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Effects of Continuous Noise on Avian Hearing and Vocal Development

(single-unit recording/noise-induced deafness/auditory feedback/masking noise/vocalization deficits)

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ABSTRACT Continuous loud noise was used to mask auditory feedback from vocal behavior of male canaries. Single unit techniques demonstrate partial deafness after noise exposure. Longer exposure caused greater deficits, with losses of high-frequency sensitivity. Males raised in noise to 40 days of age, then deafened surgically, thus totally deprived of auditory feedback from vocalization, developed significantly fewer song syllables than birds similarly raised but left intact, to mature in quiet sound-insulated chambers. Males left longer in noise, to sexual maturity at 200 days of age, sang at first like surgically deafened birds, but then increased their song syllable repertoire after noise termination. Thus, in spite of the considerable deafness resulting from noise exposure, the deficit in syllable repertoire was corrected, presumably as a result of restoration of the birds' ability to hear their own song.

Auditory feedback is important in the development of avian vocalizations. While certain species deafened early in life develop a normal repertoire, such as chickens and doves (1, 2), in others the vocalizations developed after early deafening are highly abnormal. Since the latter only develop normal song by learning from an adult model, abnormality after deafening is expected. However, the abnormalities are often much greater than those emerging if the intact young are prevented from hearing adult models (3–9). Auditory templates have therefore been postulated, to which the bird matches its own vocal output during development (10–12). For analysis of the role of auditory feedback in avian vocal development, deafening by bilateral removal of the cochlea is the method used.

Surgical deafening as developed by Schwartzkopff (13) and Konishi (3) has the drawback of irreversibility. A technique of reversible masking would permit separation of effects on development from those on mature performance and allow study of the functional significance of auditory feedback from developmental stages in early singing. To this end, we conducted experiments on vocal development of birds raised in loud noise. To interpret the results it was also necessary for us to determine the degree of hearing damage caused by noise exposure.

MATERIALS AND METHODS

The technique of recording the activity of single auditory neurons is a powerful tool for determination of auditory thresholds in normal, as well as in partially deafened, animals. The response of a neuron in the lower part of the auditory pathway is a function of sound frequency and intensity. Each neuron is most sensitive to one frequency, called here the characteristic frequency of that cell; the same neuron is progressively less sensitive to frequencies above and below the characteristic frequency. Different neurons have different characteristic frequencies. With one individual, the thresholds of different neurons can be plotted against their characteristic frequencies. The resultant distribution closely resembles the behavioral audiogram, with all of its species-specific characteristics (14–16).

When the normal neuronal thresholds for different frequencies and the orderly distribution of units in the cochlear nucleus according to their characteristic frequencies are known, shifts in single-unit thresholds can be detected systematically for the entire range of audible frequencies with ease. This method was used as a basis for determining the auditory sensitivity of canaries (*Serinus canarius*), exposed to loud noise for varying periods. Eight canaries exposed to noise and several normal canaries were subjected to "blind" neurophysiological testing by Konishi at Princeton University.

For the single-unit recording, birds were anesthetized with urethan. The floor of the fourth ventricle was exposed by removal of the cerebellum, leaving a large part of the cochlea nucleus visible. The avian cochlear nucleus consists of two major parts: nucleus magnocellularis and nucleus angularis. Since auditory neurons are more clearly arranged according to their characteristic frequencies in the nucleus angularis than in the other nucleus, single units were recorded from the former, with tungsten microelectrodes. These microelectrodes were placed on desired points in the nucleus, the head having been secured in a holder-electrode carrier assembly, under a Zeiss operating microscope. The stimuli were tone bursts 100 msec in duration. Sound was delivered by an open loudspeaker placed 20 cm from the bird's head. Sound pressure levels were measured at the position of the bird's ear with a calibrated 12-mm B & K condenser microphone in combination with a General Radio Type 1900-A Wave Analyzer. The thresholds and characteristic frequencies of auditory neurons were judged by the rate of discharge as monitored both visually and acoustically. For threshold determination the stimulus intensity was lowered until stimulus-locked variations in the number of spikes disappeared. All determinations were conducted in a sound-proof room.

Breeding pairs of canaries from an inbred strain of Belgian "Wasserschlager" were placed within acoustically insulated chambers (IAC model AC-1) in wooden cages, with white noise broadcast through an array of three 5-inch (12.5-cm) loudspeakers on one end of the cage. The birds were subjected to a total sound pressure level of 95–100 dB(B) (reference 0.0002 dyne/cm^2) at 20 cm from the speakers, set with a General Radio Type 1551-C Sound Level Meter. This pressure level

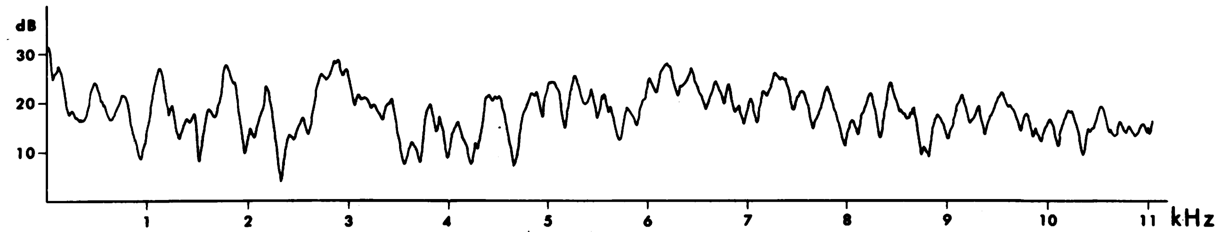

FIG. 1. Frequency spectrum of noise expressed in relative amplitudes of 50-Hz band components. Canaries were exposed to this noise at a total sound pressure level of 95–100 dB (0.0002 dynes/cm²).

corresponds to about 90–95 dB above the auditory threshold of canaries at their most sensitive frequencies. The frequency spectrum of noise under these same conditions was determined by a General Radio Recording Wave Analyzer (Types 1900-A and 1521-B) in conjunction with a calibrated 12-mm B & K condenser microphone (Fig. 1). Although the frequency spectrum was not entirely flat, it covered the hearing range of the canary and was not heavily weighted in any one part of it.

About 70 young birds were raised by their parents to independence (about 40 days after hatching) under these conditions. At this stage they were separated and sexed by laparotomy. The males were placed in one of three conditions, to remain there until they became sexually mature and began to sing at about 200 days of age. Five males in one group were surgically deafened immediately by bilateral removal of the cochlea. The operation was performed by Prof. Nottebohm of the Rockefeller University. These birds were presumed to lack any auditory feedback whatsoever from their own vocalization, thus subjected to the most complete auditory deprivation yet accomplished with birds. A second group of nine males removed from the noise at about 40 days were then housed in quiet acoustical chambers either singly or in pairs, and again left until sexually mature. These were controls for the first and third groups, having ample opportunity to receive auditory feedback during the process of song development after noise exposure as nestlings and fledglings. Lastly, a third group of 11 males was left in noise until about 200 days of age, by which time they were already sexually mature and singing. All three groups were subjected to an approximately normal photoperiod cycle bringing them into breeding condition at about the same age. On the assumption that the different treatments might have hindered gonadal development in varying degrees, all birds were implanted subcutaneously with a 10-mg pellet of testosterone propionate on the neck at about 200 days to ensure maximal motivation for singing.

Sound recordings were made of subsong and song of birds

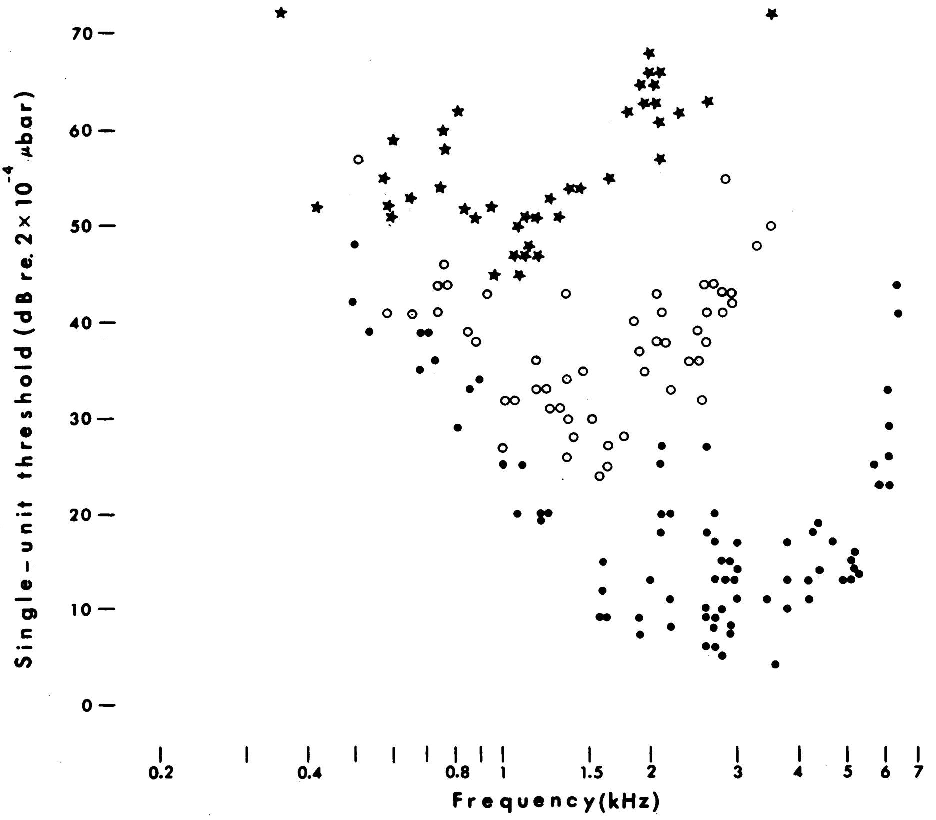

FIG. 2. Auditory sensitivity of normal canaries and canaries exposed to noise. Each symbol indicates the threshold of a single auditory neuron at its characteristic frequency. Units obtained from three different individuals are identified by different symbols: normal canary (*filled circles*), bird exposed to noise for 40 days (*open circles*), and bird exposed to noise for 200 days (*stars*).

in all conditions. Selected samples were analyzed sound-spectrographically by the Kay Electric sound spectrograph (model 6061B) and the Federal Scientific "Ubiquitous" Real Time Spectral Analyzer (model UA7B). The resulting analyses were then subjected to several different measurements, only one of which will be referred to here, namely, the syllable repertoire size. For this purpose, analyses of several good quality recordings from the first season of singing beginning at 200 days of age were selected. These were inspected serially; each new syllable type was identified as it was encountered until the number of new ones discovered reached an asymptote. Other samples from the same bird were then inspected in the same way; thus we reached an estimate of the size of the repertoire of different syllable types used by each bird during that singing season. In some cases birds were retained in acoustical chambers through a second season induced by first shortening the photoperiod for about 10 weeks and then bringing them into reproductive condition once more with long days, but without exogenous testosterone. Songs were recorded and analyzed in the same way.

RESULTS AND DISCUSSION

All birds treated with 95–100-dB noise became partially deaf as a result. The deafening involved both a general rise in thresholds and a change in the shape of the distribution of thresholds of units at their characteristic frequencies (Fig. 2). Both effects varied with the duration of exposure to noise. When thresholds of the most sensitive neurons of each bird were compared, those kept in noise for 40 days were 20 dB above normal. After 200 days of noise there was a 50–60-dB loss. The sensitivity peak also shifted towards lower frequencies, the shift being greater in the birds with longer exposure to noise.

Noise seems to have the greatest effect in the upper part of the hearing range. In fact, those areas of the cochlear nucleus that normally contain units for high frequencies did not yield any responding cells in the birds exposed to noise. Low-frequency units were much less affected by noise exposure. As seen in Fig. 2, single-unit thresholds were almost normal below about 1 kHz in the bird kept in noise for 40 days and below about 600 Hz in the individual kept in noise for 200 days. The inner ear hair cells can be selectively destroyed by loud sounds of a particular frequency range (17, 18). However, since the energy of the noise used in this experiment was distributed more or less evenly across the spectrum, the loss of high-frequency hearing is not directly attributable to emphasis on a particular noise frequency, and some other explanation must be sought.

Although not distinguished thus far, hearing was studied in two classes of birds, those placed in the noise as breeding adults and kept there, and those raised in noise from the egg. Thus some subjects received noise early in life, before they were a year old, while others were older, being 1 or 2 years of age before the first exposure to noise. In eight birds selected for hearing studies, no systematic differences relating to the age of exposure have been detected. Thus, in contrast with cats, there seems to be no particular period of increased susceptibility to noise within the age-range studied (19).

Various periods intervened between the removal from the noise and the determination of hearing thresholds, because of the studies of song development. These periods ranged from 1–2 years. While short-term recovery might have occurred, there is no evidence of improved hearing in those birds left for an extra year under quiet conditions. It seems probable that the deficits measured are permanent.

TABLE 1. *Syllable repertoire sizes of male canaries hatched and raised in noise*

	Noise to 40 days*		Noise to 200 days†	
	Then operated 1st season A	Not operated season B	Intact 1st season C1	Intact 2nd season C2
Number of subjects	5	9	11	
Range of syllable repertoires	1–8	6–19	2–6	6–22
Mean number of syllable types per bird	5.0	13.9	3.5	11.4
Standard deviation of the mean	2.74	5.45	1.44	5.28

* *A*. Deafened immediately on removal from noise by removal of both cochleas. *B*. Left intact in quiet acoustical chambers after removal from noise. Both groups were housed either singly or in pairs.

† C1 Songs from the first reproductive season, within about 2 months after termination of the noise. C2. Songs from the second season beginning about 3 months later. In addition to the 11 subjects in noise for 200 days, a twelfth died between the first and second seasons and is, therefore, omitted from the table.

Song development in young males hatched and raised in noise was studied; the effect of the various treatments on the syllable repertoire size at sexual maturity is shown on Table 1. When we compare, first, the two groups that were left in noise for the first 40 days and then either left intact in acoustical isolation or deafened, there is a striking and highly significant reduction in the repertoire size of the surgically-deafened birds—a mean of 5.0 syllable types as compared with 13.9 for the intact birds ($P < 0.01$, *t*-test of independent means). In addition, the deafened birds share with other bird species so treated instability in syllable morphology. The song varied widely in loudness, and sometimes birds that appeared to be singing produced no recordable sound. These qualities were rare or lacking in the individuals left intact after 40 days of noise. This result suggests that the latter could hear their own voices in spite of the 20-dB hearing loss we know them to have suffered. Recorded again 1 year later, the deaf birds showed no recovery of ability to sing as nondeafened birds do.

When we now compare the behavior of males left in noise to about 200 days of age, and then recorded and analyzed during their first singing session, the result is similar. The mean syllable repertoire size of 3.5 is not significantly different from that of the 5.0 mean of birds exposed to noise for 40 days and then deafened ($P > 0.1$, *t*-test of independent means). This finding is consistent with the hypothesis that a level of noise at 90–100 dB is indeed effective in masking these birds' hearing of their own vocalizations. At this stage they were in fact behaving as though deaf and showed little recovery during this first season of singing.

We know that these birds exposed to noise for 200 days suffered a 50–60-dB loss in hearing when measured about a year after removal from the noise. Their high-frequency sensitivity was severely curtailed but, although they were probably deaf above 4 kHz, their hearing range still encompassed most of the frequency span in which the long-term average acoustic power of normal Belgian Wasserschlager canary song falls (16). This loss seems to represent a permanent threshold shift. At the time of song recording, up to 2 months after removal from noise, their thresholds may have been even higher. Mammalian studies of noise effects demonstrate not only permanent threshold shifts, but also temporary threshold shifts that disappear slowly after removal from noise. In chinchillas exposed to 100-dB noise for 7 days, the temporary threshold shifts took 5 days to disappear, less for shorter noise exposures (20). It is thus conceivable that, after noise for 200 days, the canaries suffered both a permanent and also a temporary threshold shift throughout the first period of song recording.

These 11 birds were retained in acoustical chambers and brought into a second cycle of singing some months later. At this time there was a striking change in their behavior. Without exception, every individual developed a larger syllable repertoire than had been used in the first season. The mean number of syllables in the repertoire increased from 3.5 to 11.4 ($P < 0.001$, *t*-test of related means). The increased mean size of 11.4 is not significantly different from the 13.9 means of birds exposed to noise for 40 days with hearing intact ($P > 0.3$, *t*-test of independent means). The ideal comparison would have been with data we did not gather, on controls singing in a *second* cycle. Surgically deafened birds showed no syllable repertoire increase in a second season. We conclude that, notwithstanding the hearing deficits imposed by 200 days of noise, these birds nevertheless have sufficient auditory feedback from their own vocal behavior to restore a syllable repertoire of similar size to the controls.

With levels of singing measured at about 13 cm from a bird's head around 85 dB (reference 0.0002 dynes/cm^2), even a bird with a 60-dB hearing loss should be able to hear some of its own song. The increase in repertoire, taking place several months after removal from noise experienced for the first 200 days of life, is one line of evidence that there is sufficient hearing after noise exposure for restoration of a syllable repertoire size similar to that of controls. There is also evidence that birds left in noise for only 40 days have sufficient hearing for one male to imitate another in spite of their 20-dB hearing deficit. Of the nine males kept in quiet chambers after noise up to 40 days, five were housed singly and four in two pairs. The latter were left together until sexual maturity and were separated only for the purposes of actual recording. Upon analysis of their song it was clear that one or both members of the two pairs had learned songs from the other since each pair's songs were almost identical. Obviously they were able to hear each other well enough for this accomplishment.

We conclude that a 95–100-dB noise is indeed effective in masking a male canary's hearing of his own voice. In spite of a degree of irreversible damage to hearing, correction of at least one abnormality characteristic of deaf birds' songs occurred after termination of the noise. While other problems remain to be explored, such as possible retardation of reproductive development by masking noise, with repercussions for song development, and possible effects of partial deafness on fine structure of song, it seems conceivable that exposure to white noise will prove to be a useful technique for masking auditory feedback from particular phases of vocal development.

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