



## Auditory discrimination learning in zebra finches: effects of sex, early life conditions and stimulus characteristics



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A meta-analysis was conducted to investigate whether sex differences, developmental history, stimulus number and/or characteristics affect the speed of auditory discrimination learning of zebra finches, *Taeniopygia guttata*, as tested in a Go/No-go task. Our results indicate that sex, early life conditions (brood size and juvenile body size), the number of stimuli, type of stimuli (constructed from zebra finch song elements or human speech syllables) and type of discrimination (based on phonetic characteristics or sequential structure of sounds) significantly influenced learning speed. Learning speed was faster if birds were female, reared in larger broods or were larger as juveniles. Greater numbers of stimuli and human speech-based stimuli were harder to learn than fewer stimuli and stimuli consisting of zebra finch song elements. Stimuli differing in phonetic characteristics were learned faster than those varying in structure. Additionally, there was some evidence of stable individual differences in performance across experiments. Our findings demonstrate that discrimination learning can be affected by factors that have been suspected to, but not yet definitively shown to, have impacts on learning. We suggest that examining the learning process itself in more detail by quantifying individual differences in learning strategies may provide more information on how various factors affect variation in learning abilities.

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Songbirds have been extensively studied for their song-learning abilities, which have provided fundamental knowledge about the behaviour, neurobiology and genetics underlying vocal learning processes (Brainard & Doupe, 2013; Doupe & Kuhl, 1999). Songbirds are also frequently used in studies of auditory perception that examine their abilities to discriminate or categorize both conspecific vocalizations and other types of sounds (e.g. ten Cate, 2014; ten Cate & Okanoya, 2012; Comins & Gentner, 2013; Sturdy, Bloomfield, Farrell, Avey, & Weisman, 2007; Weisman et al., 1998; Weisman, Njegovan, Williams, Cohen, & Sturdy, 2004). This includes studies in which the ability of birds to identify speech sounds or detect language-related grammar patterns are compared with those of humans (starlings, *Sturnus vulgaris*, Comins & Gentner, 2013; Gentner, Fenn, Margoliash, & Nusbaum, 2006; Bengalese finches, *Lonchura striata*, Lipkind et al., 2013; Seki, Suzuki, Osawa, & Okanoya, 2013; zebra finches, *Taeniopygia guttata*, Chen, Jansen, & ten Cate, 2016; Chen, van Rossum, & ten Cate, 2015; van

Heijningen, de Visser, Zuidema, & ten Cate, 2009; Kriengwatana, Escudero, Kerkhoven, & ten Cate, 2015; Ohms, Gill, Van Heijningen, Beckers, & ten Cate, 2010; Spierings & ten Cate, 2014; Spierings, de Weger, & ten Cate, 2015). Studies of these processes often demonstrate variation between individuals. The source of such variation is often not clear and the number of individuals in an experiment usually does not permit a further analysis of its origins. Sex differences in song are regularly observed, with the long-standing view being that song production is primarily a male trait: males sing and females do not (or do but to a much lesser extent). In line with this view, sex differences in songbird song and/or auditory perception are often implied; however, convincing evidence of this sex difference is lacking. Also, most analyses concentrate on the effects of the variables under study in a specific experiment, but do not compare their effects across experiments. However, an understanding of factors that produce individual variation or variation between otherwise comparable experiments may provide valuable additional insights into the processes affecting auditory discrimination and learning abilities in general. Determination of such factors is not only valuable from a theoretical perspective, but it would also allow researchers to control for these factors a priori in future experiments.

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Against this background, we conducted a meta-analysis of an extensive data set to examine several factors that may potentially have an important influence on auditory discrimination learning by zebra finches. These include sex differences, early life conditions, and the characteristics and number of the auditory stimuli. Our approach of combining data from several experiments in a meta-analysis allows us to address a variety of questions and has significant advantages over qualitative reviews and descriptions of results from isolated studies. With a meta-analysis, we are able to systematically analyse a large data set to detect how learning is influenced by our variables of interest in spite of slight differences between experiments. Consequently, we can draw much stronger conclusions to answers to our questions, which is especially valuable when results of past studies are ambiguous and/or contradictory and obtained with small sample sizes (which unfortunately is often the case). Moreover, across all experiments our measure of learning is defined using a single standardized criterion. This yields more precise comparisons of learning across different studies, and therefore a clearer picture of which factors influence auditory discrimination learning.

#### *Are there sex differences in auditory discrimination learning?*

Responses to different evolutionary pressures may have produced adaptive sex differences in learning and behaviour (Buss, 1995; Jones, Braithwaite, & Healy, 2003), which are found in the auditory learning abilities of songbird species that show a spectrum of sex differences in song production (Searcy & Brenowitz, 1988). Learning to discriminate and remember songs is essential for songbirds to produce songs. Song production is almost dogmatically seen as a male trait, which has spawned important but untested assumptions that sex differences in perception may play a part in sex differences in production. In songbirds found in the temperate zones of Europe and North America, female song is rarely observed (Riebel, Hall, & Langmore, 2005) and this sex difference in behaviour parallels striking sex differences in the volume of regions in the song control system (SCS), with females having significantly smaller neural volumes (that are sometimes even absent) than males (Ball & MacDougall-Shackleton, 2001; Nottebohm & Arnold, 1976). Based on these differences in brain and behaviour, it is possible that the significantly greater investment in development and maintenance of neuroanatomical structures and behaviour required for song learning and production by males compared to females results in males forming more detailed representations of phonetic and/or syntactic structure of songs.

Yet, contrary to the dominant view that song is a primarily male trait, females of many songbird species do in fact sing (Riebel, 2003; Riebel et al., 2005) and there is new evidence suggesting that in some species with sexual dimorphism in song production, there has been a loss of song production in females rather than the evolution of song production in males only (Odom, Hall, Riebel, Omland, & Langmore, 2014). This means that sex differences in song production may not necessarily be associated with sex differences in song learning and perception. Indeed, even in non-singing females, learning to discriminate and remember songs is essential for forming song preferences for important decisions such as mate choice (Riebel, 2003). To choose a suitable mate, females must carefully evaluate male songs, as features of male song may reliably indicate his qualities as a mate. For instance, in various songbirds, higher song complexity, greater spectral and temporal consistency and higher song rate are preferred by females because they may indicate quality in terms of developmental history (Nowicki, Peters, & Podos, 1998; Nowicki & Searcy, 2004; Nowicki, Searcy, & Peters, 2002), endocrine function (MacDougall-

Shackleton et al., 2009; Schmidt, Furlonger, Lapierre, MacDougall-Shackleton, & MacDougall-Shackleton, 2012), paternal effort (Bartsch, Weiss, & Kipper, 2015; Buchanan & Catchpole, 2000), body condition (Schmidt et al., 2012), cognitive abilities (Boogert, Giraldeau, & Lefebvre, 2008; Farrell, Weaver, An, & MacDougall-Shackleton, 2012), and age and reproductive success (Nemeth, Kempenaers, Matessi, & Brumm, 2012). Sex differences in processing of song are also evident at the neural level (e.g. Bailey & Wade, 2003; Yoder, Phan, Lu, & Vicario, 2015) and neural responses to song in females are often reflected in their behaviours towards male songs and linked to preferences for specific features in male songs (Eda-Fujiwara et al., 2003; Farrell, Kriengwatana, & MacDougall-Shackleton, 2015; Farrell, Morgan, & MacDougall-Shackleton, 2015; Farrell, Neuert, Cui, & MacDougall-Shackleton, 2015; Gentner, Hulse, Duffy, & Ball, 2001; Maney, MacDougall-Shackleton, MacDougall-Shackleton, Ball, & Hahn, 2003).

Therefore, studying sex differences in auditory learning and perception is crucial for understanding patterns of sex differences in song production, and why and how sex differences in song production evolved. Our study is the first systematic investigation of sex differences in auditory discrimination learning in a songbird, the zebra finch. This songbird shows extreme sexual dimorphism in song production (i.e. only males sing and have markedly larger brain regions involved in the control of song), making it the perfect species to test the hypothesis regarding sex differences in song and auditory perception in relation to sex differences in song production. Given these strong sex differences in zebra finch song production, we have two contrasting predictions about whether males or females would be better at auditory discrimination. If song production capabilities and greater investment in neural growth and maintenance enhance auditory learning, then zebra finch males might outperform females' discrimination of conspecific songs and/or human speech stimuli that possess song-like characteristics. On the other hand, if zebra finch females are motivated to critically analyse songs of potential mates, then females might outperform males on auditory discrimination tasks. Note that there are two separate aspects involved in auditory discrimination learning: first, the stimuli should be identifiably different to the bird, and next it should be able to learn to discriminate and treat them differently. Thus, the two sexes may discriminate and process conspecific songs similarly but differ in their ability to learn that certain stimuli are associated with different outcomes (e.g. reward or punishment; see Cynx, Williams, & Nottebohm, 1990), or the reverse, or differ in both auditory discrimination and discrimination learning.

While several studies in different species have reported sex differences in neural responses to conspecific song and general auditory stimuli (e.g. Gall, Brierley, & Lucas, 2011; Henry & Lucas, 2010; Noirot et al., 2009; Terleph, Mello, & Vicario, 2007), these do not seem to yield predictable sex differences in behavioural discrimination of conspecific vocalizations. Gall et al.'s (2011) study suggests that female red-winged blackbirds, *Agelaius phoeniceus*, and brown-headed cowbirds, *Molothrus ater*, may do better in auditory discrimination tasks as they have better auditory sensitivity. Braaten, Miner, and Cybenko (2008) also showed that female zebra finches had better memory of conspecific songs than males (but these results are based on results of three females and seven males as their study was not intentionally focused on sex differences). However, Henry and Lucas (2010) found that male Carolina chickadees, *Poecile carolinensis*, had greater auditory sensitivity, whereas females had more selective auditory filters. In zebra finches, Terleph et al. (2007) found no sex differences in responsiveness of a brain area important for song memories to pure tones, but did find that the primary auditory area of female brains was tuned to a wider range of frequencies than that of males. Given the

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