Vocal learning in Budgerigars (*Melopsittacus undulatus*): Effects of an acoustic reference on vocal matching

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Budgerigars were trained to produce specific vocalizations (calls) using operant conditioning and food reinforcement. The bird's call was compared to a digital representation of the call stored in a computer to determine a match. Once birds were responding at a high level of precision, we measured the effect of several manipulations upon the accuracy and the intensity of call production. Also, by differentially reinforcing other aspects of vocal behavior, budgerigars were trained to produce a call that matched another bird's contact call and to alter the latency of their vocal response. Both the accuracy of vocal matching and the intensity level of vocal production increased significantly when the bird could hear the template immediately before each trial. Moreover, manipulating the delay between the presentation of an acoustic reference and the onset of vocal production did not significantly affect either vocal intensity or matching accuracy. Interestingly, the vocalizations learned and reinforced in these operant experiments were only occasionally used in more natural communicative situations, such as when birds called back and forth to one another in their home cages. © *2008 Acoustical Society of America.* [DOI: 10.1121/1.2835440]

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I. INTRODUCTION

The interaction between hearing and vocal production has been widely studied in birds, especially those that develop their vocalizations through learning. Much of what we know about vocal production and vocal learning in birds comes from experiments that examined song behavior following deafening (during either the nestling period or in adulthood), rearing in isolation, or selective exposure to particular types of vocalizations during development (see, for example, Kroodsma and Miller, 1982; 1996). Together, these approaches reveal considerable variation in the styles of vocal learning and vocal development in birds.

We also know from both field and laboratory studies that a number of passerine and psittacine species learn or mimic one another's calls (Dooling, 1986; Farabaugh and Dooling, 1996; Mammen and Nowicki, 1981; Mundinger, 1970; Trillmich, 1976a, b). This phenomenon is less well studied than song learning in songbirds, and there is less information on how quickly such learning can occur (but see Farabaugh *et al.*, 1994; Mammen and Nowicki, 1981). Songbirds have often been used as subjects in these experiments, but psittacids also show call learning (see the review in Farabaugh and Dooling, 1996).

Budgerigars, for example, have a complex vocal repertoire that includes learned calls and a long rambling nonstereotyped warble song. In these birds, both sexes show considerable vocal plasticity throughout life (Farabaugh and Dooling, 1996; Hile and Striedter, 2000; Hile *et al.*, 2005). The contact call is the most frequently used call in the budgerigar vocal repertoire (Brittan-Powell *et al.*, 1997; Brockway, 1964a, b, 1969; Farabaugh and Dooling, 1996; Farabaugh *et al.*, 1992, 1994; Hall *et al.*, 1997; Heaton and Brauth, 1999; Heaton *et al.*, 1999; Hile *et al.*, 2000; Hile and Striedter, 2000; Hile *et al.*, 2005; Striedter *et al.*, 2003; Wyndham, 1980). Studies have shown that birds housed together in small groups come to share contact calls with their cagemates in a matter of a few weeks (Brown *et al.*, 1988; Farabaugh *et al.*, 1994; but, see also, Hile *et al.*, 2000; Hile and Striedter, 2000). Playback experiments in the laboratory show that budgerigars call more frequently in response to a mate's call (Ali *et al.*, 1993).

The above-cited studies, as with almost all vocal learning studies in birds, relied on spontaneous behavior and vocalizations with little experimental control over the bird's motivation, calling behavior, or reinforcement contingencies. It is a relatively simple matter to direct a human to produce (or learn) a specific vocalization as a means of investigation. While it is more difficult to accomplish the strict equivalent in animals, recent studies have brought budgerigar vocal behavior under experimental control (Manabe *et al.*, 1997; Manabe and Dooling, 1997; Manabe *et al.*, 1995) by using operant conditioning with positive reinforcement. Budgerigars can be readily trained to produce specific vocalizations for food and to modify both the spectrotemporal pattern (Manabe and Dooling, 1997) and the intensity (Manabe *et al.*, 1998) of their calls by selective reinforcement. Moreover, they can be trained to do this without first being presented with an acoustic reference of the modified call they eventually come to produce. This offers an opportunity to address questions of call learning in budgerigars in a very different and much more controlled context than afforded by normal social interactive situations involving a number of birds.

Here, we train budgerigars to produce specific calls for food reinforcement (i.e., calls that match an acoustic refer-

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ence or template) and then assess the effect of allowing the bird to hear the call (i.e., the template) it is supposed to mimic immediately prior to producing it. We also track the effects of changes in the template on call production, and we examine the effect of operant training of call production on calls the birds produce in more natural, unrestricted social situations that evoke calling behavior.

II. GENERAL METHODS

A. Subjects

The subjects in these experiments were adult budgerigars obtained from a local pet supplier and maintained in an aviary at University of Maryland. Each bird was caged separately and had free access to water and grit in their home cages. During these experiments, food was used to reinforce the vocal behavior; therefore, the birds were maintained at 90% of their free-feeding body weights. The Animal Care and Use Committee at the University of Maryland approved all animal use.

B. Apparatus

Birds were trained in a small experimental chamber (14 cm wide × 12 cm high × 17 cm deep) constructed of wire mesh and mounted in a small sound isolation chamber (Industrial Acoustic Company model AC1). A light emitting diode (LED) was affixed to each corner of a 3 cm × 3 cm square piece of sound attenuating foam. This foam was in turn mounted on the side of the cage at the level of the bird's head. An Electret condenser microphone (Sony ECM-77B), set in the middle of the foam square, detected the bird's calls. A food hopper containing hulled millet was mounted on the floor at a depth of 3 cm from the front mesh.

C. Procedure and analysis

1. Recognition of calls

The output of the Sony microphone was sent to a digital signal processing board (National Instruments AT-DSP2200). Analog data were low-pass filtered at 80 kHz before being digitized with a 16 bit analog-to-digital (A/D) converter. The digital signal was low-pass filtered at 12 kHz, using a digital filter (IIR) to reduce the frequencies in the signal and eliminate aliasing before digitizing. A/D conversion at a rate of 24 kHz was initiated when sound intensity exceeded a preset value and continued for 266 ms.

Serial power spectra were calculated using the fast Fourier transform (FFT). The FFT was performed on approximately the first 10 ms of the call while the second 10 ms of data were being sampled to RAM, and so on. For each spectrum in the series (i.e., 10 ms sample), the intensities were normalized with the peak intensity set to one (Manabe *et al.*, 1997). In all, 25 successive serial power spectra were calculated over the entire sample.

The incoming signal was classified as a contact call if the following conditions were met: (1) The duration of the entire signal was greater than 96 ms, (2) 70% of the distribution of frequencies from about 188 to 10031 Hz were between 938 and 6844 Hz, and (3) there were no call components shorter than 21 ms in the first 75 ms of the call. All signals that were classified as contact calls were stored on disk for later analysis. Call intensity (peak amplitude) was calculated on the stored digital data. All programs for experimental control and data collection were written in Microsoft C.

2. Shaping of calling behavior

The birds were habituated to the experimental chamber and then trained to eat millet from the food hopper. Once the birds reliably ate from the hopper when it was raised, manual shaping of vocalizations began. In this phase of training, typical aviary sounds were played in the test chamber to induce the birds to produce a contact call. Whenever the birds called back to the aviary tape with a contact call, the experimenter activated the hopper. When birds began to produce contact calls reliably in the absence of playback calls, the calls were reinforced automatically.

3. Generation of a call template

After several sessions in which all sounds produced by the birds met the criterion of a contact call by the call recognition software, a typical contact call produced by the bird was selected as a "template" call (see, Manabe and Dooling, 1997). The bird's call was compared to the template, with the similarity index defined as the sum of the overlapping areas of each of the 25 serial power spectra from the two calls. This index is zero if there are no overlapping areas and one if the calls were spectrally identical. In actuality, a call was compared with slight temporal variations of the onset of the other calls (e.g., five different temporal offsets of about +10, +5, 0, −5, and −10 ms to minimize the effect of slight variations in onset or intensity levels). The highest similarity index of the five temporal offsets was taken as the similarity index between the two calls. A matrix of similarity values was constructed from all calls produced in a test session. This matrix was analyzed using multidimensional scaling algorithms (MDS, Systat) and plotted in two-dimensional space. The call in the center of the largest cluster in this two-dimensional space was selected as the template call for the next phase of training.

4. Template call training

Using this template call as a model for what the bird should mimic, the next phase of training consisted of reinforcing only those calls the bird produced that were similar to the template call (i.e., above a criterion similarity index). In this phase, activating the LEDs signaled the onset of a trial and each trial was separated by a 2 s intertrial interval. Vocalizations occurring during the intertrial interval were not reinforced and delayed the onset of the next trial by 1 s. For each call produced during a trial, a similarity index was calculated in real time as described earlier with the criterion initially set very low (e.g., 0.01) so that even calls barely similar to the template were reinforced. As the bird's performance improved (i.e., more calls meeting criterion), the criterion was gradually increased to a maximum value of about 0.5 depending on the experimental conditions. All test ses-

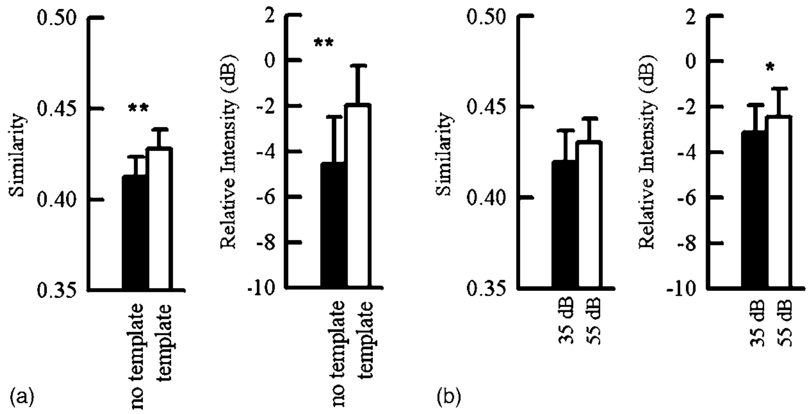

FIG. 1. (a) Mean and standard deviation of call similarity and relative intensity of contact calls from three birds. Closed bar indicates no template sound (no temp) and open bar indicates audible template (temp) presented at 55 dB. Double asterisks represents significance level of 0.001. (b) Mean and standard deviation of call similarity and relative intensity of contact calls from three birds. Closed bar indicates audible template presented at 35 dB and open bar indicates audible template presented at 55 dB. Single asterisk represents significance level of 0.05.

sions were concluded after delivery of a specific number of reinforcements (usually 48) or 20 min, whichever came first. Subjects were tested in two daily sessions, six days per week. Sessions were always separated by at least 4 h.

III. EXPERIMENT 1: EFFECTS OF TEMPLATE SOUND PRESENTATION ON THE INTENSITY AND ACCURACY OF CALL PRODUCTION

The first experiment examined the effects of presenting an acoustic reference or template (an external acoustic model of the call to be matched) to the bird and consisted of two parts. We sought to determine: (1) the effect of the presence or absence of acoustic reference on the precision of vocal accuracy and (2) the effect of the intensity level of acoustic reference on the vocal output of the test subject. We hypothesized that an acoustic reference would increase the accuracy of call production in an operant situation and that the intensity of the vocalization would depend on the intensity of the acoustic reference presented.

A. Methods

Subjects. Three male budgerigars were used for this experiment.

B. Procedure

Once the birds were trained to asymptotic levels of performance on the template-matching paradigm described earlier, a new training phase was introduced in which the template call was played to the bird before each trial. The sound pressure level of the template sound was measured with a General Radio Model 1982 Sound Level Meter and 3 m extension cable with a $\frac{1}{2}$ in. microphone placed in the position of the bird's head in the test apparatus. For the first part of the experiment, the sound pressure of the template call was set to a peak of 55 dB SPL (fast rms) at the bird's head. There were two types of trials: a nonsound template trial and a sound template trial. A total of 48 trials, 24 trials of each type, were presented randomly during a single test session. In all, each bird ran between 20 and 49 sessions for this experiment.

In the second part of the experiment, the template call was played to the bird on each trial but at one of two different intensities. The template was presented at a peak sound pressure level of either 55 dB SPL or 35 dB SPL rms at the bird's head just before the trial onset. The two different trial types occurred in a random order within a session and a total of 24 trials of each type occurred.

C. Results and discussion of experiment 1

Figure 1(a) shows the mean similarity index and the mean call intensity of three birds for each of the two trial types. The mean similarity index between all calls produced by the birds and the stored template call was significantly greater when the template was audible than in trials when the template was not presented to the bird [one-way repeated measures (RM) ANOVA; $F(2,1)=552.3$, $p<0.002$]. The mean intensity of the calls produced by the three birds in trials with an audible template was also significantly greater than in trials when the template was not presented [one-way RM ANOVA; $F(2,1)=130.6$, $p<0.008$]. This experiment shows that presenting birds with an acoustic reference results in small but significant increases in both the precision of call matching and the intensity of call production.

Figure 1(b) shows the mean similarity index and the mean call intensity of three birds. The mean similarity index between the birds' calls and the template call in high intensity trials was not significantly different from those produced in low intensity trials [one-way RM ANOVA; $F(2,1)=5.67$, $p>0.1$]. On the other hand, the mean intensity of the birds' calls in high intensity trials was significantly greater than calls produced by the birds in the low intensity trials [one-way RM ANOVA; $F(2,1)=28.1$, $p<0.03$]. These results show that while the precision of call matching remains the same for both intensities of the acoustic reference, the intensity of call production is dependent on the intensity of the

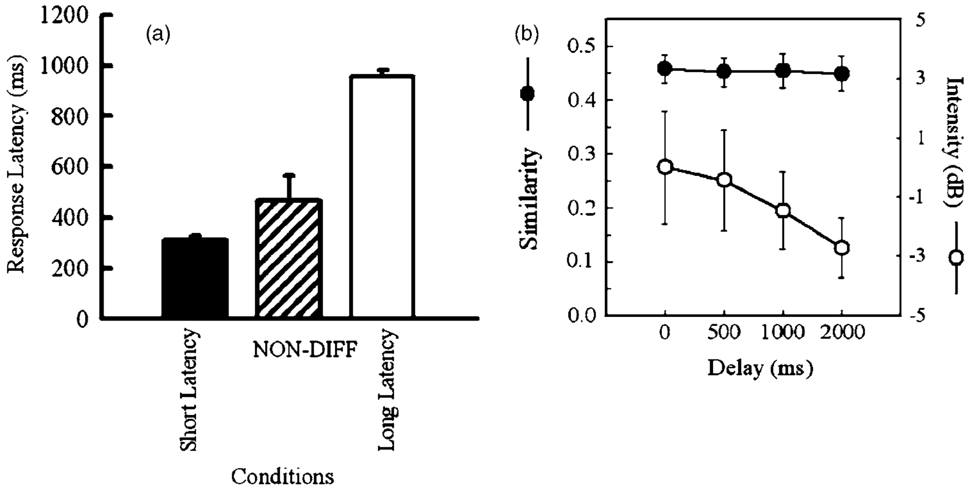

FIG. 2. (a) Mean and standard deviation of callback latency for three birds under three different conditions. Closed bar indicates the differential reinforcement of short latency, the striped bar indicates the nondifferential reinforcement condition, and the open bar indicates the differential reinforcement of long latency. (b) Mean and standard deviation of call similarity (closed circles) and intensity (open circles) across delay for three birds.

acoustic reference. Taken together, these results show that the bird's own call heard immediately prior to call production affects certain aspects of the quality of the bird's vocalization.

IV. EXPERIMENT 2: EFFECTS OF DELAY BETWEEN HEARING THE ACOUSTIC REFERENCE AND CALL PRODUCTION ON THE INTENSITY AND ACCURACY OF THE CALL

Experiment 1 showed that providing an acoustic reference before vocal production can increase both the precision of matching to the template and the intensity of vocal output. Casual observation of budgerigars in more "natural" situations, as when they are calling back and forth to one another in a large vivarium, suggests that they have control over a number of features of their calling behavior such as how quickly they respond to the call of another bird. In the following experiment, we examined whether the bird's latency to respond (vocally) to hearing a contact call was amenable to control through differential reinforcement. Moreover, if a bird's vocal response latency can be controlled by differential reinforcement, it provides an opportunity to examine other aspects of calling behavior, such as the role of memory, in guiding the precision of vocal production in matching the acoustic reference.

A. Method

Subjects. The same three birds from the previous experiments were used in this experiment.

B. Procedure

The latency with which the bird responded to the template was differentially reinforced. First, the latency of the bird's response to the template was measured in a normal test session (as described earlier). In this phase, there were no reinforcement contingencies on latency, and every call the bird produced was reinforced. Once performance reached asymptotic levels, calls were reinforced only when the latency to respond *was shorter* than the average delay value obtained in phase one. The value of the response delay criterion was gradually decreased from 1000 to 400 ms. Then, calls produced by the bird were reinforced only when the response latency *exceeded* a criterion value. Here, the criterion value was gradually increased from 400 to 700 ms.

In the second part of the experiment, a trial delay was imposed after the presentation of template sound and before the LED was lit. At first, calls matching the template were reinforced if the response occurred within 1000 ms after the LED was lit. Then, four delay intervals (0, 500, 1000, and 2000 ms) were imposed between the presentation of the template sound and the lighting of the LED. Calls produced during these delay intervals (i.e., prior to lighting the LED) were not reinforced. Furthermore, calls produced during the delay interval canceled the current trial and initiated a new trial sequence. The four delays were randomly mixed within a session, and the number of trials at each delay was set to 24. The birds were required to wait until the LED was lit to vocalize. The birds ran between 20 and 60 sessions during this experiment.

C. Results and discussion of experiment 2

Figure 2(a) shows mean response latency of three birds. These results show that differentially reinforcing response latencies was effective in both increasing and decreasing the birds' normal response latency. While the mean latency was well controlled by differential reinforcement [one-way RM ANOVA; $F(2,2)=59.9$, $p<0.002$], neither the mean similarity index [one-way RM ANOVA; $F(2,3)=1.27$, $p>0.36$] nor the mean call intensity [one-way RM ANOVA; $F(2,3)=2.54$, $p>0.10$] were significantly different across delay intervals [see Fig. 2(b)]. These results provide no evidence for a decay in auditory memory as a factor in the precision of vocal production in budgerigars. An obvious explanation for this result is that these birds, as with humans producing speech, had extensive experience with producing particular call types such that they were, in effect, "overtrained" on the

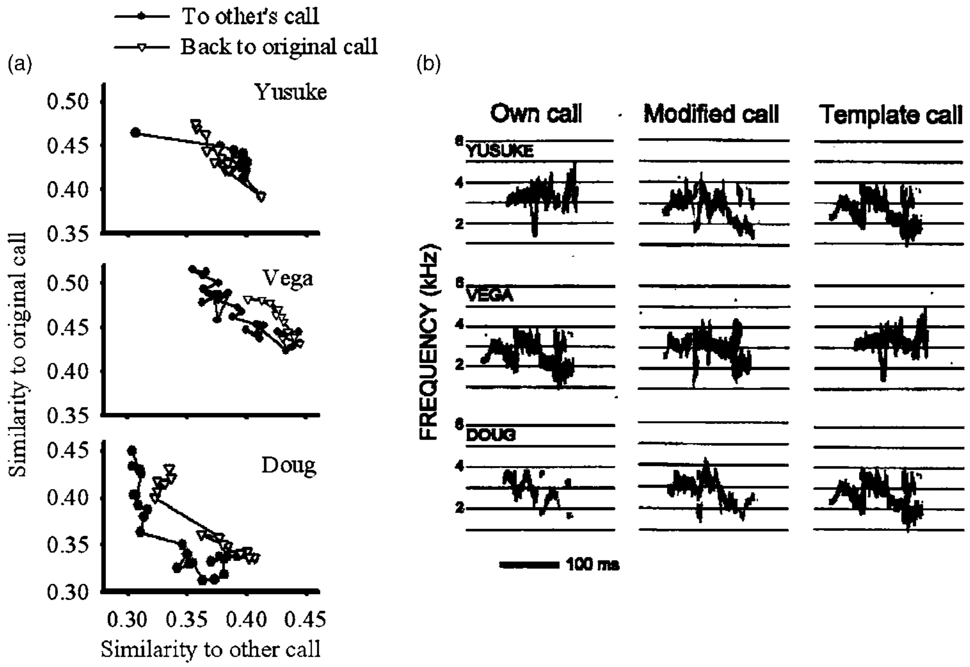

FIG. 3. (a) Mean similarities to original call and the template call for three birds. Closed circle indicates the training to make the template call. The open circle indicates training back to the original call. The line in each graph represents the average similarity between the original call from the previous training (i.e., no template sound) and the template call. (b) Sonograms of own call (original call), modified call, and template call from three birds.

motor patterns required to produce these calls. Thus, there was little lost, at least in terms of vocal precision and vocal level, from imposing a delay of up to 2 s in responding following presentation of an acoustic reference.

V. EXPERIMENT 3: EFFECTS OF CHANGING THE TEMPLATE AND ACOUSTIC REFERENCE

If providing birds with an acoustic reference or auditory template prior to vocalizing increases the precision of vocal matching, this might reflect a mechanism birds use in social situations to learn one another's contact calls. The present study examined this question by training birds to produce calls under operant control and then changed the reference sound from one of their own calls (experiment 1) to the call of another bird. The purpose of this experiment was to determine whether birds could learn new calls through a process of selective reinforcement of spectrotemporal changes in the acoustic reference that eventually converge on the contact call of another bird. In effect, this study simulates a situation that might exist when a bird is housed with a new cagemate and learns the new cagemate's contact call.

A. Method

Subjects. Two birds from the previous experiment (Yusuke and Vega) and one new bird (Doug) were used in this experiment.

B. Procedure

These birds were trained to produce a call to match an audible template call within 1000 ms after onset of LED. Once the birds' performance reached asymptotic levels, the stored template for a particular bird was changed to the stored template of one of the other two birds. In other words, the template for Yusuke was switched from his original template call to Vega's template call, the template for Vega to Yusuke's call, and the template for Doug to Vega's call, respectively. The similarity between Yusuke's original template and Vega's original template was 0.35, and the similarity between Doug's original template and Vega's original template was 0.31.

As described earlier, calls were reinforced only when the similarity between the call and the new template call met a predetermined criterion. Initially, the criterion was set low to around 0.30 and gradually increased up to a maximum of about 0.45 as the bird's performance improved. After the birds reached asymptotic levels of performance on this new template, the old template was reinstated and retraining began on the original template call. In this retraining phase, the initial criterion was set at 0.35 and again gradually increased to about 0.45 depending on the bird's performance.

C. Results and discussion of experiment 3

Figure 3(a) shows the mean similarity index between all calls produced in the two sessions and the two templates. The ordinate represents the similarity to the original call template while the abscissa represents the similarity to the new call template. Each data point is the mean similarity for all calls produced in a single daily session after the call template was switched. Changes in call similarity are significantly different across the testing sessions [ANOVA, $F(2,8)=28.14$, $p<0.05$]. In the first phase, changing the call template from "original" to "other" results in a significant decrease in similarity to the original template ($t=7.05$, $p<0.05$). Then, in a retraining phase, the template the bird had to match was switched from other back to original for all three birds.

Changing the call template back to the original template significantly decreases similarity of birds' calls to the other template ($t = -5.75$, $p < 0.05$) and inceases similarity to the original template calls over a period of about 10 days.

Sonograms of each bird's original template, its new template, and the modified call resulting from changing the template are shown in Fig. 3(b). The modified call for each bird never matches the new template call perfectly but becomes more similar to the template call than to the bird's original call. Some features of the calls changed more than others. Vega's modified call, for instance, retained the constant frequency 2 kHz segment in the original call and became more like a combination of the bird's original call and the template call. This kind of recombination of segments is not unusual and may be one of several ways that budgerigars come to share contact calls in small social groups under more "natural" conditions (Farabaugh *et al.*, 1994; Hile *et al.*, 2000; Hile and Striedter, 2000).

VI. EXPERIMENT 4: CALLS IN AND OUT OF THE OPERANT CONTEXT

The previous experiments demonstrate that budgerigars can learn new contact calls under operant control using selective reinforcement and that hearing an acoustic reference prior to vocalizing affects the precision and level of vocal output. The strictly controlled operant test environment is highly unnatural so it is an open question whether vocal learning in this context is similar to what might occur in more natural social contexts. Experiment 4 examined two aspects of this problem. First, we sought to determine the extent to which calls learned in an operant context were produced in a more natural context (as when birds call back and forth to one another in their home cages). Second, we compared operant learning of contact calls in birds that had extensive learning experience in a natural context with birds that were housed in social and acoustic isolation. In all, we trained four budgerigars using the operant procedures described in the following. During the course of these experiments, the calls produced by the birds outside of the operant context were recorded on a weekly basis.

A. Method

1. Subjects

Four experimentally naive female budgerigars, all several years old, served as subjects. Two birds (There and Here) were caged separately in a large aviary that housed 50–100 other adult budgerigars. Two other birds (Bart and Maggie) were reared normally to the age of 10 months but then housed for over a year in a restricted social and acoustic environment where they could not interact visually or acoustically with other budgerigars.

2. Audio recording

During these experiments, each bird's natural vocal repertoire was recorded weekly in a seminatural situation. The two birds normally housed in the large aviary (There and Here) were moved to small, individually isolated, recording boxes (21.5×23×23 cm), which had three walls, lined with acoustic foam, a front wall of Plexiglas, and a top of wire mesh. These small boxes were housed within a larger sound isolation chamber (Industrial Acoustic Company model AC1). Calls were elicited from these birds by opening the doors to the sound isolation chambers slightly (so the birds could hear one another). The two birds (Maggie and Bart) maintained in acoustic and social isolation (i.e., already housed in similar IAC chambers) were recorded individually and stimulated with a tape of running water rather than other bird vocalizations.

In all cases, the recording boxes were fitted with an omnidirectional Realistic Electret Microphone (model 33-1063) connected to separate tracks of a four-channel Marantz tape recorder (PMD740), and 20–30 calls were recorded per bird per session. A Kay Elemetrics model 7800 Digital Kay Sonagraph was used to print spectrograms (300 Hz bandwidth; expanded mode). Contact calls are distinctive and highly stereotyped making it easy to visually categorize vocalizations into call type categories.

B. Procedure

The birds' initial contact call repertoire was sampled and classified into types (by EBP). Three of the four birds produced only one contact call type. The remaining bird (Bart) already produced several call types at the time these experiments were initiated. Bart was trained immediately on the template task described earlier in Sec. II.

The three birds that produced only one contact call were trained on a "1-back procedure" described previously (Manabe *et al.*, 1997; Manabe and Dooling, 1997). This procedure induces birds through selective reinforcement to produce more than one call type. Briefly, a call was reinforced only when it was different from the last reinforced call. Call difference, or dissimilarity, was quantified in terms of the sum of the overlapping area of 20 successive serial frequency distributions (Manabe *et al.*, 1997). Initially, all calls that varied a predetermined amount from the previous call were reinforced, even if the newly produced call differed only slightly from the last reinforced call. As the bird's performance improved, the criterion for qualifying as different became stricter. Once a bird consistently produced two, and sometimes more, acoustically distinct calls, one of the new call types was chosen to be the bird's new template call and the second phase of training began.

In this phase of the experiment, the bird was only rewarded in the operant chamber for producing the new template call. In other words, the bird's call production was only reinforced when the similarity index to the template was above a certain criterion. This criterion was increased gradually to a maximum of 0.45 as the bird's performance improved. In this experiment, the template call was not audible to the bird; in other words, there was no external acoustic reference for the bird's production. The point of this template training was to induce precise learning and reliable production of a new call type in the operant context.

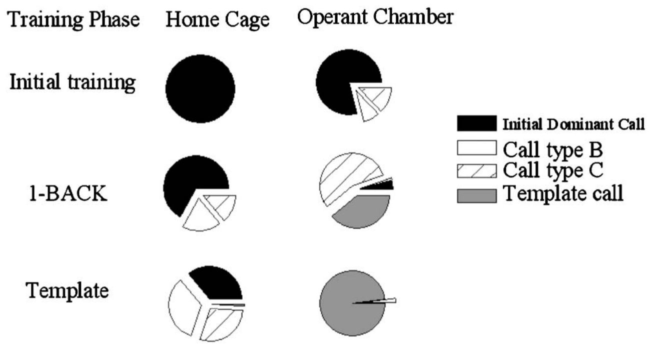

FIG. 4. Data for four birds showing percentages of calls produced (by type) in the home cage and the operant chamber. As template training concludes, the birds produce the template call the majority of the time within the operant chamber but rarely in the birds' natural repertoires.

C. Results and discussion of experiment 4

1. The effect of restricted social and acoustic conditions on learning

The two different birds, housed in small cages within sight and earshot of 50–100 birds (There and Here), readily learned both the 1-Back and template operant tasks. Surprisingly, two birds reared in restricted conditions (Bart and Maggie) failed to learn either experimental task. Specifically, these two birds did learn to associate calling with food reward but failed to reach criterion on any of the tasks. Attempts to train the birds in the operant task continued daily for approximately 8 months. The birds were then returned to a large aviary with other birds for a period of 6 months. Within a few weeks of interacting with the birds in this aviary, both birds (Bart and Maggie) produced at least two new call types in their home cage. These results show that these birds were perfectly capable of learning new call types in a more natural social situation, presumably via social reinforcement, but *not* under experimental operant conditions with food reinforcement.

2. The effect of normal social and acoustic conditions on learning

After a 6 month period in the aviary, Bart and Maggie were housed in the same room as There and Here. They were retrained in the Operant test chamber and now both learned to produce new call types in the Operant test chamber when trained on the 1-Back procedure.

All four birds learned to produce an acceptably precise match to the template call in the template task. Figure 4 summarizes the data for all four birds when housed in a normal acoustic environment. The majority of calls first produced by the birds in the Operant test chamber were the dominant contact calls (from their natural repertoire) produced in the home cage as seen in Fig. 4 (initial training). However, as the training continued, the calls in the two contexts began to differentiate until finally there was little to no overlap between calls produced in the natural and operant contexts (Fig. 4 1-Back). At the conclusion of template call training, the four birds rarely produced the template call outside of the operant context (Fig. 4, template). In other words, food reinforcement of a specific call type in the operant context did not increase its use in more natural communication contexts for these four birds. This is surprising given the demonstrable vocal plasticity of budgerigars throughout adulthood.

The overlap between call types produced in a natural calling situation and the Operant test chamber was characteristic of the earliest stages of training as shown in Fig. 4. As the criterion for reinforcement of a specific call type becomes more restrictive in the Operant test chamber, all other nonreinforced calls cease to be produced. By contrast, the number of call types produced outside of the Operant test chamber remained virtually unaffected during the last stages of this experiment (e.g., moving from the 1-Back procedure to the template training procedure). Taken together, the results from this experiment show that (1) social interactions with other birds can affect training in the Operant context and (2) training in the Operant context can influence the diversity of calls birds produce in a normal social context.

VII. GENERAL DISCUSSION

Budgerigars can be trained by food reward to modify the spectrotemporal qualities of their species-specific contact calls (Manabe *et al.*, 1995, 1997; Manabe and Dooling, 1997) and to control the intensity of their vocal output (Manabe *et al.*, 1998). The present experiments extend these findings in a number of important ways: (1) Hearing an external acoustic reference independently increases the accuracy and intensity of call matching, (2) delays of up to 2 s between template presentation and trial onset does not affect either vocal intensity or matching accuracy, (3) response (calling) latency is susceptible to modification by selective reinforcement, (4) production of other budgerigars' contact calls can be learned in an operant context through selective reinforcement, (5) calls learned and exclusively reinforced in an operant context are not used in more natural communicative contexts, and (6) birds kept in social and acoustic isolation do not readily learn new calls in an operant context.

One of the most productive areas of research in vocal learning in songbirds has been studies devoted to understanding what songs and calls birds can learn, and when, and from whom they learn. Compared to song learning, call learning in birds is much less well studied. In budgerigars, call learning, and subsequent production of contact calls, is not widely separated in time perhaps because budgerigars leave their parents and join juvenile flocks shortly after fledging (Wyndham, 1980). The development of shared vocalizations may be necessary, especially in such gregarious species, for social bonding (e.g., Farabaugh *et al.*, 1994). In most social situations, however, it is difficult to identify the key variables in vocal learning and study them separately. The present studies show that many aspects of calling behavior, including learning multiple contact call types, can be quite easily influenced through selective reinforcement procedures involving food. Presumably, in natural contexts, social reinforcement takes the place of food reinforcement. In addition, the fact that the four birds in experiment 4 came to use different contact calls in the operant environment compared to their natural home environment also highlights another point—the contact call repertoire in these birds is context dependent.

The present results provide some insight into two general mechanisms by which budgerigars could learn new contact calls as adults. One, a "memory-based" process, might involve repeated presentation of the model to be learned, the subsequent formation of an auditory memory, followed by vocal-motor attempts to match that auditory memory. Another quite different mechanism, akin to "action-based" learning (e.g., Marler and Nelson, 1993), could involve selective reinforcement of call variations, through visual and social cues, which guide vocal productions so that they ultimately converge on the call type to be learned. For budgerigars, this mechanism has been suggested by previous work showing that social and visual interaction is key to contact call sharing in adult budgerigars and that acoustic interaction alone is not sufficient (Farabaugh *et al.*, 1994). The present experiments strengthen this hypothesis considerably by showing that budgerigars learn new calls in an operant context by selective reinforcement of call variation by food reinforcement eventually producing a contact call which matches another bird's contact call.

Finally, parrots almost certainly do not normally learn new vocalizations for food reinforcement in nature. Rather, they probably learn new vocalizations by mechanisms that involve various social reinforcers or other manipulations of their social environment (Brittan-Powell *et al.*, 1997; Farabaugh and Dooling, 1996; Farabaugh *et al.*, 1994; Rowley and Chapman, 1986; Treisman, 1978). But, the present experiments, by bringing a number of aspects of contact call learning under strict experimental control, do offer new opportunities to examine the biological bases of vocal learning, the operation of specific sensory and motor circuits underlying learning, and the critical role that auditory feedback plays in both the learning and maintenance of an adult vocal repertoire.

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