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Automated auditory recognition training and testing

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Laboratory training and testing of auditory recognition skills in animals is important for understanding animal communication systems that depend on auditory cues. Songbirds are commonly studied because of their exceptional ability to learn complex vocalizations. In recent years, mounting interest in the perceptual abilities of songbirds has increased the demand for laboratory behavioural training and testing paradigms. Here, we describe and demonstrate the success of a method for auditory discrimination experiments, including all the necessary hardware, training procedures and freely available, versatile software. The system can run several behavioural training and testing paradigms, including operant (go–nogo, stimulus preference and two-alternative forced choice) and classical conditioning tasks. The software and some hardware components can be used with any laboratory animal that learns and responds to sensory cues. The peripheral hardware and training procedures are designed for use with songbirds and auditory stimuli. Using the go–nogo paradigm of the training system, we show that adult zebra finches, *Taeniopygia guttata*, learn to recognize and correctly classify individual female calls and male songs. We also show that learning the task generalizes to new stimulus classes; birds that learned the task with calls subsequently learned to recognize songs faster than did birds that learned the task and songs at the same time.

The sensory and perceptual functions of the auditory system can be investigated by measuring behavioural responses to sounds. Among nonhuman animals, sound processing and perception are of particular interest in birds because many species communicate using complex vocalizations and show the rare capability of vocal learning (Doupe & Kuhl 1999; Dooling et al. 2000; Brenowitz & Woolley 2004; Dooling & Lohr 2006). Songbirds that learn to produce and recognize complex vocalizations are commonly used in laboratory studies of natural sound processing, vocal learning and vocal motor production (Williams 2008). Laboratory studies examining the role of vocalizations in reproductive behaviour also commonly use songbirds because of the importance of song in sexual competition and mate choice (Hauber et al. 2010). A history of auditory training and testing techniques using small birds exists (Hulse 1995; Dooling et al. 2000), but the increasing popularity of the songbird for studying the perception of learned vocalizations suggests that an automated, well-described and fully tested method for training and testing small birds on auditory recognition tasks will facilitate studies investigating vocal perception.

Songbirds offer several practical advantages to the study of vocal communication. Many species can be bred and reared in captivity, allowing for highly controlled developmental manipulations, detailed analyses of behavioural development and comparisons across species. Some species develop rapidly (<100 days), allowing laboratory experiments to be conducted throughout the life span of an individual and across generations (Campbell & Hauber 2009; Feher et al. 2009). Furthermore, behavioural and neurophysiological experiments can be combined; the neural circuits that control song processing, learning and production are well described (Nordeen & Nordeen 2008).

The zebra finch, *Taeniopygia guttata*, an Australian estrildid finch, is the most commonly studied songbird in the laboratory (Williams 2008; Warren et al. 2010). Only males sing and use their songs to court females (Zann 1996). Females use the acoustic properties of male songs for mate selection (Forstmeier & Birkhead 2004; Spencer et al. 2005; Boogert et al. 2008; Holveck & Riebel 2007, 2010). Males and females also produce calls, which are learned in males but not in females (Vicario 2004; Vignal et al. 2004, 2008). Both males and females can distinguish between the songs and calls of different individuals, as demonstrated by operant conditioning experiments (Okanoya & Dooling 1991; Cynx & Nottebohm 1992; Riebel 2009). In zebra finches, operant conditioning experiments have examined the temporal and spectral characteristics of calls and songs that are necessary for

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discrimination (Cynx et al. 1990; Lohr & Dooling 1998; Dooling & Lohr 2006; Riebel 2009; Nagel et al. 2010), developmental (Braaten et al. 2006) and experiential (Benney & Braaten 2000) changes in song discrimination, and female preferences for male songs as they relate to mate choice (Riebel 2009). Several studies have shown that female song preferences measured using operant testing paradigms predict which songs evoke female sexual responses such as copulation solicitation displays and mating (Riebel & Slater 1998; Holveck & Riebel 2007, 2010; Anderson 2009).

Behavioural auditory training and testing paradigms that are manually controlled are impractical and vulnerable to data collection and analysis errors. Commercially available training and testing systems that are automated are expensive and use hardware and software that may not have the flexibility to accommodate a wide range of experimental designs. For example, depending on the number of input and output lines necessary for a given paradigm, a single interface module may only control one or two training chambers, requiring the user to purchase multiple modules. Additionally, commercially available hardware components that are necessary for successful discrimination training, such as feeders, are often unsuitable for small birds (Njegovan et al. 1994). To overcome these issues, laboratories implement custom-designed software and/or hardware systems (Okanoya & Dooling 1988; Scharff et al. 1998; Houx & ten Cate 1999; Gentner et al. 2000; Sturdy & Weisman 2006; van Heijningen et al. 2009; Nagel et al. 2010). These custom-designed solutions are not available for all scientists and are challenging to develop and employ, especially for small birds.

We have developed an auditory recognition training system (ARTSy) that uses inexpensive hardware and custom software that is flexible, high-throughput and freely available to scientists. ARTSy can be used to train and test any animal species that learns to recognize and respond to sensory cues. For example, the hardware can be modified to address questions regarding the discrimination of visual or olfactory cues. Here, we describe the system with hardware designed for training small birds to recognize and respond to individual sounds or sound sequences, how to assemble the hardware and use the software. We demonstrate the success of the system by describing the recognition training and testing of male and female zebra finches using female calls and male songs. Results also show that task learning in adult zebra finches generalizes to other sound classes.

METHODS

Overview

The training system can be used for a variety of behavioural paradigms, including operant (go–nogo, two-alternative forced choice, preference) and classical conditioning tasks. Here, we tested the go–nogo paradigm with male and female zebra finches. The basic parameters that we define and the procedures we describe for go–nogo are similar for the other training paradigms. In the go–nogo paradigm, the subject is rewarded for responding to the correct (go) sound and is punished for responding to the incorrect (nogo) sound. Subjects are rewarded with food and punished with a period of complete darkness. Zebra finches typically learn the go–nogo task after 600–3000 trials, which is consistent with the results from studies using systems designed for use in individual laboratories (Cynx & Nottebohm 1992; Cynx 1995; Braaten et al. 2006). First, we trained subjects on the go–nogo task with female long calls. We reasoned that training birds with one class of sounds that is separate from the class of sounds that are of experimental interest is advantageous because learning the go–nogo task and learning to recognize and discriminate between specific sounds are two separate problems that the subjects must solve. Dissociating the learning of the task and the sound recognition learning that is required for discrimination allows the experimenter to directly compare discrimination performance on different types of experimental stimuli. After subjects reached a criterion of 80% or better correct responses to long calls (Fig. 1a), we then tested their ability to generalize the go–nogo task to zebra finch songs (Fig. 1b). We also trained a separate group of birds using songs and compared task learning using long calls as stimuli to task learning using songs as stimuli because these stimuli differ in duration, acoustic complexity and salience. We predicted that the automated system would successfully train birds to discriminate between different sounds in a comparable number of trials as previously described in the literature and that task learning would generalize to another sound class such that birds would learn to recognize songs faster if they learned them after learning the task on calls than if they learned the songs and the task simultaneously.

Subjects

We trained nine (2 male, 7 female) adult zebra finches that were hatched and reared in the breeding colony in the Department of Psychology at Columbia University. All birds were naïve to discrimination training. Birds were raised in six different family cages (some subjects were from the same lineage) and housed as adults in same-sex aviaries so that they could see and hear other zebra finches of both sexes in the room. The colony photoperiod was maintained on a 14:10 h light:dark cycle. Colony room temperature was maintained between 23 and 29 °C. Mixed seed, water, cuttlebone and grit were freely available; the birds were also supplemented three times a week with lettuce and twice a week with eggs and shells. We trained two separate cohorts of adult zebra finches with different sounds on the initial go–nogo task. The first cohort ($N = 4$, 1 male, 3 female) was trained with songs and the second cohort ($N = 5$, 1 male, 4 female) was trained with long calls. Subjects in cohort 2 were tested for their ability to generalize the task to songs after they were trained to recognize long calls. The ages of subjects in cohort 1 (420 ± 8.49 days, $N = 4$) and 2 (227.20 ± 101.92 days, $N = 5$) were recorded at the start of the experiment. The mean weight of the females in cohort 2 recorded at the start of the experiment was 14.18 ± 0.80 g, $N = 4$; the weight of the male was 16.64 g. All animal procedures were approved by the Columbia University Institutional Animal Care and Use Committee (IACUC) and met all applicable state and federal guidelines.

Apparatus

Training events were conducted in a custom-built wire cage ($43.18 \times 30.48 \times 30.48$ cm) housed in a sound-isolation cubicle (outside dimensions: $78.74 \times 53.34 \times 53.34$ cm; inside dimensions: $67.31 \times 41.91 \times 44.45$ cm) lined with acoustic foam (see Supplementary Material, Fig. S4; H10-24A, Coulbourn Instruments, Allentown, PA, U.S.A.). A custom-built, acrylic response panel (30.48×30.48 cm) replaced one wall of the cage. An infrared slot sensor was mounted on the left side of the response panel (SLO30VB6Y, Banner Photoelectric Sensors, Prime Inc., Oradell, NJ, U.S.A.). A custom-built solenoid-driven feeder delivered food reinforcement during training (Supplementary Material, Fig. S5). A fluorescent lamp (137076, www.jcwhitney.com) mounted on the back of the isolation chamber was used for light reinforcement during training. An overhead fluorescent lamp (13707G, www.jcwhitney.com) was used to illuminate the chamber when the subjects were not training. A speaker (KFC-1377, Kenwood USA Corporation, Kenwood, CA) was placed on the top of the wire cage,