Control of vocal intensity in budgerigars (*Melopsittacus undulatus*): Differential reinforcement of vocal intensity and the Lombard effect

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Call production in budgerigars was studied using operant conditioning. In several experiments, budgerigars were reinforced with food for producing calls that were above or below a criterion level of intensity. This differential reinforcement procedure was successful in controlling vocal intensity in both directions showing that the intensity with which budgerigars produce vocalizations is under voluntary control. In additional experiments, call intensity maintained by food reinforcement was measured both in the quiet and in the presence of various levels of broadband noise. Call intensity in budgerigars increased significantly in noise, paralleling the well-known Lombard effect in humans which is the reflexive increase in speech intensity during communication in noise. Call intensity was measured in broadband noise and in a notched noise (no energy between 1.5 and 4.5 kHz) with the same overall level. Results show that noise in the spectral region of contact calls is most effective in causing an increase in vocal intensity. In aggregate, these experiments show that budgerigars have voluntary control over the intensive aspect of their vocalizations, that they normally monitor their vocal output though external auditory feedback, and, like humans, they exhibit the Lombard effect. © *1998 Acoustical Society of America.* [S0001-4966(98)04402-6]

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INTRODUCTION

While there is an extensive and popular literature on animal models of human speech perception (see, for example, Kuhl, 1989), there has been much less work on animal models of human vocal production. In large part, this is because, with the exception of humans, vocal learning at either the phonological or syntactical level does not occur in mammals. Evidence of vocal learning appears to be widespread among birds, probably occurring in over half of the 9000 known species (Kroodsma and Miller, 1982, 1996). For this reason, there have been a number of studies over the years of the effect of hearing loss on the quality of vocal output in both young and adult birds (see, for example, Konishi, 1963, 1964, 1965a,b; Marler *et al.*, 1972, 1973; Nottebohm, 1968; Nottebohm and Nottebohm, 1971). Results show that permanent deafening (i.e., cochlear removal) has a profound effect on the characteristics of vocal output in both young birds and depending on the species, adult birds as well (Nordeen and Nordeen, 1992; Kroodsma and Konishi, 1991). But, aside from these studies that have examined the effects of complete hearing loss on vocalizations, there has been little study of more subtle interactions between hearing and vocalizations in animals. Understanding these more subtle interactions between hearing and vocalizations is probably essential for the full understanding of vocal development, vocal learning, and acoustic communication in both animals and humans. Profound hearing loss in humans can cause tremendous deficits in speech (Binnie *et al.*, 1982; Lane and Webster, 1991). In humans there are also numerous examples of more subtle interactions between hearing and speech production. One such interaction is the Lombard effect in which speakers adjust their vocal output or speech intensity depending on background noise level (Lane and Tranel, 1971).

As far as we know, there have only been three attempts to look for similar phenomena in animals. Sinnott and her colleagues (Sinnott *et al.*, 1975) showed that two old world monkeys (a female *Macaca nemestrina* and a male *Macaca fascucularis*) could be trained to vocalize for food and increased their vocal intensity when exposed to white noise. Japanese quail (*Coturnix coturnix japonica*) produce louder separation calls when they are visually and acoustically separated from their mate under noise conditions than in the quiet (Potash, 1972). Recent studies of the zebra finch (*Taeniopygia guttata*) also provide evidence that background noise level affects the level of vocal output (Cynx *et al.*, 1997). These studies suggest that some primates and birds may have the ability to monitor their vocal output and adjust their vocal intensity in reference to background noise level.

It is well accepted that changes in speaking level in humans is normally composed of at least two components: a voluntary component and a reflexive component. Clearly humans are able to adjust the intensity of their vocal output in a completely voluntary way in a wide variety of circumstances. But it is also the case that humans adjust their speech intensity in certain situations (increase in background noise, when wearing ear protectors, following temporary threshold shift from noise exposure, etc.) without being consciously aware of making an effort to do so. This ''reflexive'' increase in vocal intensity provides compelling evidence that humans normally monitor the level or intensity of their vocal output.

We have known for many years from observations and recordings under laboratory conditions that budgerigars show considerable variability in the peak intensities of their contact calls (ranging from 80 to 100 dB SPL) (Dooling, 1986; Sadr, 1996). Such variation in calling level both between and within birds suggest that budgerigars can control their vocal intensity. The present series of experiments were undertaken to determine whether budgerigars (*Melopsittacus undulatus*), small parrots native to Australia, can adjust the intensity of their vocalizations both voluntarily and in response to environmental conditions such as noise.

I. EXPERIMENT 1

Previous experiments on vocal learning in a wide variety of species of birds, including budgerigars, have shown that many aspects of the spectrotemporal pattern of vocal output are learned (Dooling, 1986; Farabaugh *et al.*, 1994). The intensive features of bird vocalizations, and whether or not these features are learned, have received far less attention (but see Cynx *et al.*, 1990; Williams *et al.*, 1989). Previous experiments in this series have shown that budgerigars can modify the spectrotemporal pattern of their contact calls for food (Manabe and Dooling, 1997; Manabe *et al.*, 1995, 1997). The purpose of the present experiment was to determine whether budgerigars are capable of changing the intensity of their calls in order to obtain food.

A. Method

1. Subjects

Four adult male budgerigars (*Melopsittacus undulatus*) were maintained at 90% of their free-feeding weights. The birds were obtained from a local pet supplier and maintained in an aviary at University of Maryland, under a light–dark cycle correlated with the season. Each bird was caged separately and had free access to water and grit in their home cages.

2. Apparatus

The apparatus and procedure have been detailed previously and are only briefly described here (Manabe and Dooling, 1997).

a. Experimental chamber. Birds were trained in a small experimental chamber (14 cm wide ×12 cm high ×17 cm deep) made of wire mesh which was then housed in a sound-attenuating box (Industrial Acoustics IAC-1). A LED was mounted on each corner of a 3 cm ×3 cm square piece of foam mounted on one side of the test cage just above the food hopper. An electret condenser microphone (SONY ECM-77B) mounted in the middle of the square foam equidistant from the four LEDs was used to record bird's call. The food hopper mounted on the floor at a depth of 3 cm from the front panel delivered yellow millet.

b. Sound sampling. The output of the microphone was sent to a digital signal processing board (National Instruments AT-DSP2200). The board low-pass filtered the analog data at 80 kHz prior to 16-bit digitization. The digital signal was then low-pass filtered at 12 kHz before further processing. When sound intensity exceeded a pre-set criterion, A/D conversion commenced at a sampling rate of 24 kHz for a total duration of 266 ms.

Serial spectra were calculated using the fast Fourier transform (FFT). Calculations for the first 10.67 ms were carried out while the second 10.67 ms of data were being sent to RAM, and so on. For each successive 10.67-ms segment of sound, a power spectrum was calculated (cf. Manabe *et al.*, 1995, 1997; Manabe and Dooling, 1997). In all, 25 successive spectra were computed constituting the entire 266 ms (i.e., 25×10.67 ms) of sound analyzed from the beginning of each call. Peak amplitude from the whole call was calculated in real time. Each serial spectrum was normalized to a peak intensity of one for subsequent comparison to the values of the stored template.

In practice, three criteria had to be met in order for a sound to be classified as a contact call. The sound had to have a duration greater than 96 ms, at least 70% of the total energy between 187.5 Hz and 10031.25 Hz had to fall within the range of 937.5 Hz–6843.75 Hz, and no individual call components occurring in the initial 74-ms sampling period could be shorter than 21.3 ms. During testing, every incoming sound classified as a call by these criteria was stored in digital form on disk for further analysis. Programs for experimental control and data collection were written in Microsoft C.

B. Procedure

1. Shaping of vocal responses

After the birds habituated to the experimental chamber, they were allowed to eat millet from the floor-mounted feeder. When the birds became accustomed to eating millet from the feeder whenever it was activated, hand shaping of vocal production began. Typical aviary sounds were played in the test cage to induce the birds to call (cf. Ginsburg, 1960). Whenever the bird produced a contact call, the experimenter activated the feeder. When the birds began to emit calls reliably in the absence of the aviary tape, call productions were reinforced automatically. A test session ended when call productions resulted in a total of 48 reinforcements. Since all calls meeting the criterion for a call were reinforced, this phase was called nondifferential reinforcement of call production. Calls from the last three test sessions were used to establish the call intensity used by each bird in the nondifferential reinforcement of call production phase.

2. Differential reinforcement of call intensity

After the bird's performance stabilized in the nondifferential reinforcement of call production phase, differential reinforcement of high intensity calls was implemented. In this procedure, only calls with an intensity above a pre-set criterion were reinforced. Initially, this criterion was set to the mean intensity of all calls produced in the last three test sessions of nondifferential reinforcement (as described above). Once the bird was producing calls that met or exceeded the criterion intensity level on at least 66% of the trials in a given session, the intensity criterion was increased for the subsequent test session. The intensity criterion chosen for this subsequent test session was set to the mean intensity of calls produced in the previous test session. This procedure

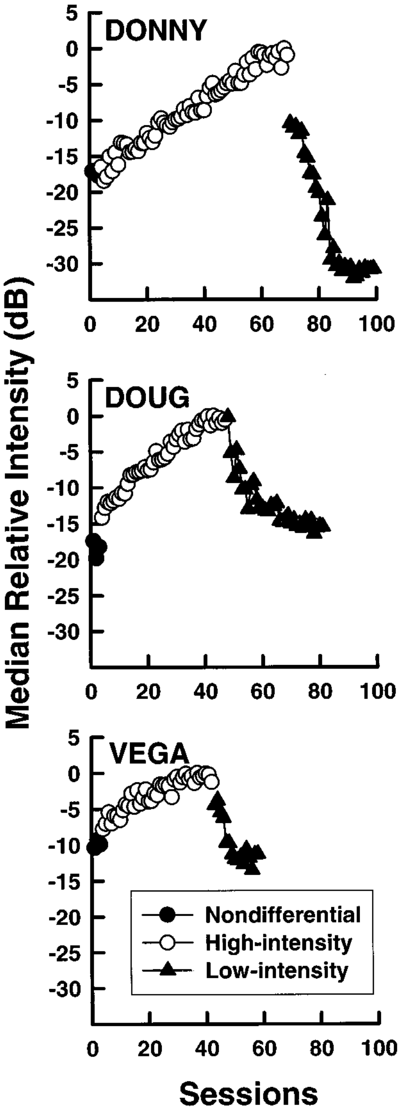

FIG. 1. Median relative call intensities in the nondifferential, differential-reinforcement-of-high-intensity, and differential-reinforcement-of-low-intensity trials. Closed circles show the call intensities produced during nondifferential reinforcement of call intensity, the open circles intensities in differential reinforcement of high intensity schedule and closed triangles intensities in differential reinforcement of low intensity schedules.

continued until there was no increase in intensity over nine successive test sessions. Once this asymptotic level of performance was reached in producing high intensity calls, a second procedure involving the differential reinforcement of low intensity calls was implemented. This procedure was the exact opposite of the first procedure except that the procedure began after the bird reached an asymptotic high intensity call level as opposed to the call intensity level used in test sessions involving nondifferential reinforcement of call production. Now, in the differential reinforcement of low intensity procedure, only calls with intensities below a preset criterion were reinforced.

C. Results and discussion of experiment 1

Figure 1 shows the median call intensity in dB per session for each bird. The call intensities of all birds increased in the high intensity reinforcement condition and decreased in the low intensity reinforcement condition. The relative difference in intensity between two differential schedules was about 30 dB for DONNY, 20 dB for DOUG, and 11 dB for VEGA. A significant difference was found across conditions [one-way repeated measures ANOVA $F(2,1)=9.29$, $p<0.04$]. In a multiple comparison test, the call intensities in the differential reinforcement of high intensity schedule were significantly greater than those produced in either the nondifferential or differential reinforcement of low intensity schedules (Student–Newman–Keuls method; $p<0.05$). On the other hand, there was no significant difference between nondifferential and differential reinforcement of low intensity schedules. In the present experiment, quiet calls under a predetermined amplitude did not trigger the system. Such calls were therefore never reinforced even under a schedule of differential reinforcement of low intensity calls. Therefore, the lower limit of call intensity probably maintained call intensity above a certain level. Subject DONNY showed a large decrease in intensity during differential reinforcement of low intensity compared to the other two birds. Since Donny's call intensity was much higher than the call intensity of the other birds by 2–17 dB, this bird obviously had sufficient room to decrease call intensity.

II. EXPERIMENT 2

In experiment 1, the birds' call productions were sampled with the microphone in a fixed position on the cage panel. Normally the birds would position themselves on a perch along side the floor-mounted food hopper and facing the fixed microphone on the cage panel. But, with the microphone in a fixed location and the bird free to move about within a few centimeters, there are other possible sources of variation in intensity measured at the microphone other than a variation in output from the bird. It might be possible, for instance, for the bird to affect the intensity of recorded calls by moving closer or farther away from the microphone or turning its head. Because we occasionally observed such behaviors in the birds, experiment 2 was designed to measure the amount of variation that could potentially be attributed to the bird's movement relative to the microphone.

To obtain a measure of call intensity independent of head movement, the distance between the bird's beak and the microphone was fixed. This was accomplished by using a small audio FM transmitter and microphone attached to the bird's head with super glue. We compared the variance in call intensity measured by a microphone on the bird's head with the variance in call intensity recorded from a microphone on the front panel, to see how head movement affected measured call intensity.

A. Method

1. Subjects

Three male adult budgerigars (*Melopsittacus undulatus*) were used.

2. Apparatus

a. Experimental chamber. The same experimental chamber was used as in experiment 1 except for a coil antenna made from audio cable mounted just under the ceiling of the test cage.

b. FM Transmitter. A small audio FM transmitter (1.0 ×0.5×0.5 cm) was constructed from a circuit modified from Lancaster *et al.* (1992) for use in bats. The transmitter contained a built-in electret microphone (Knowles Electronics 3068) and a small battery (LR364) so that the bird had complete freedom of movement in the test apparatus. The weight of the transmitter including the microphone and battery was about 1 g and was attached on bird's head by glue during the test sessions. The FM transmissions were monitored with a small FM radio (Radio Shack 12-174), the output of which was sent directly to the DSP board (National Instruments AT-DSP2200). The output level of the FM receiver was calibrated to 0.1-V peak amplitude using a 2-kHz 114 dB SPL pure tone prior to each test session. The tone was produced 4 cm from a microphone on the transmitter. During a test session, contact calls were distinguished from background sounds using the same criteria as described in experiment 1.

B. Procedure

All three birds in this experiment were experienced with the procedure, so shaping of calling behavior for food was not necessary. A transmitter was attached to the bird's head during training sessions. Despite some initial apparent discomfort occasioned by gluing the transmitter to the head, all three birds habituated sufficiently so that useable data could be obtained over the course of an entire test session. Once habituated to the transmitter on its head, the bird was trained to produce a specific call. At first, every call was reinforced if it met the criteria for a contact call as in experiment 1. This phase continued for three sessions, during which the intensity of the bird's calls were measured by a microphone on the front panel of the test cage and by a microphone attached to the transmitter on the bird's head.

C. Results and discussion of experiment 2

The coefficient of variation of call intensities for each bird from a single test session as sampled from both the stationary microphone and the head-mounted microphone are shown in Fig. 2. The variation in call intensity measured by a microphone on the front panel was significantly greater than that measured by a microphone on the head [one-way repeated measures ANOVA $F(2,1)=18.7$, $p<0.05$]. We conclude that up to one-third of the variance in call intensity measured by a microphone on the front panel could be due to the movement of the bird in relation to the stationary microphone.

III. EXPERIMENT 3

The results of experiment 2 suggested that the birds could use more than one strategy to affect the intensity of contact calls recorded by a stationary microphone. To establish, unequivocally, whether birds could increase vocal intensity independent of any small changes in position, we selected one bird from experiment 2 who adapted particularly well to having the transmitter attached to its head for extended testing. With this bird, we repeated the differential reinforcement of high intensity calls used in experiment 1 with the head transmitter in place. We examined call productions both within a test session and across test sessions.

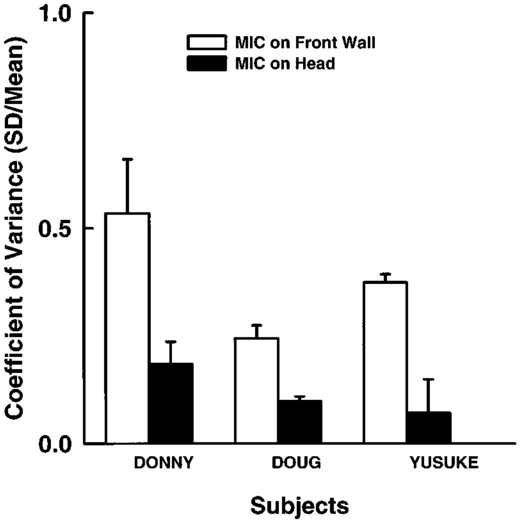

FIG. 2. Coefficient of variance in call intensity. Open bars show coefficient of variances, standard deviation divided by mean call intensity measured by a microphone on the front panel, closed bars coefficient variances measured by a microphone on the bird's head, respectively.

A. Method

One male adult budgerigar (*Melopsittacus undulatus*) from experiment 2 was used.

B. Procedure

This experiment was conducted exactly as described for the intensity increase portion of of experiment 1.

C. Results and discussion of experiment 3

Figure 3 shows intensity changes across trials measured from a microphone attached to the bird's head in the last test session in which the nondifferential reinforcement procedure was in effect (when every call production was reinforced with food) and the first test session when the differential reinforcement of high intensity procedure was introduced (in which only calls with high intensity were reinforced). There was clearly no increase in call intensity during the nondifferential reinforcement of call intensity procedure. On the other hand, there was a marked increase in call intensity within 45 trials of the introduction of the differential reinforcement of high intensity calls.

As in experiment 1, the intensity criterion was adjusted on subsequent test sessions toward higher intensity calling. Figure 4 shows the changes in call intensity across sessions for this bird. Call intensity clearly increased when a procedure involving the differential reinforcement of high intensity calls was instituted thus confirming the results of experiment 1.

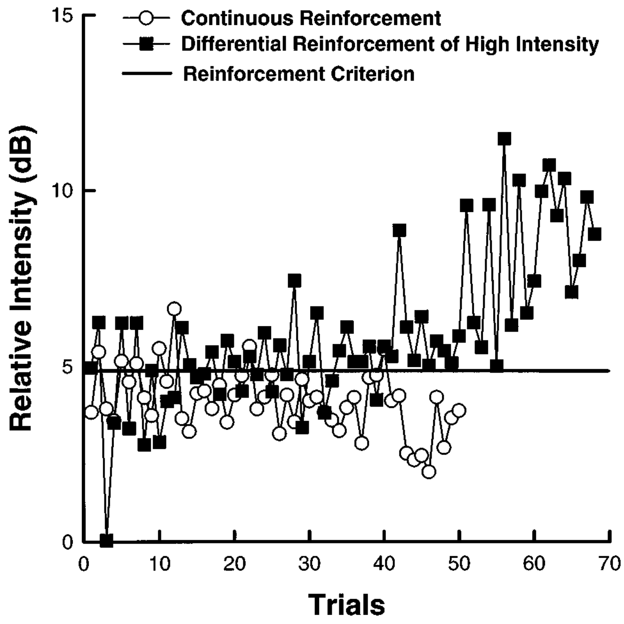

FIG. 3. Relative call intensities across trials in the continuous reinforcement procedure and in differential reinforcement of high intensity procedure using a microphone on the bird's head. Open circles indicate intensities in nondifferential reinforcement, closed circles ones in differential reinforcement of high intensity procedures. The horizontal line indicates the reinforcement criterion.

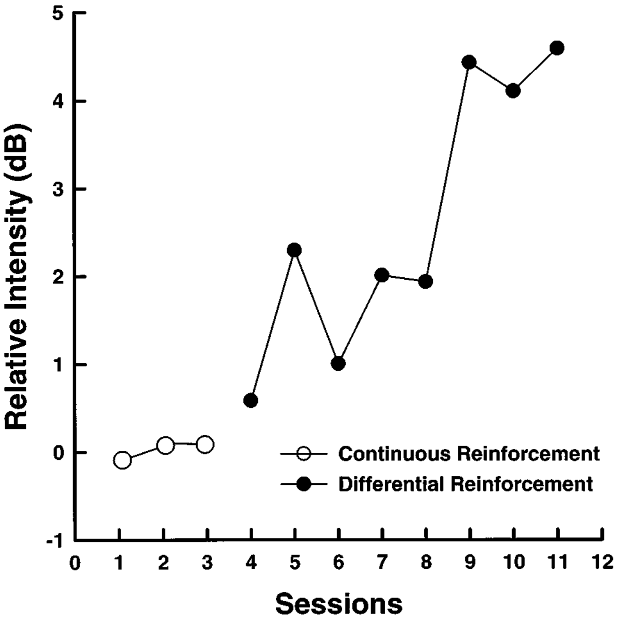

FIG. 4. Relative call intensity in the nondifferential reinforcement and in the differential reinforcement of high intensity procedure. Open circles indicate calls from the nondifferential session and closed circles represent calls from the differential sessions.

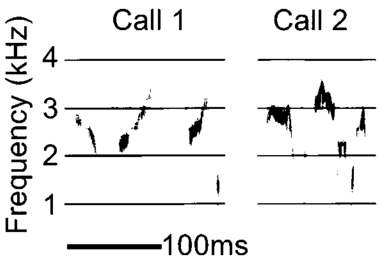

FIG. 5. Sonagrams of calls produced by a bird in the differential reinforcement of high intensity procedure.

Interestingly, examination of the calls produced by this bird revealed that it used a strategy not seen in the birds used in experiment 1. This bird produced at least two different calls during training sessions in experiment 3. The sonograms of these two call types—one longer and one shorter—are shown in Fig. 5. Initially the bird made only the longer call during early training sessions (shown in Fig. 4). It began to produce the shorter call as well only in the later sessions when the intensity criterion was being increased from session-to-session depending on the bird's performance. The intensity of the shorter call was also greater than that of the longer call. One interpretation of this result is that there is a tradeoff in vocal production between intensity and duration. That is, it appears that in order to produce a more intense call, the bird shortened its production. The results of this experiment establish unequivocally that budgerigars can increase the intensity of their vocal productions independent of other strategies such as changes in location.

IV. EXPERIMENT 4

The experiments described above show that budgerigars, like humans, can be directed (or trained) to modify the intensity with which they produce vocalizations. But with humans, there are also clearly instances where the intensity of vocal output is increased in a more reflexive way, as when humans are trying to communicate in a background of noise. This effect, known as the Lombard effect, has been the subject of numerous studies over the years (see, for example, Lane and Tranel, 1971; Dreher and O'Neill, 1958; Picket, 1958; Gardner, 1964, 1966).

A. Method

1. Subjects

Two female and three male adult budgerigars (*Melopsittacus undulatus*) were maintained at 90% of their free-feeding weights as described in experiment 1.

2. Apparatus

a. Experimental chamber. Birds were trained in the same experimental chamber as in experiment 1.

b. Background noise. White noise was introduced into the test chamber as follows. Noise was digitally generated by the DSP board (National Instruments AT-DSP2200) and delivered through a small 1-in. speaker (Panasonic EAS-45P36S) mounted in foam above and behind the recording microphone and pointed at the bird's head when sitting on the perch. In these experiments, the noise was delivered at two levels and was calibrated using a sound level meter and a 1/2-in. microphone (GenRad Incorporation GR 1982 precision sound-level meter and analyzer) before the experiments.

c. Recording and measurement of call intensity. Since sound intensity recorded by a microphone on the bird's head could be affected by movement relative to the speaker that was producing the noise in this experiment, a separate, stationary microphone (Radio Shack 33-1063) described above was used to record the birds' calls. The output of this microphone was fed to a tape recorder (Marantz PMD 740). At the end of each session, vocalizations recorded on tape were analyzed with a Kay Sonagraph model 7800 real time analyzer. The intensity of each vocalization was measured using this analyzer.

B. Procedure

After the birds' performance stabilized, a series of test sessions was conducted in which white noise of various levels was presented during the test session. In the first phase, no noise was presented for the first third of the test session, then a noise was presented at an overall level of 55 dB(A) during the middle third of the session, and finally, the noise was turned off again during the last third of the session (A–B–A test sequence). In the second phase, a no noise condition was alternated with a noise presented at a level of 70 dB SPL in the middle third of the session in the same ABA sequence. In the third phase of this experiment, the noise level alternated between 55 dB and 70 dB SPL. Each alternation involved 25 trials resulting in a total of 75 trials in each test session. During these test sessions, every call the bird produced was reinforced by the experimenter rather than automatically, since the masking noise in the test chamber would sometimes trigger the call recognition system.

C. Results and discussion of experiment 4

Call intensities reported in this experiment were normalized to the highest intensity call produced across all test sessions for all birds. The mean relative intensities of the five birds in this experiment are shown in Fig. 6. The significant effects in intensity were found in all three conditions, in the 0–55–0 dB condition [repeated measures one-way ANOVA; $F(4,2)=5.79$, $p<0.03$], in the 0–70–0 dB condition [repeated measures one-way ANOVA; $F(4,2)=13.3$, $p<0.01$] and in the 55–70–55 dB condition [repeated measures one-way ANOVA; $F(4,2)=7.69$, $p<0.02$]. In a multiple comparison test, there was no significant difference in call intensity between the first and the last noise level (two A's) in the A–B–A sequence (Student–Newman–Keuls method) in any of the three conditions. On the other hand, the call intensities produced in the middle third of the test sessions (the ''B'' noise levels) were all significantly greater than the calls produced in the first or last third of a test sessions (Student–Newman–Keuls method; $p<0.05$). These results show that the intensity with which budgerigars produce their vocalizations is affected by background noise level even when the acoustic dimension of intensity is made irrelevant for the bird obtaining food.

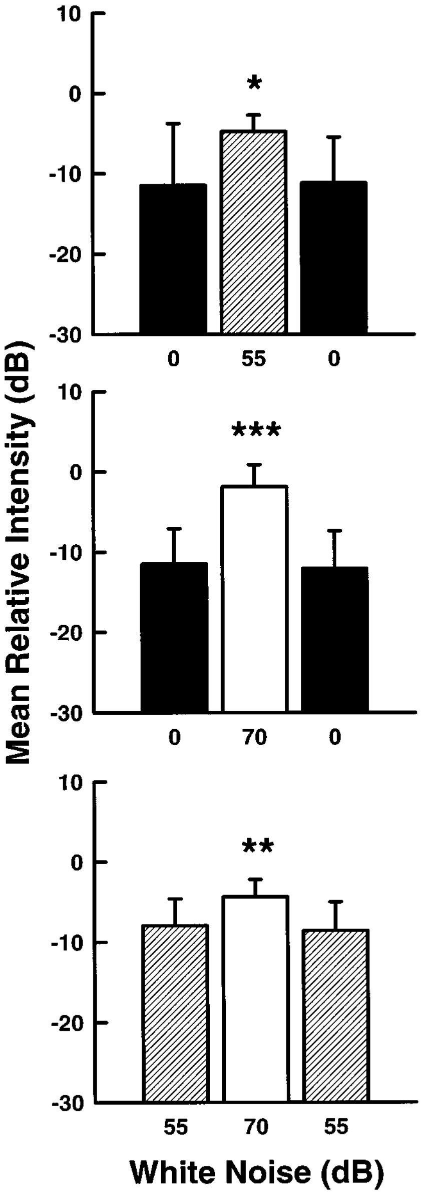

FIG. 6. Mean relative call intensities within a session. The top panel shows relative intensities in the 0–55–0 dB noise condition. The middle panel shows the relative intensities in 0–70–0 dB noise condition and the bottom panel shows the relative intensities in 55–70–55 dB noise condition.

V. EXPERIMENT 5

Experiment 4 showed that budgerigars have a reflexive increase in vocal intensity in the presence of noise. Experiment 5 was designed to further address this issue by examining whether it is overall noise or noise in the spectral region of vocalizations that is effective in producing the Lombard effect. If only noise in the spectral region of vocalizations is effective inducing the Lombard effect, this suggests that budgerigars, like humans, are assessing the signal-to-noise ratio between their vocal output and background noise.

A. Method

Subjects and apparatus were the same as in experiment 3.

B. Procedure

In this experiment, noises of two different spectral shapes, but the same overall level, were generated. One noise was the same as the white noise described above which had

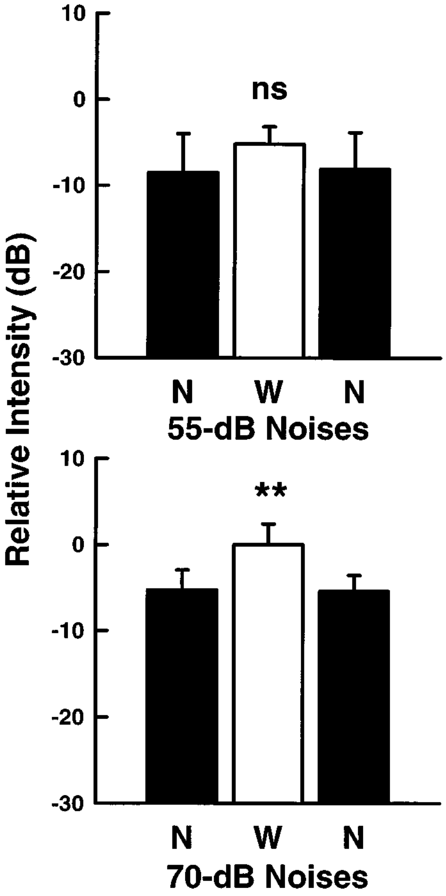

FIG. 7. Mean relative call intensities in notched-white-notched noises condition. The top panel shows relative call intensities produced in the 55-dB noise. The bottom panel shows relative intensities in the 70-dB noise.

a relatively flat spectra. The second noise contained a spectral notch of reduced energy between 1.5 kHz and 4.5 kHz. This spectral notch was greater than 40 dB deep with slopes of 100 dB/octave. The spectral energy of budgerigar contact calls is almost exclusively restricted to this spectral region. Within a single test session, broadband white noise and notched noise were alternated in an A–B–A sequence. The overall sound level of two noises was set either at 55 dB or 70 dB. Each noise condition was tested for 25 trials for a total number of trials in a test session of 75.

C. Results and discussion of experiment 5

The mean relative call intensity of the five birds in the two different sessions is shown in Fig. 7. A significant effect in call intensity was found in the 70-dB background noise condition. [one-way repeated measures ANOVA; $F(4,2) = 6.82$, $p < 0.02$]. A multiple comparison test (Student–Newman–Keuls method) also shows a significant difference in call intensity between notched noise and white noise ($p < 0.05$). On the other hand, there was no significant effect of placing a notch in a noise presented at level of 55 dB SPL [one-way repeated measures ANOVA; $F(4,2) = 2.05$, $p > 0.10$]. These results suggest that it is intense noise in the spectral region of the budgerigar's contact call that is the critical factor for inducing the Lombard effect.

VI. GENERAL DISCUSSION

Understanding the relation between hearing and vocal production in humans depends in large measure on adequate animal models. Hearing loss results in abnormal vocalizations in some birds including the budgerigar (Dooling *et al.*, 1987; Heaton *et al.*, submitted; Konishi, 1963, 1964, 1965a,b). In humans, hearing loss can clearly have a profound effect on the speech of both children and adults (Binnie *et al.*, 1982; Cowie and Douglas-Cowie, 1983; Goehl and Kaufman, 1984; Lane and Webster, 1971; Monsen, 1978a,b, 1979; Waldstein, 1990). The present experiments were designed, in part, to extend the parallels between vocal production in budgerigars and vocal production in humans by examining more subtle aspects of the role that hearing plays in vocal production.

Previous experiments in this series have shown that 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). The present experiments extend these findings by showing that budgerigars can also be trained to control the intensity of their vocal output just as they can control the spectrotemporal aspects of their complex contact calls. Additional experiments on call production in the presence of background noise also suggest that budgerigars demonstrate a Lombard effect—an increase in vocal intensity in the presence of a background noise.

The Lombard effect, even in humans, is probably the result of very complex processes and it is worthwhile to consider the possible mechanisms that might underlie this specific phenomenon in budgerigars and the general problem of voluntary control of vocal intensity in birds. The experiments in this paper support a case for budgerigars acoustically monitoring their vocal output and making adjustments on the basis of auditory feedback. Other explanations are possible. Most alternative explanations—which we consider unlikely—will probably require additional experiments to resolve. For instance, placing a notch in masking noise in the spectral region of contact calls provides strong evidence that it is energy in the spectral region of the contact call, rather than outside it, which is effective in inducing the Lombard effect. Additional controls might include a systematic investigation of spectral notches placed in other regions of the background noise. Another issue is the extent to which budgerigars can increase or decrease their vocal intensity without auditory feedback. It should be possible to train a bird to change its vocal intensity using operant conditioning, deafen the bird by extirpation of the basilar papillae, and see whether increases and decrease in vocal intensity are still possible under operant control. Although kinesthetic and proprioceptive feedback from the vocal production apparatus could conceivably continue to guide vocal production, such feedback pathways have not been well described in birds. It is well known that deaf humans, even those born deaf, can be trained, albeit with difficulty, to modulate the intensity of their vocal output (Martony, 1968).

In partial support of the hypotheses about nonauditory feedback, recent experiments on vocal production following treatment with the ototoxic drug kanamycin in budgerigars (which induces extensive but temporary hearing loss) show that call structure is affected by drug-induced hearing loss and that this structure recovers considerably well before significant hearing recovery has occurred (Dooling *et al.*, 1997). This observation argues either for some kind of alternative, non-acoustic feedback in maintaining call phonology or, perhaps, some kind of precise auditory-vocal memory that requires little veridical sensory input in order to maintain well learned behavior patterns.

Another issue is the extent to which birds are stimulated by the addition of background noise to call more frequently and/or produce louder vocalizations independent of external auditory feedback. It is common knowledge among aviculturists that low level background noise such as running water, etc. can be used to elicit calling from birds. Although we did not observe any such tendencies in our operant situation, whether such a phenomenon may have influenced our results simply cannot be determined. Taken together, we think that the results from tests with different noise levels, coupled with the effect of using noise with a notch in the frequency region of vocalizations provide support for the fact that it is the level of auditory feedback (rather than the change in signal-to-noise ratio through auditory feedback) which is the mechanism by which background noise leads to an increase in vocal intensity.

A final issue concerns the fact that several different strategies were employed by budgerigars to affect the intensity of calls as recorded from a stationary microphone. The most obvious strategy was to increase and decrease the intensity of their vocal output. But this strategy in experiment 1 was probably also combined with the second strategy, which was for the bird to alter its location with respect to the stationary microphone. As evidence, consider that the amount of intensity increase for budgerigar DOUG was about 15 dB in experiment 1 but only 5 dB in an identical procedure (experiment 3) when a transmitter was attached to his head. Moreover, a detailed analysis of the call structure produced by this bird across test sessions, revealed yet another possible strategy in that the bird eventually changed call types. In other words, in later sessions, when the bird was producing the highest intensity calls, it was using a different call type. There are several possible interpretations of this latter finding. One is that there is a trade-off between intensity and duration as has been described for humans, such that producing a more intense call requires producing a shorter call. Another possibility is that particular call types that are restricted to a particular intensity may have evolved or developed under functional exigencies. Thus reinforcing the bird for producing a higher intensity call may simply induce it to select a more intense call from its repertoire. Such a strategy could be combined with one of moving closer or further away from a stationary microphone as in experiment 1.

Finally, we think these results are interesting for several reasons. Whether budgerigars monitor their vocal output in the same manner as humans is a critical issue in trying to develop an animal model for understanding the relation between hearing, vocal development, and vocal learning. Birds in general, and budgerigars in particular, are important to consider in the context of such a model because they exhibit the phenomenon of hair cell regeneration and the return of auditory function following hair cell replacement. Budgerigars, like humans, also show remarkable behavioral plasticity in being able to learn new species-specific vocalizations throughout life. Thus, these birds may provide a unique animal model with which to both assess the effects of temporary hearing loss and hearing restoration on vocal output in humans. Such a model system may therefore have particular relevance for the study of the auditory and vocal sequella of cochlear implantation.

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