrate for the two languages depends on a number of factors including proficiency and early experience with each language (Perani et al., 1996, 1998; Raboyeau et al., 2010).

Speech acquisition in human infants and birdsong learning share many behavioral, neural and genetic characteristics (Doupe and Kuhl, 1999; Bolhuis and Gahr, 2006). Songbirds and humans acquire their vocalizations during sensitive (or optimal) periods early in development. Some birds (“open-ended learners”) are able to learn vocalizations beyond the sensitive period, whereas the zebra finch (*Taeniopygia guttata*, an “age-limited learner”) learns and crystallizes its song during a specific period in development (Fig. 1D) (Bolhuis and Gahr, 2006). Early in development, juvenile male zebra finches form a representation of the song of an adult tutor (usually their father) and subsequently acquire their own song, which resembles the tutor’s song, through a

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Abbreviations: CM, caudal mesopallium; CMM, caudomedial mesopallium; dph, days post hatching; HVC, acronym used as proper name; LMAN, lateral magnocellular nucleus of the anterior nidopallium; MLd, mesencephalicus lateralis pars dorsalis; NCM, caudomedial nidopallium; Ov, ovoidalis.

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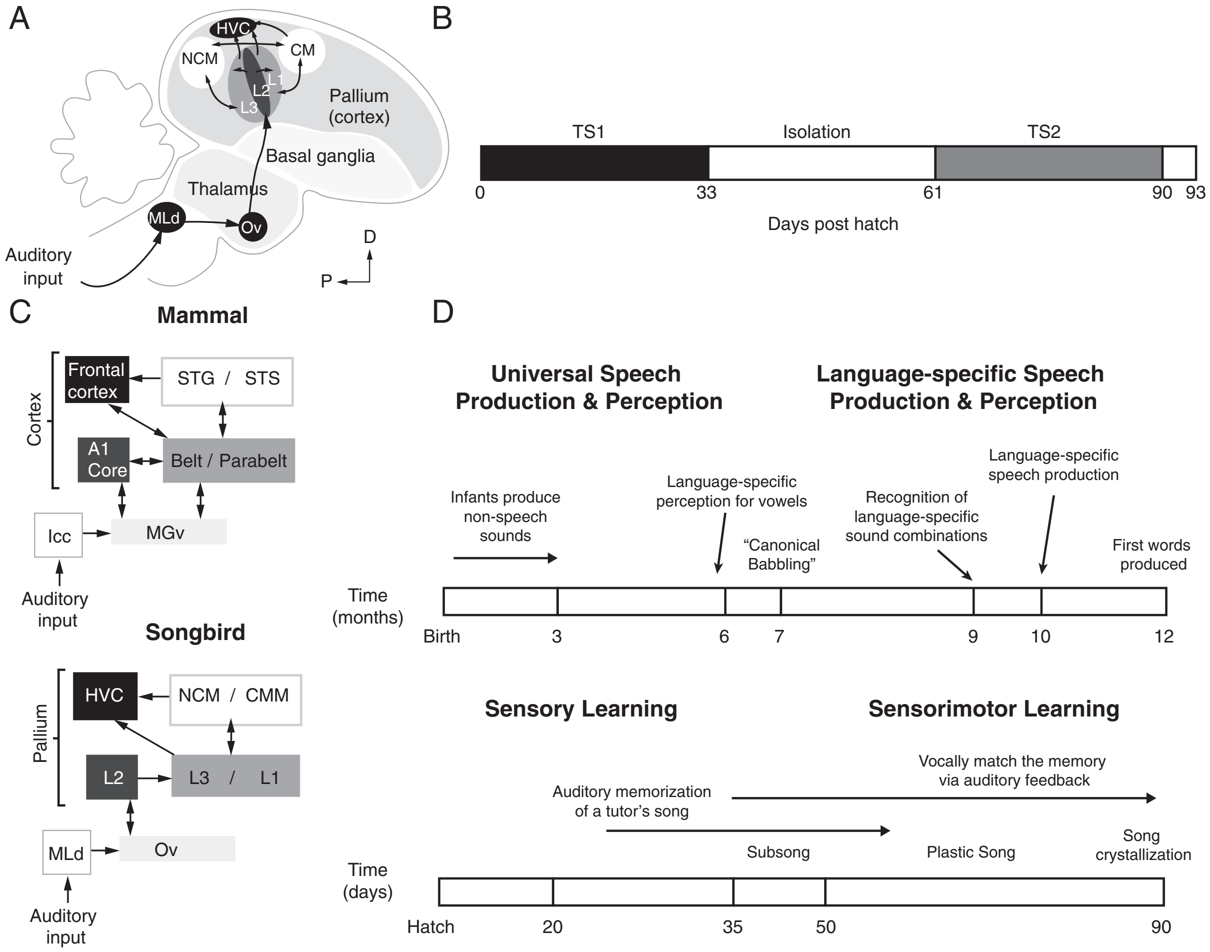

Fig. 1. Parallels between neural systems for auditory learning, and between behavioral development in both humans and zebra finches (normally raised or sequentially tutored). (A): Simplified diagram (not to scale; left) of the avian auditory system. The ascending auditory pathway (dark gray arrows) includes a midbrain nucleus (MLd), a thalamic nucleus (Ov) and several cortical regions. The primary auditory cortex (Field L2) connects to the secondary auditory regions Field L3 and L1, which in turn are reciprocally connected to regions analogous to the mammalian auditory association cortex (NCM and medial and lateral CM). Adapted, with permission from: Chirathivat et al., 2015. (B): Developmental timeline of vocal learning with sequential tutors. Juvenile male zebra finches are exposed to the first tutor (Tutor Song 1) until 33 dph and then individually isolated for 28 days. At 61 dph, they are exposed to a second tutor (Tutor Song 2) until 90 dph. Between 90 and 93 dph, zebra finches are individually isolated. At 93 dph, zebra finches were exposed to a 30-min playback of either Tutor 1 or Tutor 2. (C) Block diagram highlighting parallels between mammalian and songbird circuitry. Adapted, with permission from: Chirathivat et al., 2015. (D): Developmental timeline of human speech perception and production and songbird auditory learning and song development. Top: first, zebra finches acquire an auditory memory (or "template") of their tutor's song (between 25 and 65 days post hatching). Between days 35 and 90, zebra finches practice their vocalizations through a process of trail-and-error learning (sensorimotor learning phase). By day 90, zebra finches produce a "crystallized" song, which remains relatively stable throughout their adult life. Bottom: During the first 3 months, human infants produce non-speech sounds, which progresses to babbling by 7 months. By 12 months, infants are beginning to produce their first words, which will be retained and used throughout their lifetime. Adapted, with permission from Doupe and Kuhl, 1999.

process of trial-and-error learning akin to human babbling. Left-hemispheric dominance for memory of the bird's own song has been observed in a Wernicke-like region (caudomedial nidopallium, NCM) in the zebra finch brain (Fig. 1A), similar to the brain lateralization associated with human language (Moorman et al., 2012).

Like human infants who may be exposed to more than one language during development, wild zebra finches are exposed to several conspecific song models at the same time in their natural environment (Immelmann, 1969). Despite subsequent conflicting experiences, early exposure can exert lasting effects on neural structure and function. In swamp sparrows, a songbird species that imitates many different songs learned from multiple tutors during development, the pre-motor nucleus HVC (acronym used as proper name) maintains a neural representation of the acquired tutor songs, including those that are not part of the adult repertoire (Prather et al., 2010). This raises the possibility that neural representations of several relevant auditory models can be stored in the adult zebra finch brain.

In the laboratory, we can investigate whether brain regions contain a neural representation of tutor song by manipulating the early auditory environment and exposing juvenile zebra finches to two adult song tutors. (Yazaki-Sugiyama and Mooney, 2004). Selective auditory responses for tutor song in the lateral magnocellular nucleus of the anterior nidopallium (LMAN; part of a cortico-basal ganglia loop) are lost as the juvenile copies a new song, suggesting that the adult LMAN does not