

Species differences in the identification of acoustic stimuli by birds

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Abstract

The perceptual organization of auditory stimuli can reveal a great deal about how the brain naturally groups events. The current study uses identification techniques to investigate the abilities of two species of birds in identifying zebra finch song as well as synthetically generated speech stimuli. Budgerigars (*Melopsittacus undulatus*) and zebra finches (*Taeniopygia guttata*) were trained to differentially peck keys in response to the presentation of various complex stimuli. Although there were no clear differences in performance during the training paradigm between the two species, budgerigars were far more adept at learning to identify both sets of complex stimuli than were zebra finches, requiring far less trials to reach criterion. The non-singing but vocally plastic budgerigars vastly outperformed zebra finches at identifying both zebra finch song and synthetically designed human speech despite known similarities in auditory sensitivities between the two species and seemingly equivalent learning capacity. The flexibility that budgerigars seem to have at identifying various stimuli is highlighted by their enhanced performance in these tasks. These results are discussed in the context of what is known about both general and specialized processes which may contribute to any differences or similarities in performance.

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1. Introduction

Birds have been a particularly well-studied class of animals in the field of categorization and identification of acoustic stimuli (see recent review by Sturdy et al., 2007). Birds are one of the few groups of animals known to exhibit vocal learning, and use acoustic communication for territoriality, mate choice, offspring recognition, alarm signaling, and individual recognition. Several territorial songbirds have been shown to be very good at identifying vocalizations, including red-winged blackbirds (*Agelaius phoeniceus*), brown-headed cowbirds (*Molothrus ater*), and song sparrows (*Melospiza melodia*) (Sinnott, 1980; Stoddard et al., 1992). Territorial non-songbirds also show identification abilities for auditory stimuli. Beckers and ten Cate (2001) found that two *Streptopelia* dove species accurately identified synthetic vocalizations using both temporal and amplitude modulation structure, although they demonstrated a learning rate much slower than seen in the songbird studies mentioned above.

A lack of song learning was mentioned as a possible reason that these birds learned to identify at a slower rate than songbirds.

Bengalese finches (*Lonchura striata*) in a study by Ikebuchi and Okanoya (2000) took a long time to learn to identify song pairs relative to the song sparrows in the Stoddard et al. (1992) experiment. The authors concluded that the finches' memory capacity for new song pairs was limited because these birds were non-territorial (Ikebuchi and Okanoya, 2000). A comparison of black-capped chickadees and zebra finches (*Taeniopygia guttata*) on the categorization of conspecific and heterospecific vocalizations and found that chickadees (territorial) learned the task faster than the zebra finches (non-territorial) (Phillmore et al., 1998), supporting Ikebuchi and Okanoya's hypothesis.

Other researchers have attempted to identify the limits and abilities of non-territorial birds on identification tasks. Three non-territorial birds, domesticated pigeons (*Columba livia*), European starlings (*Sturnus vulgaris*), and zebra finches, were trained to categorize rising and falling tone sequence patterns (Cynx, 1995). The pigeons learned the task much more slowly than the finches and starlings, even though perceptual abilities were found to be similar. Pigeons are also non-vocal learners (Nottebohm and Nottebohm, 1971), however, which could again

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be one possible reason for their slower performance relative to the other two bird species.

Other studies have examined the differences between groups of birds differing in both vocal learning abilities and territoriality. It took an average of 14 sessions of 100 trials each to train budgerigars (*Melopsittacus undulatus*; non-territorial non-songbirds) to identify two budgerigar calls (Park et al., 1985). Learning to identify two canary (*Serinus canaria*) calls took another 14 sessions. Canaries (territorial songbirds) learned conspecific calls within 30 sessions but never learned the budgerigar calls. The differences in learning the identification task did not occur because of differences in learning capacity, but appeared to be specific to the type of stimuli used in testing.

These results from the canaries and budgerigars are intriguing for several reasons. First, the studies suggest the possibility that *both* differences in territoriality and mechanisms of call learning and usage may play a role in determining how well animals are able to categorize and identify acoustic stimuli. Canaries and budgerigars both produce contact calls, but the use of these calls differs widely between the two species. The learned contact calls of budgerigars are the primary ‘signature’ vocalizations of these very social, colonially breeding animals. Their contact calls are used for the formation and maintenance of social bonds and also for the coordination of reproductive behavior (reviewed in Farabaugh and Dooling, 1996). Canaries only use these types of calls when they are in visual contact. Their much longer and more complex songs, on the other hand, are used for territorial defense and mate selection (e.g., Catchpole, 1982). It could be that the budgerigars are predisposed to learn to identify the shorter call-like signals than they would be to learning longer songs, and that the reverse would hold true for songbirds.

A second reason that these experiments are intriguing is that results from studies on the perception of conspecific versus heterospecific vocalizations are mixed. Some studies show a species-specific advantage while others show no specificity. We know that animals are better at learning conspecific songs compared to heterospecific songs (Marler and Peters, 1977). This suggests that the ability to hear and memorize conspecific over heterospecific songs might be matched, but once again, results of past studies are mixed. In a study of auditory scene analysis (Benney and Braaten, 2001), zebra finches were better at detecting conspecific song than heterospecific song embedded in other songs. The zebra finches also had difficulty ignoring zebra finch songs that were used as distracters when the birds were required to detect a heterospecific target (Benney and Braaten, 2001). Okanoya and Dooling (1991) also found a species-specific advantage for discriminating calls in both zebra finches and budgerigars, and Dooling et al. (1992) showed an enhanced ability to distinguish between conspecific calls for both species. On the other hand, Phillmore et al. (2002) found no species-specific advantage in the recognition of vocalizations by black-capped chickadees for their songs or for zebra finch calls, even when both sets were degraded by recording them from a distance.

In a study on the perception of altered zebra finch song motifs, Nespore and Dooling (1997) found that zebra finches and budgerigars performed equally well, and were generally much better

than human listeners. Given that these two species of birds may be equally able to discriminate alterations in zebra finch songs, we decided to ask whether they would be equally able to learn to identify them. We extended experiments comparing non-territorial songbirds and non-territorial non-songbirds to see if performance in a non-territorial songbird could be improved by using longer, and possibly more meaningful, stimuli. Since it is somewhat difficult to compare across studies using different stimuli, apparatuses, procedures, and criteria, we chose to compare the learning of an identification task in two species of birds using identical methods. Although the experiments above were conducted on canaries, here we compare abilities of budgerigars and zebra finches. Zebra finches, like budgerigars, are non-territorial. Both birds learn their vocalizations, but budgerigars continue to modify those vocalizations throughout their lives, while zebra finches generally learn one song as juveniles and continue to use that song throughout their life (e.g., Tchernichovski et al., 2001). Zebra finches can place song notes into categories (Sturdy et al., 1999, 2001), and a recent study by Braaten et al. (2006) showed that adult and juvenile zebra finches can also properly categorize songs versus reversed songs.

Another reason for extending previous studies (Park and Dooling, 1985; Park et al., 1989) using different model species is that many more comparisons of auditory capabilities have been conducted on budgerigars and zebra finches than on canaries. Most of these studies of the basic abilities of budgerigars and zebra finches show similarities between what the two birds can hear. The audiograms (Okanoya and Dooling, 1987), maximum and minimum temporal integration functions (Dooling and Searcy, 1985; Okanoya and Dooling, 1990), and discrimination and detection of calls and tones in various types of noise (Lohr et al., 2003) are similar between the two species. Masking by harmonic complexes shows more masking in finches than in budgerigars, but similar patterns between positive and negative phased maskers that differ significantly from that found in humans (Dooling et al., 2001). Discrimination of */ra/-la/* speech continua show similarities in response latencies for stimuli along the entire length of the continua and a similar peak in discrimination performance, suggested to be the categorical boundary (Dooling et al., 1995). Weisman et al. (2004) found similarities and high accuracy in absolute pitch discrimination in zebra finches and budgerigars. A recent study by Lohr et al. (2006) highlighted the sensitivity of both species of birds at discriminating temporal fine structure of zebra finch call-like harmonic sounds. Zebra finches and budgerigars could detect changes in periods as short as 1–2 ms (humans were much worse at the task).

In general, the auditory sensitivity of zebra finches and budgerigars is remarkably similar. However, there are some studies that highlight the differences in hearing between the two species of animals. Zebra finches are better than budgerigars at detecting a mistuned harmonic (Lohr and Dooling, 1998) and discriminating temporal fine structure (Dooling et al., 2000). Budgerigars have better spectral resolving power than zebra finches for stimuli within 2–3 kHz (Okanoya and Dooling, 1987), are better at absolute sound localization (Park and Dooling, 1991), and at discriminating amongst stimuli

mimicking the precedence effect (Dent and Dooling, 2004). Although basic hearing abilities in the two species are not identical, the differences in ability can usually be tied to differences in interaural distance or in vocal production (reviewed in Dooling et al., 2000).

We trained budgerigars and zebra finches on two identification tasks using complex auditory stimuli. The first set of stimuli was zebra finch songs. While the stimuli are biologically meaningful to the zebra finches, they are not meaningful for the budgerigars. However, both species of birds have the abilities to discriminate amongst these stimuli, although finches sometimes show a species-specific advantage for doing this task (see above). We also know that the training of budgerigars and zebra finches on a forced-choice task using pure tones takes about the same amount of time (unpublished observations; also see Section 3 below). If the two species differ in their ability to identify zebra finch songs, this difference is unlikely to be explained by simple perceptual differences; instead, other factors must be contributing. If the budgerigars are superior, it suggests that the vocal flexibility of their repertoire and communication system plays an important role. If the zebra finches are superior, it suggests that the biological meaningfulness of the stimuli is an important factor. The second set of stimuli was chosen to be less biologically relevant to both species of birds: tokens of speech sounds. As mentioned above, discrimination of speech continua by these two species of birds suggests that the abilities to perceive them are similar. If species differences are found in the abilities to identify the stimuli, then some other important factors must account for the differences.

2. Materials and methods

2.1. Subjects

Fourteen adult budgerigars (11 males and 3 females) and 12 adult zebra finches (8 males and 4 females) were used as subjects in these experiments. Some of the birds participated in only one experiment while a few participated in both (individual numbers for each experiment are listed below). All of the birds were individually housed in a vivarium at the University at Buffalo and were kept on a day/night cycle corresponding to the season. Most of these experiments were conducted between the months of May and August. The birds were either purchased from a local pet store or bred in the vivarium. They were kept at approximately 90% of their free-feeding weight during the course of the experiment. The birds were tested 5–7 days a week in 30–40 min sessions. All procedures were approved by the University at Buffalo, SUNY's Institutional Animal Care and Use Committee and complied with NIH guidelines for animal use.

2.2. Testing apparatus

The psychoacoustic experiments took place in one of four identical psychoacoustic testing setups. The setups consisted of a wire test cage (61 cm × 33 cm × 36 cm) mounted in a sound-attenuated chamber (Industrial Acoustics Company, Small Animal Chamber) lined with sound-absorbent foam (10.2 cm

Sonex, Ilbruck Co.). The test cage consisted of a perch, an automatic food hopper (Med Associates Standard Pigeon Grain Hopper), and two vertical response keys extending downwards from the inside of the hopper in front of the bird. The response keys were two sensitive microswitches with 1 cm-square green (left key) or red (right key) buttons glued to the ends. The birds pecked the colored keys, which tripped the microswitches. A small 7-W light at the top of the test cage illuminated the chamber and served as the experimental house light. An additional 30-W bulb remained on in the chamber for the entire session. The behavior of the animals during test sessions was monitored at all times by an overhead web-camera (Logitech QuickCam Pro, Model 4000). One speaker (Morel Acoustics, Model MDT-29) was hung directly behind the subject at the level of the bird's head, 30.5 cm away from the bird during testing. The experiments were controlled by a Dell microcomputer operating Tucker-Davis Technologies (TDT, Gainesville, FL) modules and SykofizX software.

2.3. Stimuli and calibration

On each day of testing, the birds were presented with two categories of stimuli. For the song perception birds, stimuli were two songs recorded from six zebra finches from a colony at Boston University (see Best et al., 2005 for details about the stimuli and their recording). Briefly, the songs were recorded in a single-walled sound-treated booth (Industrial Acoustics Company, New York) using a single microphone (Audio-Technica AT3031) placed 7 in. above the caged bird. Five similar song motifs were selected from each bird's repertoire. Each motif was highly stereotyped for a particular bird but quite distinct from those of the other birds. The songs were between 800 and 1000 ms in duration and were output at an overall RMS level of 65 dB at a sampling rate of 50 kHz.

For the birds performing the speech task, the identification stimuli were two full-formant speech syllables, /ba/ and /wa/ (see Fig. 1). The speech sounds were generated by the

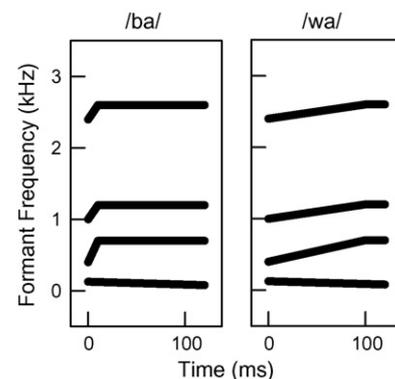


Fig. 1. Schematics of the two stimuli used in the speech perception experiment. The two stimuli differed in their transition durations of formants 1–3. For the /ba/ token, this duration was 10 ms and for the /wa/ token, it was 100 ms. For both stimuli, F1 began at 400 Hz and moved to 700 Hz over the transition period. F2 moved from 1000 to 1200 Hz, and F3 moved from 2400 to 2600 Hz over the same time periods. F0 fell linearly for both stimuli over the duration of the stimuli from 125 to 80 Hz.

cascade/parallel software synthesizer described by Klatt (1980) according to the parameters of Dent et al. (1997). The syllables were 120 ms in duration and the main differences between the stimuli were the durations of the frequency transitions for several of the formants. The duration of the initial formant transition was always 10 ms for the /ba/ tokens and 100 ms for the /wa/ tokens. All stimuli were presented at a peak sound-pressure level of 65 dB with a sampling rate of 50 kHz.

Stimulus calibration was performed with a Larson-Davis sound level meter (Model 825) and 20-ft extension cable. For all measurements, a 1/2-in. microphone was placed in the position normally occupied by the bird's head during testing.

2.4. Procedures

The birds were trained using operant conditioning procedures to peck the microswitches for food reinforcement. First, they pecked at the left key to start a trial. After a variable interval of 2–7 s, a sound was presented from either category with equal probability. The birds were trained to peck the left key again when they heard certain stimuli and peck the right key when they heard other stimuli. The entire stimulus sound played through, regardless of when the animal responded. If they correctly identified the sound within 1.5 s following its presentation, they were rewarded with 1.5 s access to hulled millet from the illuminated food hopper for 70% of the correct trials. They were rewarded with the hopper light only for 1.5 s in the other 30% of the correct trials. If they responded later than 1.5 after the sound's completion, no reward was given. If they responded incorrectly by indicating the wrong category of the stimulus, the house light was extinguished for 5 s. As soon as the reinforcement or punishment phases were completed, the animals could immediately initiate another trial by pecking the left key.

The birds were randomly assigned to the zebra finch song or human speech identification experiment. In the zebra finch song experiment, the birds were presented on every session with the 5 motifs from each of two songs (10 song types per session). Each bird was randomly assigned two songs to classify. The 'left' and 'right' assignment for each song was also randomly assigned and differed between birds, but was held constant for each bird across sessions. The percent correct score was calculated for each bird in 100-trial blocks. Criterion was reached and the experiment for that subject was ended when the bird scored at least 85% correct for three successive 100-trial blocks, but the first block above 85% was counted for each bird as the 'blocks to criterion' threshold. A total of 10 budgerigars and 10 zebra finches were used in this experiment.

In the human-speech perception experiment, the birds were only presented with 1 possible token each of the /ba/ and /wa/ syllables. In this experiment, the 'left' assignment was always given to the /ba/ sound and the 'right' assignment was always given to the /wa/ sound. This experiment was part of a larger speech perception experiment that will not be discussed further here. Again, percent-correct scores were calculated for 100-trial blocks, the birds were stopped when they reached three successive 100-trial blocks at 85% correct or better, and the first block was counted for each bird. A total of 5 budgeri-

gars and 4 zebra finches were used in this experiment. One of the budgerigars and two of the zebra finches in this experiment were previously used in the zebra finch song perception experiment.

2.5. Data analysis

The number of 100-trial blocks to reach criterion was calculated for each subject. A one-way ANOVA was used to determine if there were differences between the species in the number of blocks required to reach criterion for both the zebra finch song perception and the human speech perception experiments.

3. Results

3.1. Training

To ensure that any differences in learning to identify the test stimuli were not related to general cognitive capabilities of the birds, we analyzed the training data and calculated the average performance for each species to reach several training milestones. Training the birds in our laboratory progresses through a series of phases, ranging from shaping the animal to eat out of the food hopper, to pecking the left key to initiate a trial, and then pecking the left or right key appropriately to different classes of stimuli (pure tones of different frequencies) for a food reward. Unlike in the two experimental conditions (where the results are reported as 100-trial blocks), the results here are reported as 'sessions'. During training, the animals typically run only about 30–50 trials in a session but there are no differences between the species in the number of trials run (unpublished obs.).

The mean number of sessions (\pm S.E.M.) that it took our animals to reach the training phase of pecking the left key to initiate a trial and then pecking the left key again when a sound (e.g., a 2 kHz pure tone) was presented was 20.57 ± 3.06 sessions for the zebra finches and 22.56 ± 3.84 sessions for the budgerigars. A *t*-test comparing the two species showed that they were not significantly different ($t(14) = -0.31, p > 0.05$).

To reach the next training phase of pecking the left key to initiate a trial and then pecking the right key when a different (from the earlier training phase, e.g., a 4 kHz pure tone) sound was presented required an additional 3.57 ± 3.10 sessions for the zebra finches and 11 ± 4.86 sessions for the budgerigars. A *t*-test comparing the two species showed that they were not significantly different at this phase of training ($t(14) = -0.99, p > 0.05$). To reach the final phase of training, where animals are required to peck the left key to initiate a trial and then peck the left key for one stimulus (2 kHz pure tone) and the right key for other stimulus (4 kHz pure tone), the zebra finches needed 6.43 ± 3.92 more sessions and the budgerigars needed 12.77 ± 4.77 more sessions. A *t*-test comparing the two species showed that they were not significantly different at this final phase of training either ($t(14) = -1.57, p > 0.05$). These results suggest that there is little difference between the two species' ultimate ability to perform the mechanics required in our identification task, suggesting that any differences reflect differences in the ability to learn to properly identify the complex signals used as stimuli.

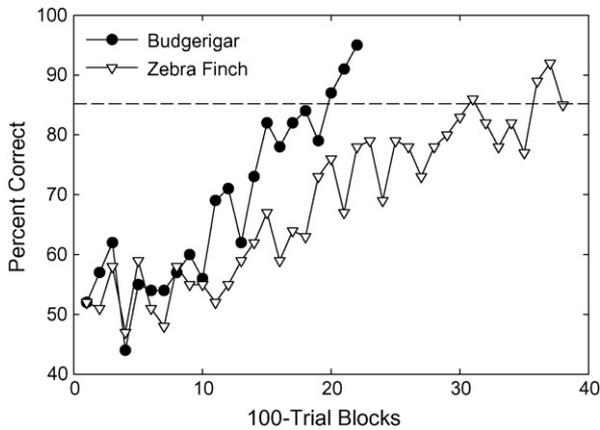


Fig. 2. Categorization of zebra finch song stimuli are shown for a representative zebra finch and a representative budgerigar.

3.2. Zebra finch song perception experiment

Although the above results demonstrate that training performance levels are similar between the two species of birds, budgerigars and zebra finches have large differences in the number of blocks it takes them to learn to identify two zebra finch songs. A representative zebra finch and a representative budgerigar are shown in Fig. 2. Both birds began at about 50% correct (chance performance) and steadily increased to criterion. Overall, the budgerigars learned this task in a mean of 2460 trials, while the zebra finches learned this task in a mean of 3590 trials. While the two species differed in their average learning rate, there was some overlap in the time it took the different individuals of the two species to learn the task. The budgerigars ranged from 12 to 42 hundred-trial blocks, while the finches had a larger range spanning 24–68 hundred-trial blocks (see Fig. 3). The differences between the two groups were statistically significant as measured by a one-way ANOVA ($F(1,18) = 5.38, p < 0.05$). Thus, the zebra finches took significantly longer than the budgerigars to learn to identify zebra finch songs.

3.3. Speech perception experiment

The budgerigars and zebra finches trained to identify the speech sounds of /ba/ and /wa/ showed even larger species

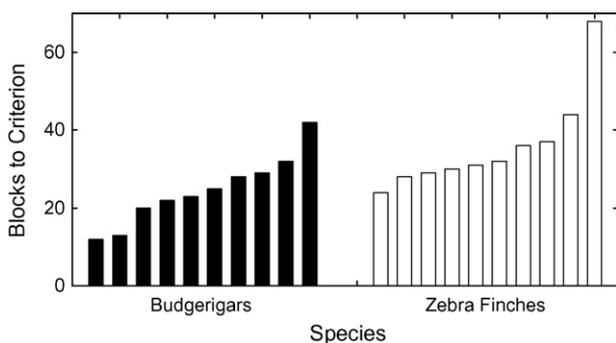


Fig. 3. Number of 100-trial blocks needed to reach criterion performance in classifying zebra finch songs. Each bar represents a different subject.

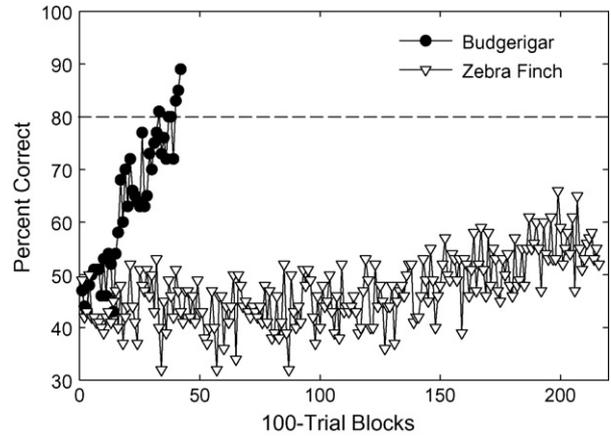


Fig. 4. Categorization of synthetic speech stimuli are shown for a representative zebra finch and a representative budgerigar.

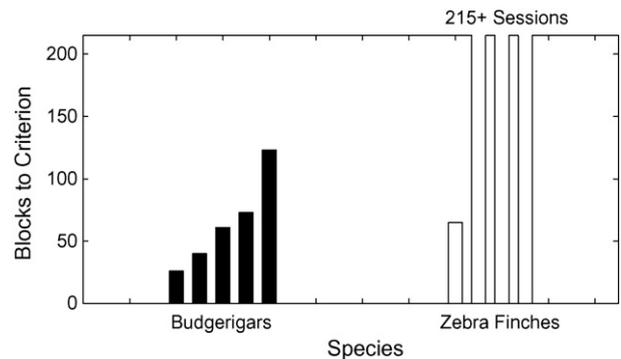


Fig. 5. Number of 100-trial blocks needed to reach criterion performance in classifying synthetic speech stimuli. Each bar represents a different subject.

differences in the same direction in this experiment than in the zebra finch song perception experiment. Fig. 4 shows a representative zebra finch and a representative budgerigar learning this task. Again, both birds start at about 50% correct. Performance steadily increases to criterion for the budgerigar; however, performance never quite reaches criterion for the zebra finch, even after more than 20,000 trials. Fig. 5 shows the range of time it took the birds to learn the task. The budgerigars ranged from 26 to 123 hundred-trial blocks, while the zebra finches had a larger range spanning 65 to >200 hundred-trial blocks. Since most of the zebra finches never learned the task, a statistical analysis would have been difficult. Therefore, the finches that took more than 200 blocks to train were assigned the conservative value of 200 blocks. The differences between the two groups were statistically significant as measured by a one-way ANOVA ($F(1,7) = 8.35, p < 0.05$). The budgerigars were not only faster at learning to identify zebra finch songs, but they were also vastly superior at learning to identify speech tokens, both in speed of learning and in the percentage of birds that achieved criterion performance within 200 training blocks.

4. Discussion

The results from our two identification experiments were quite surprising given the training-phase analyses. Those results

revealed that there were no significant differences between the two species at any of the stages of training. Thus, differences in training performance cannot explain the differences seen later in identification tasks. Another reason we were somewhat surprised at our findings is that previous studies on the *discrimination* of distance calls by budgerigars and zebra finches have shown that there is a definitive advantage to learning conspecific rather than heterospecific calls in that task (Okanoya and Dooling, 1991).

The species-specific advantages for discriminating distance calls (natural vocalizations) by budgerigars and zebra finches that Okanoya and Dooling (1991) found did not appear in our results. Instead, the budgerigars vastly outperformed the zebra finches in tasks where the stimuli being presented were either less environmentally relevant to them (zebra finch songs), or equally ambiguous for both species (speech tokens). Further, only a single zebra finch reached criterion on the speech perception task, and that was the one who first participated in the zebra finch song identification project. This hints that larger differences would be found when using only naive birds and that experience at identifying different types of auditory stimuli may enhance overall performance.

It is difficult to directly compare our results from those found in other laboratories due to differences in training, procedures, and learning criteria. For instance, animals typically have been trained on only two stimuli at a time in experiments from other laboratories. In our birdsong task, the birds were trained to place 10 stimuli into two classes. This may have lengthened the overall acquisition time in our experiments compared to earlier studies. We can compare the performance of our two species within this series of experiments, however. The large differences we found between the zebra finches and the budgerigars in the birdsong experiment were surprising given that the songs have essentially no meaning or value to the budgerigars but should be quite important to the zebra finches. Park et al. (1985) found this same difference between canaries and budgerigars. The budgerigars were good at identifying both budgerigar and canary calls and were better than the canaries at identifying canary calls. Similar to most of the zebra finches in our experiment on the human speech identification task, the canaries in the study could not be trained at all on heterospecific calls. It is most likely the case that the number of complex acoustic stimuli that budgerigars are capable of remembering is quite large and their enhanced ability to discriminate acoustic distinctions seems to be beneficial not only for species-specific stimuli, but also for non-species specific stimuli. Consistent with these previous findings, our results support the idea that budgerigars may have a superior and sophisticated memory capacity for complex acoustic stimuli, and that this enables them to learn to identify heterospecific calls as well as conspecific calls.

Finally, it is worth comparing the lifestyles of these two groups of birds. Bengalese finches took a long time to learn to categorize song pairs and their memory capacity for new song pairs was limited (Ikebuchi and Okanoya, 2000) compared to the abilities of song sparrows (Stoddard et al., 1992). Ikebuchi and Okanoya (2000) hypothesized that these differences arose because the Bengalese finches were non-territorial. Budgerigars

are also non-territorial birds, so this hypothesis, although it may apply to birds within the Passeriformes order, does not hold for all birds. The capacity for vocal learning between zebra finches and budgerigars is very different. Zebra finches learn their vocalizations as juveniles and modify these vocalizations very little throughout their lives (e.g., Tchernichovski et al., 2001), while budgerigars learn and modify new vocalizations constantly, even as adults (e.g., Farabaugh et al., 1994). Perhaps the differences between abilities to identify auditory stimuli have more to do with the learning of vocalizations than how they use them.

A recent study by Wanker et al. (2005) in spectacled parrotlets (*Forpus conspicillatus*) demonstrated that a bird closely related to the budgerigar actually produces specific contact calls for specific companions within their social system. This complex referential signaling capacity requires that animals know and recognize each other and have a specific signal to produce in that specific context. The Wanker et al. (2005) study also showed that an individual bird better recognized the signals that are usually directed towards that individual compared to signals that were typically directed towards others. Although the labeling system used by budgerigars has not been shown to be specific down to the name of an individual, the closely related parrotlets, who demonstrate call convergence to members of their own flock, clearly have the ability to identify and classify individuals. This ability must be very advanced since animals are constantly changing their signals for each other, learning new signals, and producing different signals in different situations (Farabaugh et al., 1994). The tremendous vocal plasticity that budgerigars possess offers a possible explanation for the large species differences shown in these experiments, differences that cannot be explained by considering only simple auditory capacities or learning abilities.

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