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Effect of auditory stimuli on conditioned vocal behavior of budgerigars

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Abstract

The budgerigar (*Melopsittacus undulatus*) is a highly social species and serves as an excellent model of vocal learning and production. This species can be trained to vocalize as a conditioned response using an operant conditioning paradigm. In addition, the birds can be trained to produce different vocalizations in response to different visual signals. Budgerigars may be fairly unique in the capability for vocal production under operant control. Whether acoustic features of the bird's natural social milieu can influence this conditioned vocal output is uncertain. The present study asked whether conditioned vocal behavior in budgerigars can be influenced by hearing vocalizations of other birds. The results show that birds vocalizing under operant control produced louder calls in the presence of vocalizations from other birds, than in pure tones or in quiet. The acoustic variation of the conditioned vocalization also increased when it in the context of hearing other bird's calls. These results reveal a functional connection between the vocal production under operant control and the perceptual mechanisms subserving vocal production in the budgerigars' natural social milieu.

Keywords

vocal conditioning; vocal learning; parrots

Introduction

The budgerigar can acquire and incorporate novel vocal patterns in its repertoire throughout life. The capability for vocal production learning is not very common in the animal kingdom, so the budgerigar is becoming more popular as an animal model in vocal production research.

As with most animal communication signals, vocalizations in this species are mainly used for communicating with other individuals (Farabaugh and Dooling, 1996). A number of studies over the years have reported on the budgerigars' imitation of the contact calls of

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other budgerigars in a social context (Farabaugh et al., 1994; Hile et al., 2000; Hile and Streidter., 2000; Moravec et al., 2006) and incorporation of other sounds in warble (Gramza, 1970). Clearly, budgerigar natural vocal behavior is strongly influenced by interaction with other birds and its acoustic milieu.

Budgerigars can be trained to produce specific calls as a conditioned response under operant control. Budgerigars learn to vocalize to obtain food rewards. In addition, they can also be trained to use two different vocal patterns in response to two different visual stimuli (Manabe and Dooling, 1997; Manabe *et al.*, 2008; Manabe *et al.*, 1995, Manabe *et al.*, 1997). In such operant experiments, each budgerigar typically produces its own vocal patterns that were previously acquired as an open-ended vocal learner under more natural social circumstances.

We know that budgerigars often produce calls in response to another birds' call (Ali et al., 1993, Eda-Fujiwara et al., 2011). This raises a questions about the budgerigars' vocal behavior. If another bird's call was played back just before production of a trained vocal response in an operant procedure, is the conditioned vocalization affected? To answer this question, we observed budgerigars' conditioned vocal response in an operant procedure under several different conditions, varying social context.

Methods

Subjects

One male and 4 female budgerigars were used. Birds were kept in individual cages in a 12/12 light/dark cycle in an aviary at the University of Maryland. For the experimental period, the body weight was maintained at 85–90% of the bird's own free-feeding weight.

Apparatus

The apparatus and procedure have been detailed previously and are briefly described in the Supplemental information. An experimental cage (19cm×17cm×22cm) was placed in a sound attenuation chamber (AC-1, Industrial Acoustic Company, NY). Subjects could access food from a hole within the floor of the cage when the food hopper was in the up position. A plate with 3 red LEDs and a microphone (ECM-77B, Sony, Japan) were attached on the cage wall 2 cm above the hole that gave access to food. Sound signals were acquired at a 24 kHz sampling rate by the microphone and sent to a signal processor (RP2.1, Tucker-Davis Technology (TDT), FL) after band pass filtering (450-10kHz; Model 3550, Krohn-Hite, MA) via amplifier (MA-3, TDT, FL). A loud speaker (40–245, Archer, Korea) was attached on the cage wall directed to the subject. Another loudspeaker (40–1289, Realistic, Japan) for background sound was placed in a corner of the chamber. The RP2.1 was also used to control the sound stimuli, LED illumination and the hopper. The background noise level was 33dB SPL.

Stimulus

Stimulus calls were previously recorded from a female flock-mate by the same recording system. The system was calibrated by adjusting the amplitude of a 200 ms (about the

duration of a budgerigar contact call), 1 kHz pure tone to 72dB SPL at the bird's head position. The levels of the other sounds were adjusted via root mean square (rms) to have the same energy as this pure tone. The flock sound of many birds singing was presented at a level of around 40–45 (maximum 50) dB SPL at the bird's head.

Procedures

Four birds had previously been trained to produce only their primary contact call in response to a lit LED (here “primary” refers to “the most frequently produced in the experimental box”). Another bird had been trained to produce any call in its repertoire (Osmanski and Dooling, 2009) but even this bird consistently produced only one vocalization in natural situations.

Birds were reinforced by 0.7–0.8s of food access when they vocalized after LED illumination. The inter-trial-interval (ITI) was 3 seconds. When they vocalized within the ITI, the vocalization was not reinforced and the time count was reset for the next 3 seconds. We recorded all reinforced vocalizations.

Once the appropriate vocal behavior was established, the subject was tested in a silent condition (1st SLT condition) where no auditory stimuli preceded the lit LED and no background sounds. One session consisted of 50 reinforced vocalizations. A morning and an afternoon session were completed in two successive days (4 sessions total). In the next 2 days, we ran 4 sessions in which there was a presentation of a budgerigar call just before LED illumination and presentation of budgerigar flock sounds through the sessions as well (1st CALL-FLK). The stimulus call presented was randomly chosen from 5 natural variations of the stimulus call. Thus, the acoustic patterns were a good approximation of sound patterns captured in natural settings.

We immediately observed difference in calls produced during the 1st SLT and 1st CALL-FLK conditions (see Results), therefore, birds were tested in 5 additional conditions: a 2nd CALL-FLK condition a 2nd SLT condition, a call presentation only (CALL) condition, a flock background only (FLK) condition, and a 1 kHz pure tone (PT) condition, in this order. Every condition was tested for 4 sessions, consisting 50 trials each.

Analyses

Vocal intensity—For each vocalization, the intensity was measured as dBV rms. Mean intensity of the SLT conditions for each bird was used as a baseline and the difference of the intensity of each vocalization from the baseline was calculated.

Vocal variation—we categorized vocal patterns by visual inspection of the sound spectrograms. Then, to quantify this categorization, 2D-correlation-based similarity indices among the sound spectrograms in each condition were computed (Osmanski and Dooling, 2009).

For statistical analyses, a Mann-Whitney U-test was used for the comparison between 1st SLT and 1st CALL-FLK. Kruskal-Wallis and Steel-Dwass multiple comparison tests were

used for the following 5 conditions. The distance of the clusters of the MDS was evaluated by one-way MANOVA (Wilks Lambda).

Results and Discussion

Vocal intensity

Between the 1st SLT and 1st CALL-FLK conditions, the vocalizations were significantly louder in CALL-FLK (Two-tailed, $U=163400$, $p<.0001$). Moreover, a significant difference of the intensity was shown across the conditions ($\chi^2=1308$, $df=4$, $p<.0001$). The vocal intensity in CALL-FLK was significantly ($p<.0001$) greater than in all other conditions (CALL ($t=14.6$), FLK ($t=14.1$), SLT ($t=26.8$) and PT ($t=28.5$)). Intensity was also greater in CALL than in SLT ($t=14.6$) and PT ($t=17.7$). Intensity in the FLK condition was greater than in SLT ($t=18.4$) and PT ($t=21.5$) (Figure 1a).

While budgerigars exhibit a robust Lombard Effect (Manabe et al., 1998; Osmanski and Dooling, 2009), this is unlikely to have been a factor in either the CALL-FLK or FLK conditions, because the birds vocalized more loudly in the CALL condition. Thus, the change in sound intensity cannot be explained by a Lombard Effect alone. Sound stimuli preceding the visual cue also affected the conditioned vocal behavior in more complex ways - both vocal intensity and variation in the CALL condition was larger than in the PT condition for instance. Interestingly, the results showed that the PT condition actually had the effect of reducing vocal intensity compared with the SLT condition ($t=4.12$, $p<.0001$).

Vocal variation

By visual inspection of spectrograms, three birds also produced non-primary calls in addition to their primary calls (examples in Figure 2). Statistical tests supported our visual-inspection-based categorization (Wilks' Lambda = 0.766, $\chi^2 = 212.57$; Wilks' Lambda = 0.246, $\chi^2 = 1117.50$; Wilks' Lambda = 0.350, $\chi^2 = 835.41$; $df = 3$, $p<.0001$ in all tests). We compared the probability of producing non-primary calls in the various conditions in these 3 birds. A significant difference was shown across the conditions ($\chi^2=34.40$, $df=4$, $p<.0001$). Between 1st SLT and 1st CALL-FLK, the probability was significantly higher in CALL-FLK (Two-tailed, $U=27.0$, $p<.001$). The probability was significantly different among the following 5 conditions. It was higher in CALL-FLK condition than in SLT ($t=4.28$, $p<.001$), FLK ($t=3.84$, $p<.01$) and PT ($t=4.23$, $p<.001$). It was also higher in CALL than in SLT condition ($t=2.97$, $p<.05$), FLK ($t=2.77$, $p<.05$) and PT ($t=3.11$, $p<.05$) (Figure 1b).

These results show that the operant control of vocal production in budgerigars is significantly influenced by natural vocalizations occurring between or during the stimulus (the LED) and the response (the bird calling). CALL-FLK condition evoked louder calls than CALL and FLK conditions. A likely reason is that the CALL-FLK condition more closely approximates the more natural situation for call production. Likewise, CALL-FLK and CALL conditions evoked more non-primary calls than did the FLK condition. This suggests that these conditions were also a closer approximation to a natural communicative context in which multiple variations of contact calls might be produced in response to the

calls of other birds, even though only a single conditioned behavior was linked to LED illumination.

The significance of this finding is that it shows that the operant control of vocal behavior in this species is still amenable to natural communicative contextual cues. While it is easy to train budgerigars to produce vocalizations under operant control, it is proving much more difficult to drive vocal learning in this species by operant control alone. The present results hold out the promise that the entire vocal communicative system, from perception to production, may be approachable using operant learning principles in this species.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Highlights

We trained budgerigars to produce calls as a conditioned response under operant control.

We asked whether the behaviour is influenced by hearing vocalizations of other birds.

Birds vocalized louder in the context of hearing another bird's call than to hearing the presentation of pure tones, or hearing no other sound at all.

The acoustic variation also increased when it in the context of hearing another bird's call.

The operant control of vocal behavior is not disconnected from the natural vocal communicative behavior.

Figure 2.

Primary and non-primary calls. (a) Examples of the spectrogram. (b) MDS space generated from similarity indices of vocalizations in SLT and CALL-FLK sessions for two birds (800 vocalizations total for each bird). Each dot represents a vocalization. Similar vocalizations clustered together. Non-primary sounds were rarely vocalized in SLT but were vocalized in the CALL-FLK condition.