TEMPORARY DEAFNESS IN BIRDS

BY CHARLES W. BRAY AND W. R. THURLOW

IN 1875 Wurm described a condition, well-known to hunters, of temporary deafness in the Capercaillie (*Tetrao urogallus*). At the climactic points of the mating song the bird, in a paroxysm of muscular effort, opens its mouth widely in a more than usually loud and strident note. During these periods, each lasting 3 or 4 seconds, it fails to react to the sound of nearby gunshots, the shouts of hunters or the noise of breaking branches. A few seconds later, and while still in the rutting ecstasy, marked reactions, even to the slightest noises, occur. According to Wurm, the deafness is "complete" for the few seconds of its duration. No similar temporary blindness or failure of the other senses was observed to accompany the deafness.

A considerable controversy arose over the source of the deafness (see Schwalbe and Ehrlich). One of the most reasonable explanations, from the modern point of view, is that of Ewald. He discovered that when the mouth of the pigeon is opened and closed the pressure of the fluids of the inner ear rises and falls. This occurs, according to Ewald, because the eardrum is attached, by way of the skin of the meatus, to the skin covering the lower jaw. When the skin of the jaw is stretched, as the mouth is opened, it pulls on the eardrum. The pressure so created is transmitted to the inner ear by the columella. Ewald suggested that the temporary rise in inner ear pressure creates a temporary deafness. Thus, he believed, the Capercaillie becomes deaf during its mating song because its mouth is stretched open so widely. Ewald's suggestion seems to have been disregarded by most later authors and the controversy over the temporary deafness continued.

The experiments to be reported here were designed to test Ewald's theory by measuring the effect of opening the mouth of the pigeon (*Columba domestica*) on the sensitivity of the ear of the bird to sound.

METHOD

The electrical responses of the cochlea furnish a reliable method for the measurement of the activity of the inner ear. When the ear of a pigeon is stimulated by sound, electrical changes occur in the cochlea. These vary in accordance with the frequency and intensity of the sound stimulus. Within certain limits the cochlear response mirrors with extraordinary fidelity the characteristics of the stimuli affecting the ear (Wever and Bray, 1936; Bray and Thurlow). In experiments on mammals, it has been shown that the cochlear responses represent a vital activity and that they probably arise in the hair cells of the organ of Corti. It has also been shown that numerous conditions which affect hearing affect the cochlear response in similar ways (see Wever). The response is an excellent index of the functional activity of the peripheral portions of the auditory system.

In the present experiments the inner ear of the anesthetized pigeon was exposed by an operative procedure described in a previous publication (Wever and Bray, 1936). An active electrode, consisting of a small piece of silver foil, was placed on the bone in the neighborhood of the oval and round windows of the cochlea. An inactive electrode was placed in the skin or muscle tissue of the head. The electrical responses of the ear were led from the electrodes through an amplifier to a wave analyzer (General Radio, Type 736A) for measurement. Suitable calibration of the recording circuit permits the statement of response values in terms of voltage at the electrodes.

Tonal stimuli were delivered to the ear of the pigeon by means of a loud speaker and a tube terminating at a standard distance from the ear. Calibration of the stimulus system is in terms of the pressure of the stimulus expressed as dynes per sq. cm. at the ear of the bird.

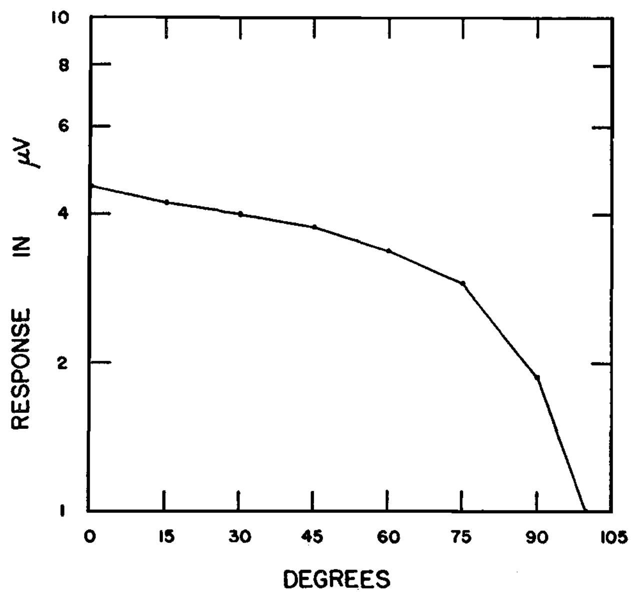
The head of the pigeon was attached, as securely as possible, to a specially constructed holder. A string was tied to the tip of the lower jaw in order to control the size of the mouth opening. It was found that it was impossible to open the mouth widely without simultaneously moving the head as a whole over a distance of 1 or 2 mm. Control tests showed that this general movement of the head did, in itself, affect the measurements of the cochlear responses. The error so introduced was small, amounting on control tests to 1 decibel or less, and can be disregarded for the purposes of the present experiments.

Studies were made on six ears in as many pigeons. Urethane anesthesia was used throughout.

RESULTS

The effect of opening the mouth of the pigeon while presenting a sound of constant intensity to its ear is to reduce the magnitude of the cochlear response. Typical results for a tone of 1000~ (cycles per second) are shown in Text-fig. 1. The tone was presented at a stimulus level of 1.0 dyne per sq. cm. which, with the mouth closed, elicited a response of about 4.5 microvolts. Response values are shown in microvolts on the logarithmic scale of the ordinate. The mouth was pulled open, in steps judged to be 15°, up to the maximum opening that could be obtained. The amount of the opening is shown in degrees on the abscissa. The graph shows that as the mouth was pulled open the response decreased, slowly at first and then more rapidly, until at the maximum opening it had dropped to 1 microvolt. This decrease amounts to 13.1 decibels. Similar effects do not occur in the mammals (cat).

Repeated tests on the same pigeon, and tests on the other pigeons,



TEXT-FIG. 1.—Decrease in the cochlear response as the mouth is opened. The magnitude of the response to a constant stimulus of 1000~ is shown in microvolts on the logarithmic scale of the ordinate. The size of the mouth opening is shown in degrees (estimated) on the abscissa.

invariably showed a reduction in response when the mouth was opened. The amount of the reduction, however, varied considerably from trial to trial, even in the same animal. A number of tests at 1000~, on each of the six birds, gave maximum reductions ranging from 8.1 to over 40 decibels. In other words, the response with mouth open varied, in the several tests, from 40% to something less than 1% of its value with mouth closed. An approximate average for the reduction would be 20 decibels or a drop to about 10% of the value with mouth closed.

It was thought that the variability, or even the effect itself, might arise through reflex contraction of the tensor tympani muscle of the middle ear of the bird. Studies on mammals have shown that the contractions of the tensor tympani and stapedius muscles can cause very considerable reductions in the cochlear response (Wever and Bray 1937, and 1941). Consequently the experiment was repeated on one pigeon after death. The cochlear responses persist, at reduced magnitude, for some time after death, so that they can be measured at a time when all reflex interference must have ceased.

The results of the measurements after death were similar to those obtained before death. On successive trials, with stimulus intensity held constant, the reduction was found to vary from 10 to more than 22 decibels. The effect, therefore, occurs, although still in variable amounts, even when the tensor tympani must be inactive. It is possible that the variability arises from changes in the arrangement of the loose folds of skin around the lower jaw and meatus. On successive trials the skin assumes different positions and the result may be that the ear drum is stretched different amounts.

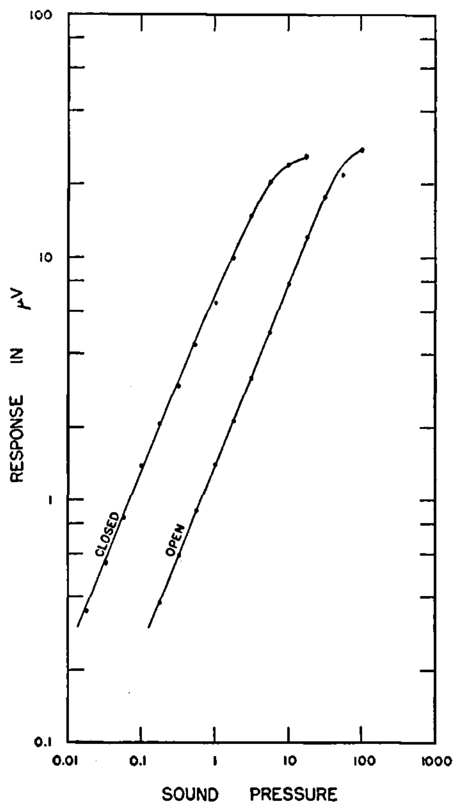
The effect of beak opening upon the responses to various intensities of a sound stimulus is illustrated in Text-fig. 2. A stimulus tone of 3000~ was presented at various pressure levels, as shown on the abscissa. Response magnitudes appear, as before, on the ordinate. The curve marked 'closed' represents what may be called the normal relation between stimulus intensity and response magnitude. At low values, the curve follows a straight-line course, which means that response varies as a power function of stimulus. In this instance the exponent of the power function is about 0.8, so that a tenfold increase in sound pressure produces only a sixfold increase in response voltage.[1]

At the higher levels the power relationship between stimulus and response fails to hold. The response fails to increase in its usual proportion as stimulus intensity is increased. This fact is shown by the departure of the curve from a straight line and its ultimate approach to a maximum. In observations on other pigeons, similar curves have been observed to pass through the maximum and bend sharply down when the stimulus level is carried slightly above that necessary to elicit the maximum response. The response, therefore, actually decreases if the stimulus is increased too far. This effect is associated with permanent injury to the inner ear and for this reason the measurements shown here ceased at the point indicated.

For the curve of Text-fig. 2 marked 'open' the lower jaw was anchored at an angle of about 75° to the upper jaw and the intensity

[1] The exponent of the power function is usually higher than that shown here and on the average is about unity (Bray and Thurlow). In other words there is a simple linear relationship between stimulus intensity and response magnitude in most of the cases studied.

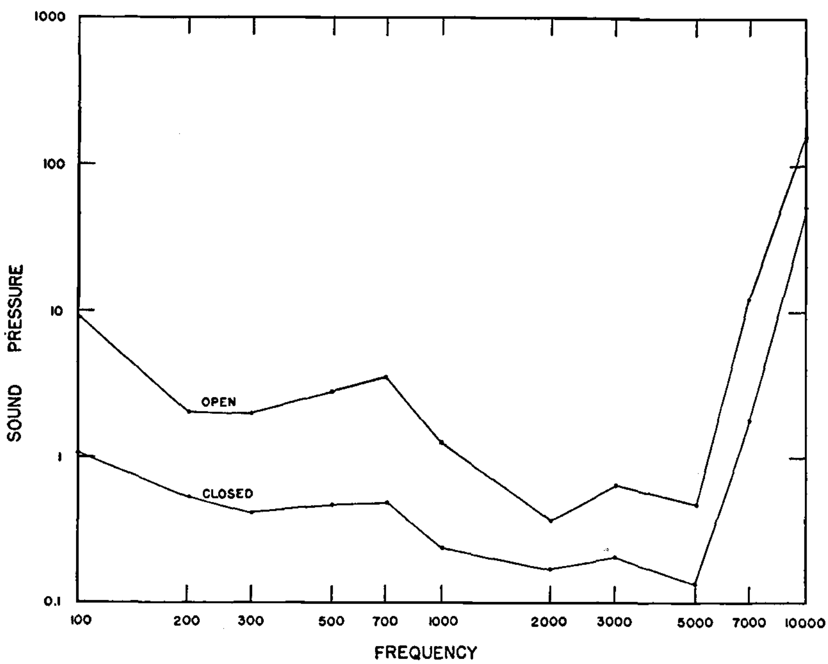
function was measured again. The curve for these measurements is shifted to the right of that for closed mouth. A loss of sensitivity, amounting to about 18 decibels, had occurred. Although sensitivity is altered, the form of the function is essentially unaffected by the change in mouth position. This indicates that the effect is constant, for any level of sound intensity, if it is considered as a reduction in the effective intensity of the stimulus. If, however, one considers the effect as a change in response, it is not constant. In Text-fig. 2 it



TEXT-FIG. 2.—The effect of opening the mouth to 75° on response to a stimulus of 3000∼ at various intensities. Response magnitudes are shown in microvolts on the ordinate and sound intensity is shown in dynes per sq. cm. on the abscissa.

is shown that, at a stimulus value of 0.18 dynes per sq. cm. (the lowest measured point on the curve for open mouth), response drops from 2.1 to 0.38 microvolts, or 15 decibels, as the mouth is opened. At 18 dynes per sq. cm. (the highest measured point on the curve for closed mouth), the drop is only from 26 to 12.5 microvolts, or a little more than 6 decibels. This change in the effect on response follows from the form of the intensity functions if the result of mouth opening is to reduce the effective value of the stimulus. Results of the same character have been observed in the mammals in studies of the effect of contraction of the tensor tympani and stapedius muscles (Wever and Bray 1937, and 1941) and in studies of the effect of air pressure in the middle ear (Wever, Bray and Lawrence).

A study was also made to determine the effect of opening the mouth on different frequencies of sound. Typical results are shown



TEXT.-FIG. 3.—The effect of opening the mouth to 75° on stimuli of various frequencies. The ordinate shows the stimulus intensity, in dynes per sq. cm., required to elicit a standard response of 1 microvolt.

in Text-fig. 3. Eleven tones in the range between 100~ and 10,000~ were presented to the ear of the bird in succession, first with mouth closed, then with mouth open at 75° and, finally, once again with mouth closed. For each frequency the ordinate of the graph shows the sound intensity required to elicit a standard response of 1 microvolt. Points on the curve marked 'closed' are the average value of the two measurements at each frequency with mouth closed. Points on the curve marked 'open' represent the single measurement at each frequency with mouth open. It should be noted that higher points in the graph indicate that greater sound intensities are required to elicit the standard response, so that the higher points mean poorer sensitivity. The curves show that sensitivity is poorer at all frequencies when the mouth is open than when the mouth is closed.

In the case shown in Text-fig. 3 some frequencies seem to be more affected than others. In other cases, however, this difference between tones could not be substantiated. Any difference which may exist between the various frequencies is less than the variability of the effect.

DISCUSSION

The results show that all sounds, within the limits of intensity and frequency here studied, are relatively reduced in intensity as they are conducted to the inner ear of the pigeon, if the mouth of the bird is opened from the closed position. The size of the reduction varies with the size of the opening. The maximum effect is about 20 decibels on the average but the variability around this average is great.

The mechanism responsible for this effect is not entirely clear. As stated above, Ewald suggested that the rise in inner ear pressure, resulting from increased tension on the ear drum, would produce just such an effect. However, in investigations of the mammals, it has been concluded that changes in inner ear pressure do not greatly affect the cochlear response. Changes of the tension of the ear drum, on the other hand, have a very considerable effect on the cochlear response (Wever, Bray and Lawrence). Possibly both factors, tension on the drum and rise in inner ear pressure, coöperate to produce the result found here, the more important factor being drum tension.

The results are of interest in suggesting that in some birds, as in the reptiles, the movements of chewing and drinking must affect hearing. Even the slight opening and closing of the mouth which sometimes occurs in breathing must have a slight effect on hearing. Movements of the jaw are ordinarily so slow that it is unlikely that they stimulate the sensory cells of the ear, especially since birds are very insensitive to sounds of low pitch (Wever and Bray, 1936; Brand and Kellogg). The movements may, however, be expected to produce slight changes in sensitivity. We have observed changes in the cochlear response of about 1 decibel accompanying the jaw movements associated with breathing. Greater reductions may be expected with other mouth activities. Drinking, especially, since it frequently involves a fairly wide mouth opening, should reduce sensitivity considerably.

The results throw further light on the problem of the temporary deafness of the Capercaillie. The wide opening of the mouth in the mating song must reduce sensitivity to sound. However, the size of the reduction in sensitivity, observed in the pigeon, is not enough to explain the 'complete deafness' attributed to the Capercaillie. Although the term 'complete deafness' is difficult to define exactly, a reduction of the order of 20 decibels would hardly produce a failure to react to nearby gunshots.

It is possible that the effect of opening the mouth is greater in the Capercaillie than in the pigeon. Variability of the effect is marked, even in the pigeon. And the differences in the accounts of the structure of the middle ear of different families of birds lead one to expect considerable variability in a delicate mechanical system such as that in question. Mouth opening affects not only the skin of the meatus but the bones to which the drum and columella are attached. It may stretch, passively, the tensor tympani and change the air pressure in the middle ear as well. In any or all of these relations variability is to be expected as we pass from family to family. Thus in the chicken, Pohlman found no reason to suppose that the drum is affected when the mouth is opened. In the pigeon, on the other hand, the change in the eardrum can readily be observed.

It is also possible that other factors enter in to increase the effect in the Capercaillie. The role of activity of the tensor tympani should be investigated, particularly in view of the muscular paroxysm of this bird at the moment of deafness. And the suggestions of the earlier writers, that the deafness of the Capercaillie arises through distraction of the attention or through the masking effect of the bird's own song, take on increased significance if external sounds are reduced in intensity at the critical moments. It is difficult to evaluate the further suggestion of the earlier writers that the meatus of the ear closes, as a result of glandular, or other, swelling combined with the pressure of the posterior process of the mandible. Wurm produced evidence that closure occurs, and was supported by others. The studies of Schwalbe and Ehrlich, on the other hand, indicate that the meatus cannot be completely closed. Pohlman, as a result of observations on the chicken, states that this bird can easily close the meatus.

Complete closure of the meatus would produce a considerable effect on hearing. In the pigeon a slight pressure over the meatus causes a drop of the cochlear response by 40 or 50 decibels. Added to the effects observed here, this would be sufficient to produce a very grave deafness indeed. Incomplete closure has little effect. Further experimentation on the possibility of closure of the meatus is indicated.

It may be concluded that temporary deafness, of noticeable degree, occurs in the pigeon and in certain other birds when the mouth opens. The effect arises primarily through tension on the eardrum.

SUMMARY

Opening the mouth of the pigeon reduces the transmission of sound to the inner ear by an amount which, at the maximum, varies around 20 decibels. The effect occurs for all frequencies and intensities of sound which have been investigated. It is suggested that the chief source of the effect is the tension on the eardrum produced by the opening of the mouth. This result suggests that the auditory sensitivity of the pigeon, and possibly of other birds as well, must vary with the position of the lower jaw. The effect throws further light on the temporary deafness which occurs in the Capercaillie during its mating song.

LITERATURE CITED

BRAND, A. R. AND KELLOGG, P. P.
1939. Auditory responses of starlings, English sparrows, and domestic pigeons. Wilson Bull., 51: 38–41.

BRAY, C. W. AND THURLOW, W. R.
1942. Interference and distortion in the cochlear responses of the pigeon. J. Comp. Psychol., 33: 279–289.

EHRLICH, H.
1907. Zur Frage der Balztaubheit bei Tetrao Urogallus. Anat. Anz., 31: 195–207.

EWALD, J. R.
1889. Zur Physiologie der Bogengänge. Fortsetzung. Ueber Bewegungen der Perilymphe. Arch. f. d. ges. Physiol. (Pflüger), 44: 319–326.

POHLMAN, A. G.
1921. The position and functional interpretation of the elastic ligaments in the middle-ear regions of Gallus. J. Morphol., 35: 229–262.

SCHWALBE, G.
1890. Ueber den Gehörgangwulst der Vögel. Arch. f. Anat. u. Entwick., 1: 42–62.

WEVER, E. G.
1939. The electrical responses of the ear. Psychol. Bull., 36: 143–187.

WEVER, E. G. AND BRAY, C. W.
1936. Hearing in the pigeon as studied by the electrical responses of the ear. J. Comp. Psychol., 22: 353–363.
1937. The tensor tympani muscle and its relation to sound conduction. Ann. Otol., 46: 947–961.
1941. Unpublished observations on the stapedius muscle.

WEVER, E. G., BRAY, C. W. AND LAWRENCE, M.
1942. The effect of pressure in the middle ear. J. Exper. Psychol., 30: 40–52.

WURM, W.
1875. Das Auerwild, dessen Naturgeschichte, Jagd und Hege. Stuttgart. (Not available to the present writers.)
1879. Die deutschen Waldhühner. II. Das Auerhuhn. Zool. Garten, 20: 38–50 (see also p. 240).
1885. Die Taubheit des schleifenden Auerhahnes. Eine Erwiderung. Zsch. f. wissensch. Zool., 41: 728–730.

Princeton Psychological Laboratory
Princeton University
Princeton, N. J.