International Journal of Comparative Psychology, Vol. 4, No. 1, 1990

PERCEPTION OF SPECIES-SPECIFIC VOCALIZATIONS BY ISOLATE-REARED BUDGERIGARS (*MELOPSITTACUS UNDULATUS*)

Robert J. Dooling, Thomas J. Park,
Susan D. Brown, Kazuo Okanoya
University of Maryland at College Park

ABSTRACT: Budgerigars were trained with operant conditioning procedures to discriminate among sets of calls from several species in a Same-Different task. Response latencies from this task were analyzed in several ways including multidimensional scaling (MDS) and cluster analysis. The pattern of response latencies from budgerigars reared in a large group of conspecifics was compared to that of budgerigars reared in acoustic and social isolation. Results show that budgerigars with previous experience with species-specific vocalizations and isolate-reared birds who had never heard such sounds can both discriminate among the categories of species-specific vocal signals. But, results from MDS and cluster analysis also show that rearing budgerigars in isolation has subtle effects on the perception of these categories of vocal signals.

INTRODUCTION

A major historical question in perceptual development is the extent to which natural perception categories are learned or innate (Gibson, 1969; Marler, 1982, 1984). This question takes on special significance for organisms that must learn their vocal signals by reference to an external auditory model (see, for example, Marler, 1987; Marler & Peters, 1989; Kuhl, 1989). Aside from humans, only birds (i.e., songbirds, parrots, and perhaps hummingbirds) have been shown to rely on learning to develop a vocal repertoire (Kroodsma & Miller, 1982).

Previous work shows that budgerigars (parakeets), when deafened as young, develop abnormal contact calls as adults (Dooling, Gephart, Price, McHale, & Brauth, 1987). Budgerigars reared in social and acoustic isolation from other birds also develop contact calls that fall outside the range of usual acoustic variation seen in this class of calls but the calls of isolate birds are not nearly as distorted

---

Address correspondence to Robert J. Dooling, Department of Psychology, University of Maryland, College Park, Maryland 20742.

as the calls of deafened birds (Dooling, Unpublished data). These kinds of experiments establish that hearing and an external auditory model are required for normal vocal development in budgerigars. The present experiments pose a different question about the role of auditory perception in vocal development. Do budgerigars who have never heard species-specific vocal signals perceive the various acoustic and functional categories of budgerigar vocalizations as experienced birds do? Or, does the perceptual grouping or clustering of complex vocal signals according to functional and acoustic categories require prior experience with the vocalizations in the appropriate social and communicative context?

METHOD

Animals

The experimental birds were nine adult budgerigars (*Melopsittacus undulatus*) obtained from a breeding colony at the University of Maryland. Following fledgling, seven of these birds (3 male, 4 female) remained in this colony of roughly 75-100 other budgerigars. Prior to experimentation, these birds were housed in large flight cages containing 10-15 other budgerigars in a large aviary. During experimentation, these birds were housed in pairs in small breeding cages. In the following experiments, we refer to these birds as normal birds.

Two isolate-reared birds (both male) were also observed. The isolate birds were in acoustic and social isolation in small animal sound isolation chambers (Industrial Acoustics Corporation) from the age of about 3 weeks and were tested beginning at the age of 8 months. These birds were housed in social and acoustic isolation during the conduct of these experiments. Yellow millet was used as reinforcer during experimental sessions and standard mixed parakeet seed was available during free-feeding times. The birds were kept on a normal photo-period correlated with the season and testing for all birds continued throughout the year.

Apparatus

The apparatus for training and testing the birds has been described elsewhere in detail (Dooling, Brown, Park, Okanoya, & Soli, 1987; Dooling, Park, Brown, Okanoya, & Soli, 1987). The birds were tested in small wire cages mounted in sound-attenuated chambers. One wall of the wire test cage was modified by the addition of a custom-built operant response panel constructed of two sensitive microswitches with light emitting diodes (LEDs) attached and a standard pigeon grain feeder. One microswitch served as an observation key and the other as a report key. A bird could trip the microswitch by pecking at the LED. All experimental events were controlled by an IBM PC-AT microcomputer. Contact calls were stored in computer memory in digital form and output at a sampling rate of 20 kHz through D/A converters during a trial.

Training and Testing Procedure

Briefly, the birds were trained on a "Same-Different" task (Dooling, Brown, et al., 1987; Dooling, Park, et al., 1987). A trial began with the illumination of the LED on the observation key. A response on the observation key resulted in the presentation of two calls separated by 300 ms and the illumination of the report key. A response on the report key within 2 s following the presentation of two different calls was rewarded with a 2 s access to grain. On the other hand, responses on the report key following the presentation of two identical calls was punished with a 20 s timeout period during which all lights in the experimental chamber were extinguished. Each trial was followed by a 1 s intertrial interval and then by a new trial sequence starting with the illumination of the observation key LED. A new trial sequence was also initiated if the bird failed to respond during the 2 s report interval. The dependent variable in these experiments was the response latency to peck the report key as measured from the end of the second stimulus.

Previous experiments with both simple pure tones and complex vocalizations have established that a budgerigar's response latencies on "Different" trials in this task are highly correlated with the discriminability of the stimuli—longer response latencies occur when the stimuli being discriminated are more similar. In other words, in this paradigm, response latency can be taken as a reliable and valid index of stimulus similarity (Dooling, Brown, et al., 1987; Dooling, Park, et al., 1987). Before being tested on the contact calls in these experiments, the birds were all trained on the Same-Different task with simple pure tones of different frequencies. Once the birds attained the concept of same-different, they transferred quickly, often without any decrement in performance, to different stimulus sets composed of vocal signals.

In the following three experiments, the test stimuli consisted of sets of 10-14 different bird calls presented at a peak sound pressure level of 72 dB(A) measured at the bird's head. We tested birds in daily sessions until all possible pairwise combinations of the different calls were presented once, resulting in a complete matrix of response latencies. In addition, trials which involved the pairing of each call with itself (i.e., "Same" trials) were repeated so that there were equal numbers of “Same” and “Different” trials in a filled matrix. In tests with a set of 10 stimuli, for example, a “filled” matrix consisted of one latency value in each “Different” or off-diagonal cell and the average of 10 latency values in each “Same” or diagonal cell. A filled matrix required 2N(N-1) trials where N is the number of stimuli in the set. Testing was continued until at least five complete matrices of response latencies were obtained. These matrices were then averaged to produce a final latency matrix from each bird for subsequent analysis.

Evidence that the birds were successfully discriminating among the stimuli in any particular set was obtained by comparing the response latencies on “Same” trials with those on “Different” trials. For all of the matrices from all of the birds used in the present experiments, response latencies in the off-diagonal cells (different trials) were always significantly shorter than response latencies in the diagonal cells (same trials). Although the dependent variable in these experiments was response latency, we also recorded percent correct and false alarm rates as a means of comparing the overall performance of the two groups of birds on the task. Typically, in these and other auditory perceptual experiments involving the “Same/Different” task, hit rate was over 80% while false alarm rate was generally below 25%.

At the end of testing, the latency values (recorded in centiseconds) from the individual matrices were subjected to a log transformation and a single matrix representing the average of all of the matrices was computed. This average matrix was then folded about its main diagonal by averaging the corresponding cell entries in the lower and upper half-matrices (i.e., A-B with B-A combinations) and discarding the values in the diagonals (i.e., latencies from “Same” trials). This resulted in a half-matrix of response latencies containing a single value for each comparison as required by the multidimensional scaling algorithm.

Data Analysis Procedures

The goal of these experiments was to determine whether budgerigars reared in acoustic and social isolation perceive complex, species-specific vocal signals differently than budgerigars reared in a large group consisting of other conspecifics. To this end, the data were analyzed in several ways.

Multidimensional Scaling. Multidimensional scaling procedures find an arrangement of points (stimuli) in multidimensional space by maximizing the correspondence between interstimulus distances (proximities) and the similarity between stimuli based on error scores, confusion indices, response latencies, or other similarity measures (Kruskal & Wish, 1978; Shepard, 1980). In these experiments, the SINDSCAL (*S*ymmetric *IN*dividual *D*ifferences *SCAL*ing) algorithm and program were used to analyze the response latency matrices. Individual differences scaling finds a common solution for a number of matrices (e.g., individual birds) by allowing each dimension of the spatial representation to expand or contract independently for each individual tested. Subject weights describe the importance of each dimension for each bird and provide an indication of the variance in each animal's data accounted for by stimulus distances along each dimension. Subject weights provide a basis of comparison among the birds in the perception of these stimuli.

Cluster Analysis. The final data matrices were also subjected to a hierarchical cluster analysis. Cluster analysis also describes the structure of similarity data but in the form of a dendrogram. Hierarchical cluster analysis groups calls according to a Euclidean distance metric with more similar calls clustered at less-aggregated levels of a hierarchy (Mezzich & Soloman, 1980). In the present experiments, we used cluster analysis to confirm the existence of a cluster or grouping of stimuli which emerged from MDS. The single dendrogram produced for socially experienced birds and for isolate-reared was accomplished by combining data across individuals. These group dendrograms provide an accurate reflection of the differences between these two groups of birds.

Category Discreteness. In the present experiments, both MDS and Cluster Analysis are used to show stimulus groupings. Since these are fairly complicated statistical procedures, another intuitively simpler measure was also developed to explore the differences between birds in the perception of stimulus categories. To obtain this measure, the average response latencies to all possible pairs of stimuli drawn from within a category (i.e., the same categories as determined by MDS and cluster analysis) are shown by a simple t-test to be significantly longer (more difficult to discriminate among) than average response latencies to all possible pairs of stimuli drawn from among the categories shown by MDS and clustering.

Percent Correct Responding. Isolate-reared birds could be abnormal in a number of ways some of which might be more directly related to performance in the operant task rather than perceptual capability. As a check on this possibility, we used the percent correct and false alarm rate to calculate a d' for each of the sessions for each bird. These values were compared for socially experienced and isolate-reared birds by an analysis of variance using a split-plot factorial design. Due to the number of comparisons, we chose to use a significance level of $p < .01$.

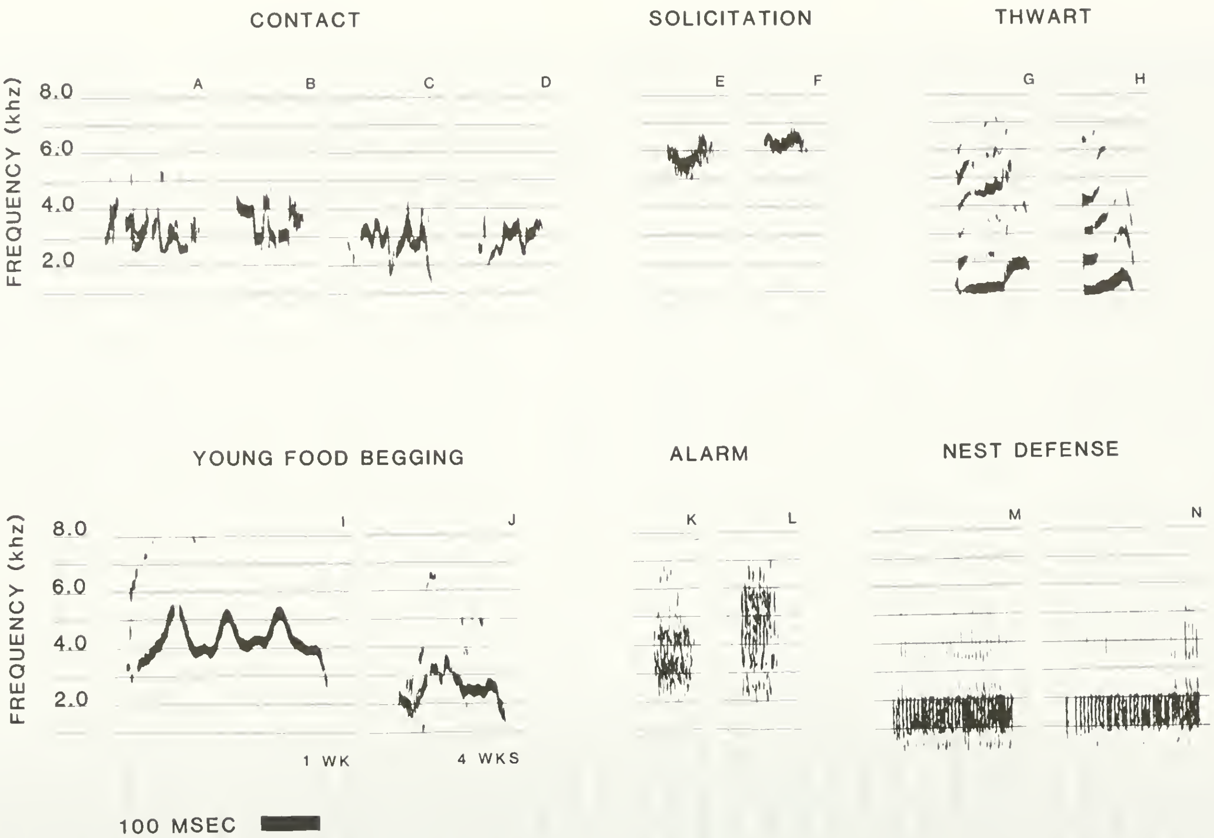


FIGURE 1. Sonograms of 14 calls drawn from the budgeriger vocal repertoire. Each call is from a different bird and given a letter designation (A-N). Time marker is 100 ms. Reprinted from Dooling, Park,

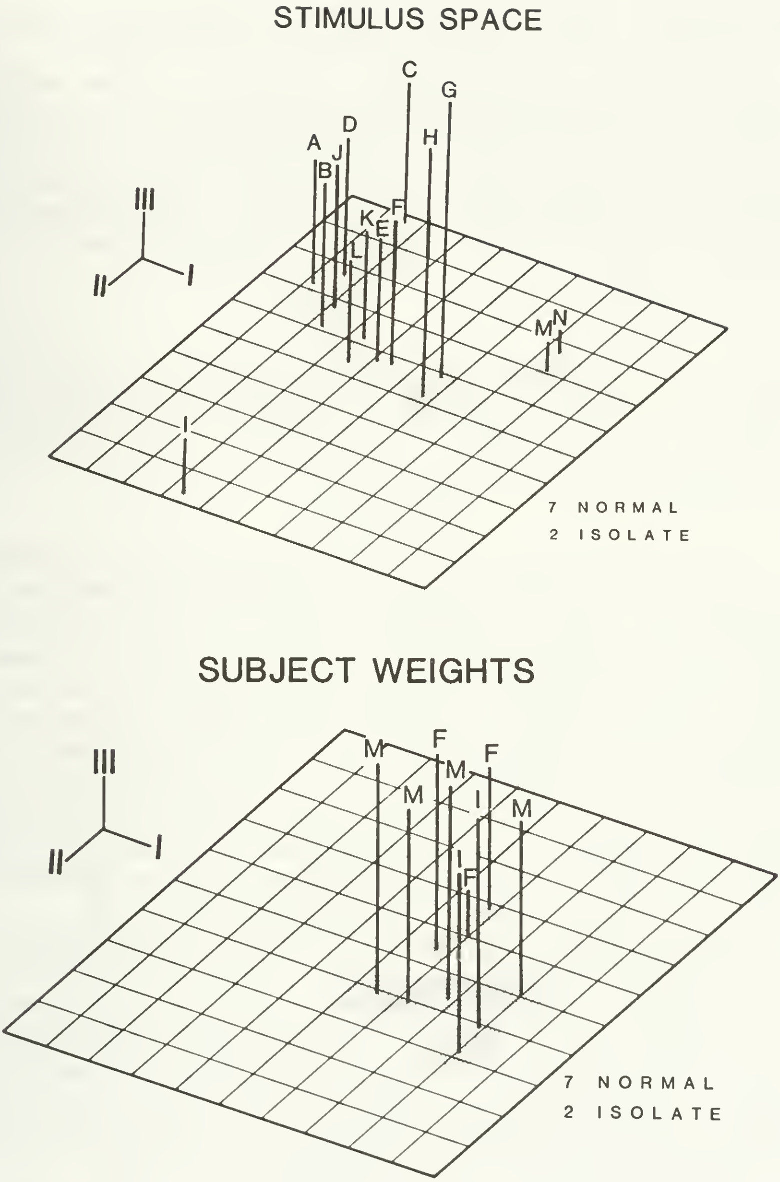


FIGURE 2 A. Three dimensional spatial representation of the perceptual similarity among 14 calls from the budgerigar vocal repertoire. Shading indicates perceptual categories as determined by a cluster analysis. B. Subject weights from the same solution.

EXPERIMENT 1: PERCEPTION OF NORMAL BUDGERIGAR CALLS

The budgerigar vocal repertoire contains a number of functionally and acoustically distinct call types. We have examined the perception of this set of calls by humans and budgerigars in an earlier report (Dooling, Park, et al., 1987). The following experiment compared the two isolate-reared budgerigars with socially-experienced budgerigars on the perception of these complex vocal signals.

Stimuli and Procedures

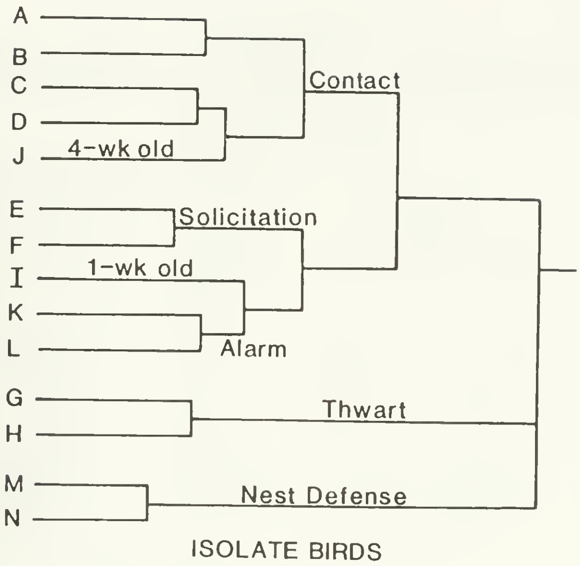
Four contact calls and two calls from each of the other major classes of vocal stimuli in the budgerigar vocal repertoire were used in this experiment. Sonograms of these stimuli are shown in Figure 1.

Results and Discussion

MDS and Clustering. The three-dimensional spatial representation generated by SINDSCAL of the perceptual similarity among these calls for the nine budgerigars is shown in Figure 2A. The distances in this solution accounted for 56.9% of the variance in response latencies with the first, second, and third dimensions accounting for 29.2%, 15.2%, and 12.6% respectively. The subject weights for this solution are shown in Figure 2B. The subject weights space shows that there are differences between male birds and female birds in the perception of these calls (as has been reported earlier for six of these birds in Dooling, Brown, Park, & Okanoya, 1990). But, the subject weights space also shows that isolate-reared birds are different from socially-experienced birds in the perception of these sounds.

The stimulus groupings are similar to those described earlier for both budgerigars and humans (Dooling, Park, et al., 1987). The results of a hierarchical cluster analysis on the average data matrix from the seven socially-experienced birds and the average data matrix from the two isolate-reared birds are shown as dendrograms in Figures 3 (Top and Bottom). Along with the differences in subject weights, the stimulus groupings obtained by a cluster analysis also show differences between normal and isolate-reared birds.

Category Discreteness. The within and between category latency comparisons reveal a similar pattern for both socially experienced and isolate-reared birds. For all birds, the response latencies to pairs of calls drawn from within categories were longer than the response latencies to pairs of calls drawn from between categories. These results are given in Table 1 as the log of the response latency (in centiseconds) times 100. Thus, a value of 150 in this table represents a "raw" or untransformed response latency of about 316 ms.



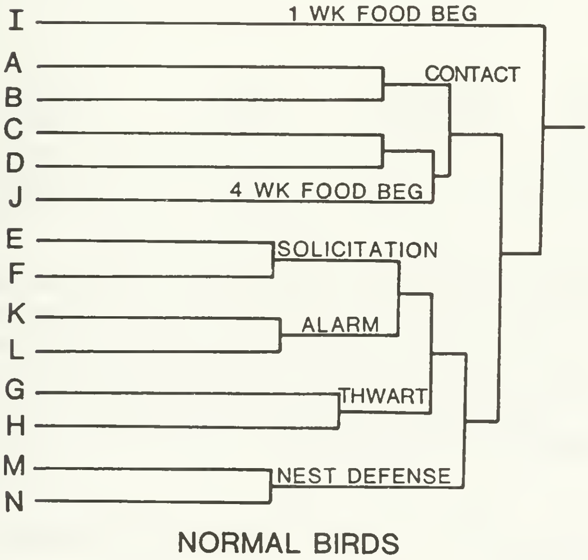


FIGURE 3. (Top). Dendrogram produced by a hierarchical cluster analysis on the latency data from two isolate-reared budgerigars discriminating among the set of 14 calls. (Bottom). Dendrogram produced by a hierarchical cluster analysis on the latency data for seven normal budgerigars.

TABLE 1
Comparison of Response Latencies (Log × 100) in Budgerigars Tested on Calls Drawn From Within and Between Categories (Assorted Calls)

	Call Pairs Relative to Categories				
	Within		*Between*		
Animal	*M*	*SD*	*M*	*SD*	*t*(89)
			Normal Birds		
P8G	154	26.7	124	22.5	4.3*
P34	177	22.5	153	11.9	5.8*
P2Y	178	23.5	170	15.4	1.6
PRW	170	29.0	135	15.4	6.6*
P74	149	40.6	124	13.8	4.2*
P21	111	38.9	73	31.7	4.0*
P39	166	25.6	136	9.7	3.8*
			Isolate-Reared Birds		
PO2	153	32.8	118	13.0	7.0*
PO4	164	21.9	138	8.4	8.1*

*$p<0.01$

Percent Correct Responding. The results of a split-plot factorial design analysis of variance of d' values with two treatments (isolates vs. normals) and five repeated measures (sessions) failed to show a significant difference between isolate-reared ($M = 2.08$) and socially-experienced ($M = 2.65$) birds ($F(1,20)=3.20$, $p>.01$).

The results of MDS show that isolation-rearing affects the perception of complex, species-specific vocalizations in spite of the fact that there was no effect in an overall measure of detection performance, d'. The results of cluster analyses also show that the stimulus groupings for isolate-reared birds are slightly different than those found for socially-experienced birds.

EXPERIMENT 2: PERCEPTION OF CONTACT CALLS OF OTHER SPECIES

The previous experiment shows that isolate-rearing affects the perception of species-specific vocal signals in budgerigars. The present experiment tests whether isolate-rearing affects the perception of a set of complex vocalizations consisting of three sets of distance calls: one set consisting of species-specific calls and the two other sets from

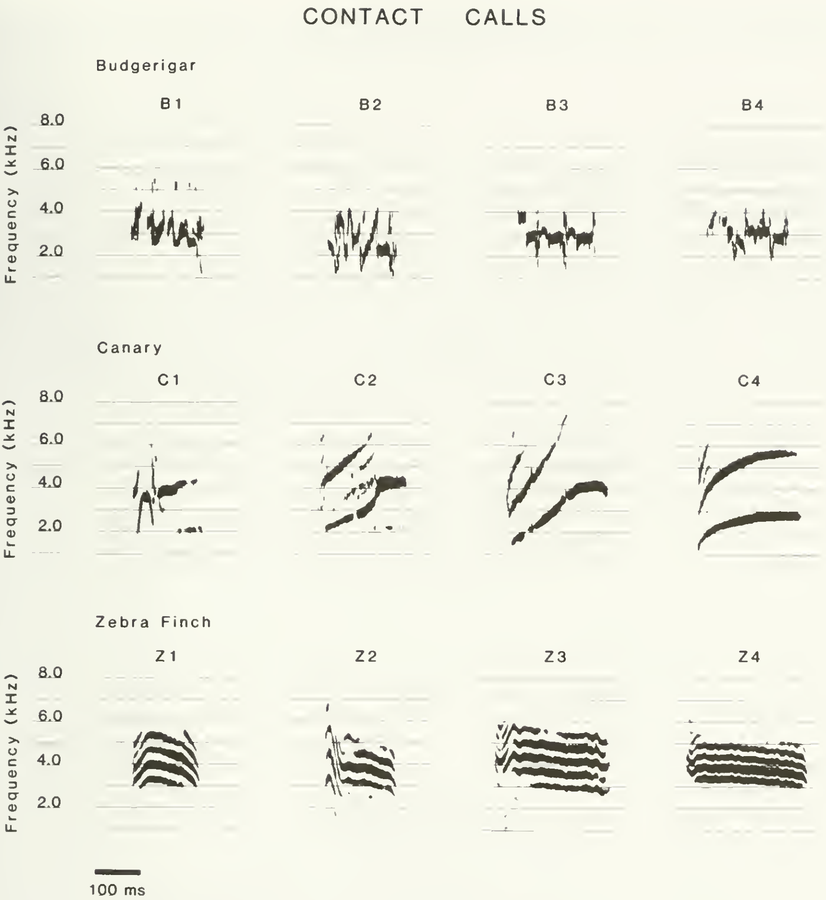


FIGURE 4. Sonograms of contact calls from four budgerigars, four canaries, and four zebra finches. Time marker is 100 ms. Reprinted from Dooling, Park, et al., 1987.

the canary (*Serinus canarius*) and the zebra finch (*Taeniophygia guttata castanotis*).

Stimuli and Procedure

The stimuli used in this experiment were contact calls from four budgerigars, four canaries, and four zebra finches. Sonograms of these stimuli are shown in Figure 4 and are identical to those used previously to test budgerigars (Dooling, Park, et al., 1987). The testing procedures were identical to those used in the previous experiment. All together, two isolate-reared birds and three socially experi-

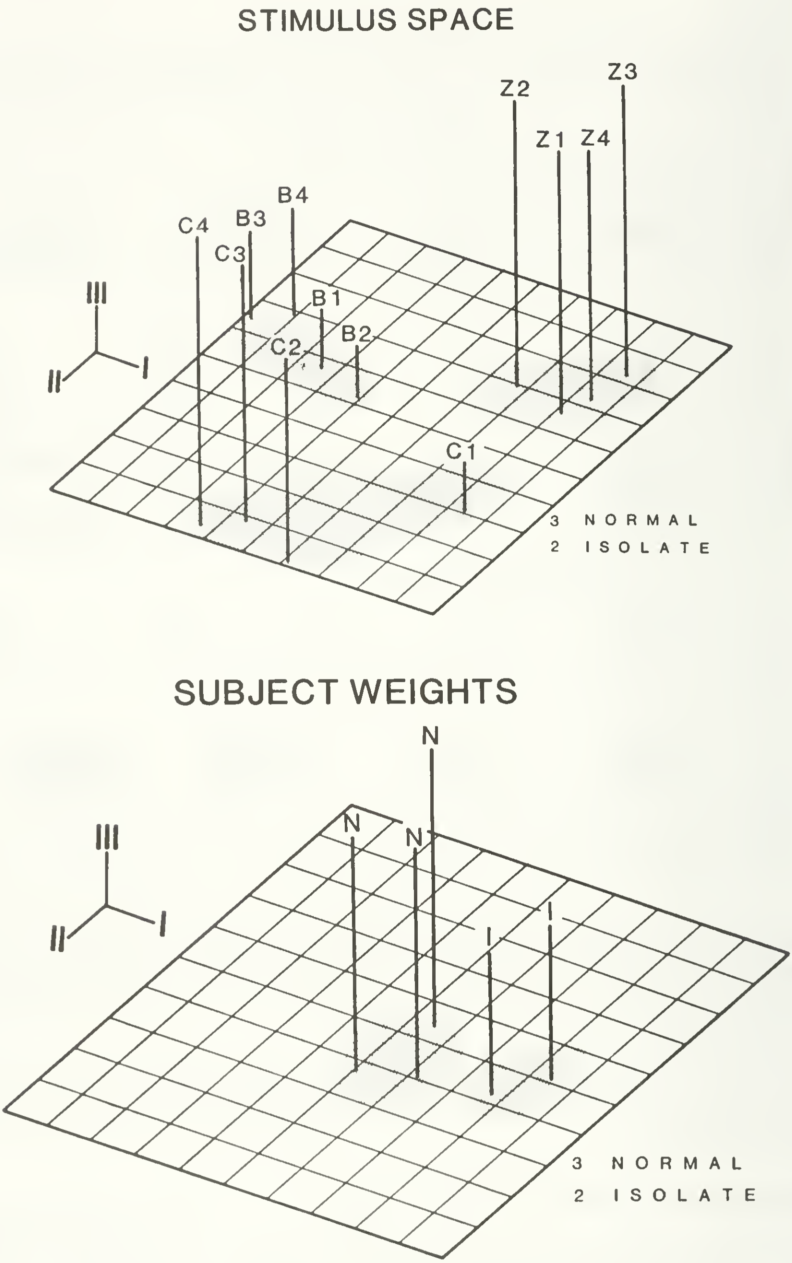


FIGURE 5 A. Three dimensional spatial representation of the set of mixed-species contact calls by three normal budgerigars and two budgerigars reared in acoustic isolation. B. The subject weights for this solution.

enced male budgerigars from the previous experiment were tested on this set of 12 mixed species contact calls.

Results and Discussion

MDS and Cluster Analysis. The three-dimensional spatial representation by SINDSCAL of the similarities among these calls perceived by the five budgerigars is shown in Figure 5A. This solution accounted for 79.3% of the variance in the birds' response latencies with the first, second, and third dimensions accounting for 42.3%, 19.3%, and 17.7% respectively. The subject weights for this solution are shown in Figure 5B. As in the previous experiment, the subject

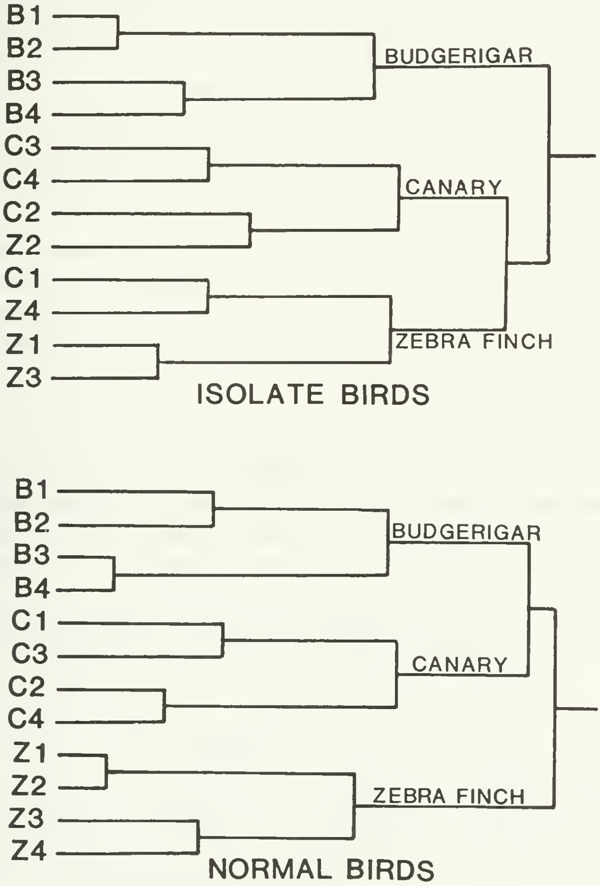


FIGURE 6 (Top). Dendrogram from the hierarchical cluster analysis of the latency data from isolate-reared budgerigars tested on mixed-species calls. (Bottom). Dendrogram from three normal budgerigars tested on same stimuli.

weights of isolate-reared birds are again separate from those of socially experienced birds.

The SINDSCAL solution for all the birds shows that the calls are grouped by species. The results of a hierarchical cluster analysis on the averaged data from isolate-reared birds and socially experienced birds are shown as dendrograms in Figures 6 (Top and Bottom). As in the previous experiment, there is a slight difference in the cluster dendrograms between these two groups of birds. Socially experienced birds group these calls by species. Isolate-reared birds show species-specific calls in one category but also show a slight intermixing of canary and zebra finch call categories.

Category Discreteness. The category-discreteness measure for both normal and isolate-reared birds reveals that the within category response latencies are significantly longer than the between category response latencies for all birds. These results (transformed values) are given for each of the five birds in Table 2.

Percent Correct Responding. An analysis of the d′ values across birds also revealed no difference between the average d′ of isolate-reared birds ($M = 1.90$) and socially experienced birds ($M = 2.22$) ($F(1,12) = 1.73$, $p > .05$).

These results parallel those of the first experiment showing differences in subject weights as well as differences in cluster dendrograms between isolate-reared and socially experienced budgerigars. These differences were found despite no statistical differences be-

TABLE 2
Comparison of Response Latencies (Log × 100) in Budgerigars Tested on Calls Drawn From Within and Between Categories (Mixed Species Calls)

	Call Pairs Relative to Categories				
	Within		*Between*		
Animal	*M*	*SD*	*M*	*SD*	*t*(64)
			Normal Birds		
P21	152	22.1	119	8.1	9.0*
P74	130	18.9	104	9.1	7.7*
PRW	166	22.2	127	12.6	9.0*
			Isolate-Reared Birds		
PO2	149	16.6	124	8.1	8.4*
PO4	140	12.6	122	9.0	6.4*

*$p < 0.01$

tween these two groups in overall detection performance as measured by an ANOVA of d' measures.

EXPERIMENT 3: PERCEPTION OF ABNORMAL CONTACT CALLS

The previous experiments show that isolate-reared budgerigars, though different from socially experienced birds, can discriminate among several biologically-relevant classes of vocalizations which make up the species repertoire and among calls from different species of birds. This experiment was designed to test a more difficult discrimination involving budgerigar contact calls from normal budgerigars, isolate-reared, and deafened budgerigars. Calls from deafened budgerigars are abnormal and even sound abnormal to human listeners while calls of isolate-reared budgerigars, though still abnormal, tend to more closely approximate those of normal budgerigars (Dooling, Park, et al., 1987; Dooling, Gephart, et al., 1987; Dooling, Unpublished Data). The present experiment addresses the question of whether isolate-reared budgerigars perceive the calls from deafened and isolate-reared birds as distinct from those produced by normal budgerigars.

Stimuli and Procedure

The stimuli used in this experiment were contact calls from 10 budgerigars. Sonograms of this set of stimuli are shown in Figure 7. The set consisted of contact calls from two deafened birds, from six birds with normal hearing and social development, and one each from the two birds reared in acoustic isolation. This stimulus set also had been used in previous tests of budgerigar perception (Dooling, Park, et al., 1987). The testing procedures were identical to those used in the previous two experiments. Three male budgerigars from Experiment 1 and the two isolate-reared budgerigars used in both Experiments 1 and 2 were tested on this set of 10 contact calls.

Results and Discussion

MDS and Cluster Analysis. The two-dimensional spatial representation of the perceptual similarity among the 10 contact calls for the five budgerigars is shown in Figure 8A. A two-dimensional solution was used in this case because the third dimension did not improve the variance accounted for by an appreciable amount. The subject weights corresponding to this solution are shown in Figure 8B. The total variance in response latencies accounted for by this spatial solution is 59.7% with the first and second dimensions accounting for

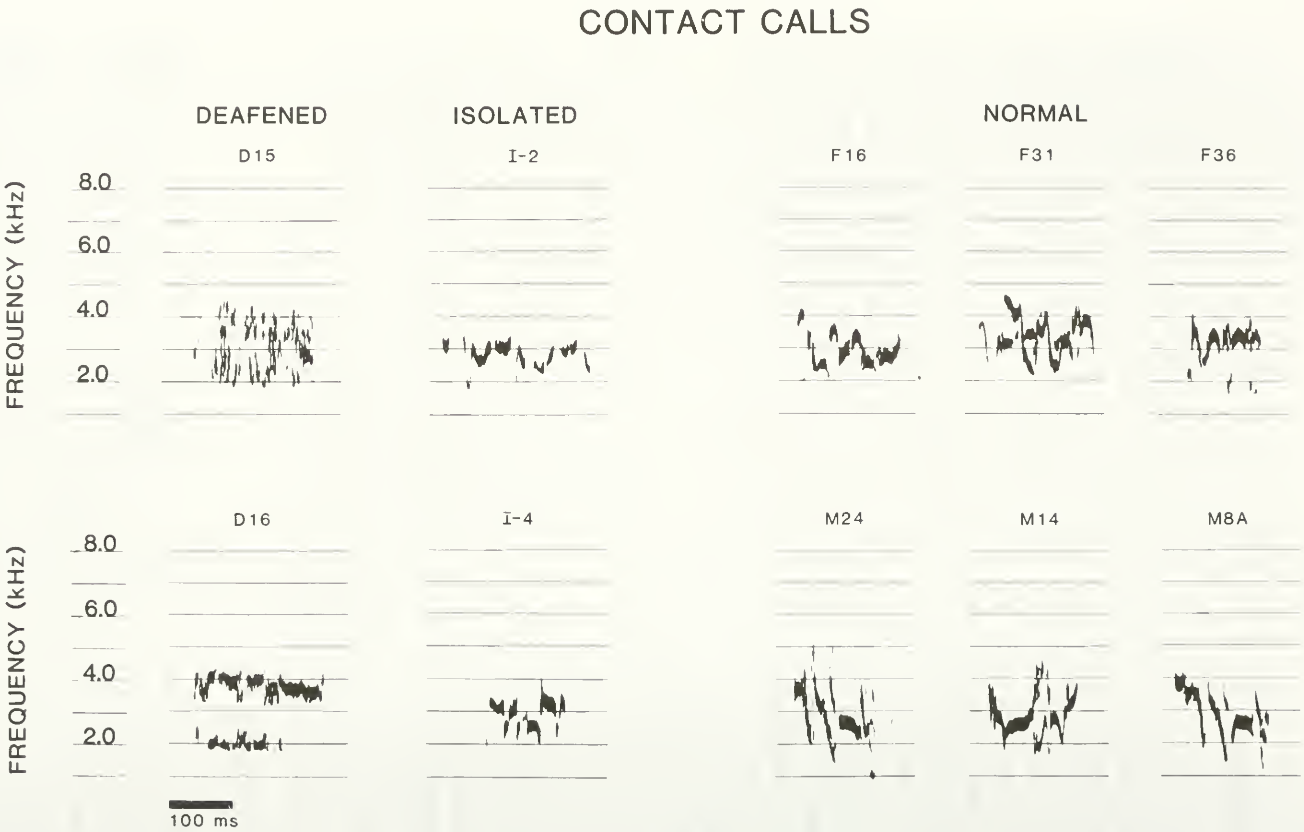


FIGURE 7. Sonograms of calls from normal, deafened and isolate-reared budgerigars. Time marker is 100 ms. Reprinted from Dooling, Park, et al., 1987.

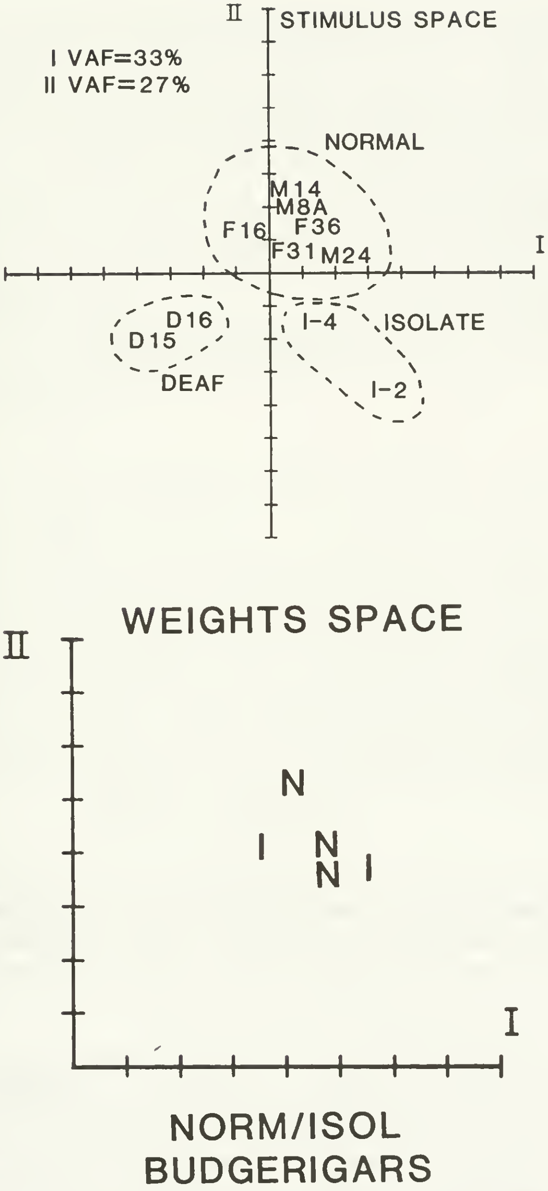


FIGURE 8 A. Two dimensional spatial representation of perceptual similarity among calls from deafened, isolate-reared, and normal budgerigars for all three normal and two isolate-reared budgerigars. B. Subject weights for the same solution.

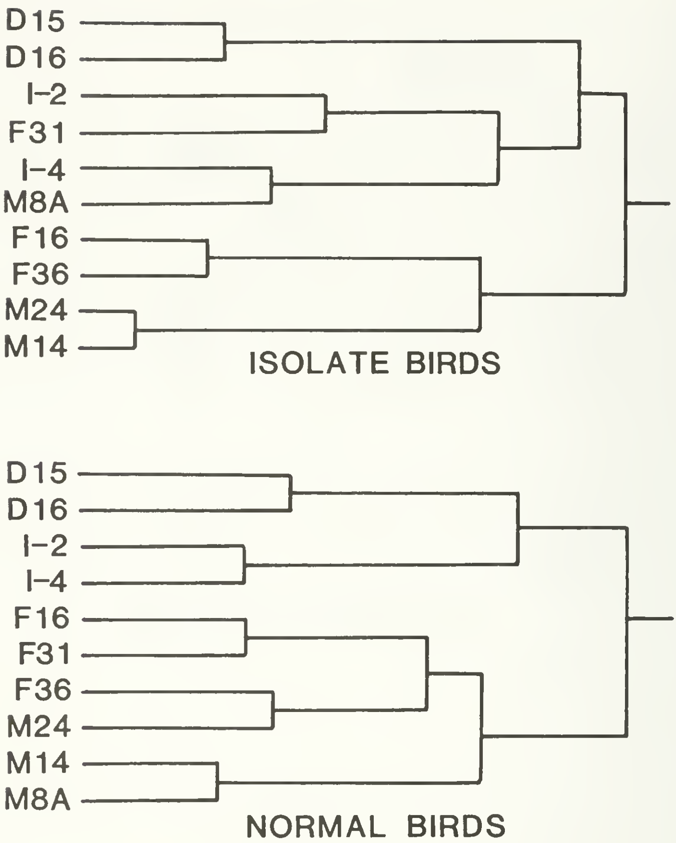


FIGURE 9 (Top). Dendrogram from a hierarchical cluster analysis of data from isolate-reared budgerigars tested on contact calls from deafened, isolate-reared, and normal birds. (Bottom). Dendrogram from three normal budgerigars tested on the same stimuli.

33.1% and 26.6%, respectively. The subject weights space reveals no systematic difference between normal birds and isolate-reared birds.

The results of a hierarchical cluster analysis on the averaged data from socially experienced birds and from isolate-reared birds are shown as dendrograms in Figures 9 (Top and Bottom). By this analysis, there are differences between the two groups of birds. Socially experienced birds show three clusters of calls corresponding to the calls of deafened, isolate, and normal birds. The clusters for isolate-reared birds show an intermixing of calls from socially experienced birds with those from the two isolate-reared birds.

Category Discreteness. On the category discreteness measure for isolate-reared and socially experienced birds, within category latencies are longer than between category latencies for all birds. These latencies (transformed) are given in Table 3.

Percent Correct Responding. The results of an analysis of d′ values across birds revealed no significant difference in the average d′ values between isolates ($M=2.01$) and socially experienced birds ($M=2.85$) ($F(1,12)=3.85$, $p>.05$).

Thus, by a cluster analysis, isolate-reared budgerigars differ from normal birds in the perceptual grouping of stimuli. However, on the basis of subject weights from an MDS analysis as well as overall detection performance, isolate birds are not systematically different from normal birds. In aggregate, then, the differences between isolate-reared and socially experienced budgerigars in this experiment are probably quite small.

DISCUSSION AND CONCLUSION

In previous experiments on budgerigars, we developed a combination of operant conditioning procedures and multidimensional scaling and hierarchical clustering analyses to assess the perception of species-specific vocal signals (Dooling, Brown, et al., 1987; Dooling, Park, et al., 1987). These earlier findings showed that budgerigars, and indeed even humans, tested on calls from different species or on call exemplars from different classes of calls in the budgerigar vocal

TABLE 3
Comparison of Response Latencies (Log × 100) in Budgerigars Tested on Calls Drawn From Within and Between Categories (Abnormal Calls)

	Call Pairs Relative to Categories				
	Within		*Between*		
Animal	*M*	*SD*	*M*	*SD*	*t*(43)
			Normal Birds		
P21	139	12.6	116	9.8	6.9*
P74	132	7.7	118	11.2	4.6*
PRW	166	15.4	144	14.0	4.9*
			Isolate-Reared Birds		
PO2	145	10.7	127	14.4	4.3*
PO4	152	19.3	135	8.8	6.4*

*$p<0.01$

repertoire, show perceptual groupings or clusters that follow closely from what an acoustical and functional analysis of the calls would suggest.

In the three experiments reported here, we extend these previous findings, using the same stimuli, to budgerigars reared in social and acoustic isolation. Both socially experienced and isolate-reared budgerigars could discriminate among these complex vocal signals and there were no differences between the two groups of birds on an overall measure of detection performance, d′. Moreover, we knew from previous experiments that these stimuli form perceptual categories for budgerigars (Dooling, Brown, et al., 1987; Dooling, Park, et al., 1987). In each of the three present experiments both socially experienced and isolate-reared budgerigars showed longer response latencies to discriminate between pairs of stimuli drawn from within categories than to discriminate between pairs of stimuli drawn from between categories. This is a simple demonstration that these stimuli tend to constitute perceptual categories for both groups of birds.

The fact that isolate-reared budgerigars, hearing the sounds which make up the species repertoire for the very first time, show evidence of perceptual groupings for species-specific vocal signals has relevance for the problem of vocal learning. These results, and the fact that humans also tend to categorize these sounds in approximately the same way as budgerigars do (Dooling, Park, et al., 1987), suggest that these stimuli from different functional classes of calls within the budgerigar vocal repertoire are acoustically designed to be easy to categorize. In other words, vocalizations which budgerigars must ultimately learn, and which make up some of the major functional classes of vocal signals in the species vocal repertoire, form acoustically distinct categories. It is largely for this reason that budgerigars perceive these stimuli in roughly the correct manner the very first time they hear them.

But our results also show, by two different measures (i.e., MDS and cluster analysis of response latency matrices), that isolate-reared birds were subtly different from socially experienced birds in the way in which they perceive the relations among these categories of species-specific calls. The subjects weights from MDS show isolate birds separate from males and females with prior social experience with these calls and the dendrogram from a cluster analysis of the data from isolate-reared birds shows an intermixing of some call categories. These perceptual results parallel what we know from studying the vocalizations of this species. Budgerigars reared in acoustic isolation develop both abnormal songs (Farabaugh, Brown, & Dooling, Submitted) and calls (Dooling, Unpublished data) though not nearly as abnormal as those of birds deafened as young (Dooling, Gephart, et al., 1987). Together the results from these experiments provide a compelling case for a role for perceptual learning in the ontogeny of the budgerigar vocal repertoire.

What do these results mean for the newly hatched budgerigar, faced with the challenge of developing a learned vocal repertoire? What does it have to cope with and what does it bring to the task? The two extremes are: (1) that nothing is specified perceptually, the bird's auditory world is a baffling, confusing assortment of acoustic stimulation, but through repeated exposure to the correct stimuli in the right context, the bird learns the appropriate perceptual categories for vocal signals, or (2) that perceptual categories for acoustic and functional categories of species-specific vocal signals are completely specified and perhaps even serve to guide the process of vocal learning. While the final answer to this question will have to await tests of very young animals, the present results from isolate-reared budgerigars are relevant to this issue since they show that, without the correct external auditory models and social situations, budgerigars fail to develop a completely veridical perception of the auditory world of complex vocal signals.

To be sure, the present results must be tempered by the fact that only two isolate-reared birds and only a selected sample of vocalizations from the species repertoire were used in these experiments. Nevertheless, these results are consistent with the notion that learning influences the auditory perceptual processes involved in vocal acquisition in this species. Elsewhere we have shown both socially-mediated perceptual learning of contact call categories in adult budgerigars (Brown, Dooling, & O'Grady, 1988) and evidence of specialized processing of these calls in adult birds (Dooling, Brown, Klump, & Okanoya, In Press). In aggregate, understanding vocal ontogeny in this species will require, in addition to auditory discrimination and categorical perception, knowledge of the important visual and social factors which serve to emphasize the biologically-relevant vocalizations for learning.

ACKNOWLEDGEMENTS

This work was supported by NIH grants DCD00198 and HD00512 to R. Dooling and NIMH Pre-Doctoral Fellowship MH09161 to T. Park. We thank S. Brauth for comments on an earlier draft and B. Gephart for help with the care and testing of birds.

REFERENCES

Brown, S.D., Dooling, R.J., & O'Grady, K. (1988). Perceptual organization of acoustic stimuli by budgerigars (*Melopsittacus undulatus*): III. Contact calls. *Journal of Comparative Psychology, 102*, 236-247.

Dooling, R.J., Brown, S.D., Klump, G.M., & Okanoya, K. (In Press). Auditory perception of conspecific and heterospecific vocalizations in birds: Evidence for special processes. *Journal of Comparative Psychology.*

Dooling, R.J., Brown, S.D., Park, T.J., & Okanoya, K. (1990). Natural perceptual categories for vocal signals in budgerigars (*Melopsittacus undulatus*). In W.C. Stebbins & M.A. Berkley (Eds.), *Comparative perception. Vol II: Complex signals.* New York: John Wiley & Sons.

Dooling, R.J., Brown, S.D., Park, T.J., Okanoya, K., & Soli, S.D. (1987). Perceptual organization of acoustic stimuli by budgerigars (*Melopsittacus undulatus*): I. Simple sounds. *Journal of Comparative Psychology, 101*, 139-149.

Dooling, R.J., Gephart, B.F., Price, P.H., McHale, C., & Brauth, S.E. (1987). Effects of deafening on the contact call of the budgerigar (*Melopsittacus undulatus*). *Animal Behaviour, 35*, 1264-1266.

Dooling, R.J., Park, T.J., Brown, S.D., Okanoya, K., & Soli, S.D. (1987). Perceptual organization of acoustic stimuli by budgerigars (*Melopsittacus undulatus*): II. Vocal signals. *Journal of Comparative Psychology, 101*, 367-381.

Farabaugh, S.M., Brown, E.D., & Dooling, R.J. (Submitted). Analysis of warble song of the budgerigar, *Melopsittacus undulatus*. Part I. Warble syllable repertoires. *Bioacoustics.*

Gibson, E. (1969). *Principles of perceptual learning and development.* New York: Appleton-Century-Crofts.

Kroodsma, D.E., & Miller, E.H. (Eds.) (1982). *Acoustic communication in birds, Vol 2: Song learning and its consequences.* New York: Academic Press.

Kruskal, J. R., & Wish, M. (1978). *Multidimensional scaling.* Beverly Hills, CA: Sage Publications.

Kuhl, P.K. (1989). On babies, birds, modules, and mechanisms: A comparative approach to the acquisition of vocal communication. In R. J. Dooling & S. H. Hulse (Eds.), *Comparative psychology of audition: Perceiving complex sounds* (pp. 379-422). Hillsdale, NJ: Lawrence Erlbaum Associates.

Marler, P. (1982). Avian and primate communication: The problem of natural categories. *Neuroscience and Biobehavioral Reviews, 6*, 87-94.

Marler, P. (1984). Song learning: Innate species differences in the learning process. In P. Marler & H.S. Terrace (Eds.), *The biology of learning*, (pp. 585-616). Berlin: Springer-Verlag.

Marler, P. (1987). Sensitive periods and the roles of specific and general sensory stimulation in birdsong learning. In J.P. Rauschecker & P. Marler (Eds.), *Imprinting and cortical plasticity: Comparative aspects of sensitive periods.* (pp. 99-136). New York: John Wiley & Sons.

Marler, P., & Peters, S. (1989). Species differences in auditory responsiveness in early vocal learning. In R.J. Dooling & S.H. Hulse, (Eds.), *The comparative psychology of audition: Perceiving complex sounds* (pp. 243-276). Hillsdale, NJ: Lawrence Erlbaum Associates.

Mezzich, J., & Soloman, H. (1980). *Taxonomy and behavioral science: Comparative performance of grouping methods.* New York: Academic Press.

Shepard, R.N. (1980). Multidimensional scaling, tree-fitting, and clustering. *Science, 210*, 390-398.