graphic Office of the Navy Department, especially because four of these diagrams (placed in a square of $2^1/_2$ degrees) cover fairly well the whole region of which Cienfuegos is the center. Unfortunately, the data collected and treated as already indicated do not seem to agree adequately with the events registered at the Observatory of Montserrat. They show nevertheless the same general dominant direction of the wind but do lack one of the secondary maxima. As all our data have been collected in the near vicinity of Cienfuegos, we have preferred to base our deductions on the more detailed records made by the Observatory.

ACTION CURRENTS IN THE AUDITORY NERVE IN RESPONSE TO ACOUSTICAL STIMULATION

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This experiment was planned in the effort to discover an answer to certain fundamental questions of auditory theory through a determination of the relationship obtaining between the character of the response of the auditory nerve and the frequency and intensity of sound affecting the ear. The cat was selected as the experimental animal, and the investigation consisted of placing electrodes on the exposed auditory nerve, and detecting the action currents in the nerve resulting from stimulation of the ear by sound.

Procedure.—The procedure was as follows: After decerebration under deep ether anesthesia by the trephine method, the skull was opened sufficiently to gain access to the right auditory nerve. An electrode, which usually took the form of a small wire hook, was then placed around the nerve, while a second electrode was placed elsewhere on the body, usually on the severed tissue of the cerebrum.

The currents picked up by these electrodes were conducted through 60 feet of shielded cable to a vacuum tube amplifier located in a soundproof room and, after amplification, were led to a telephone receiver. The ear of the animal was then stimulated, and the resulting nerve impulses detected as sound by an observer listening at the receiver in the soundproof room.

Results.—The results so far obtained in this investigation bear upon the question of the relation between the qualitative aspect of the stimulus and the nature of the nerve response. It was found that sound stimuli applied to the ear of the animal set up in the auditory nerve action currents of frequencies corresponding to those of the sound waves. These action currents, after amplification, were audible in the receiver as sounds which, so far as the observer could determine, were identical with the original stimulus.

Speech was transmitted with great fidelity. Simple commands, counting, and the like were easily received. Indeed, under good conditions the system was employed as a means of communication between operating and sound-proof rooms.

A simple tone sounded into the cat's ear gave rise to that tone in the receiver. The observer was able to detect no difference in pitch between this tone and the original stimulus. The range of frequencies to which response can be obtained has not as yet been thoroughly investigated, but the response has been observed to tones as low as 125 and as high as 4100 ~/sec. There was manifested a high degree of tonal discrimination: e.g., if two tones of adjacent frequencies, such as 3200 and 3300~, were given in succession, the observer could report accurately which was the higher.

These facts show, then, that in the nerve as a whole the frequency of response is correlated with the frequency of stimulation.

There was evidence also of a correspondence between the intensity of response in the nerve as a whole and the intensity of stimulation.

The above results are not what have been expected on the basis of recent work on other sensory nerves. The nerve responses recorded by Adrian and others on stimulation of the end-organs of pressure, pain, vision, and muscle-sensitivity, have in every case shown frequency of nerve impulse to be correlated with intensity of stimulation.[1] Here, on the contrary, we have found frequency of impulse correlated with frequency of stimulation.

Because of the divergence of our findings from what is beginning to be accepted as a general law of sensation, and the obvious suspicion aroused by what appears to be a direct correlation of stimulus and end-effect, it is necessary to produce evidence eliminating every possibility of artifact, and to supply checks beyond what have ordinarily been considered necessary in experiments of this nature in order to establish the results as in reality due to action currents in the nerve set up in the response of the ear to sound.

Experimental Checks.—The types of artifact which might conceivably be expected to give rise to the phenomena described are five in number: (1) the production of electrical currents through induction from the source of sound, (2) microphonic action of the elements of the amplifier tubes, (3) mechanical action of the electrodes, (4) movements of the nerve under influence of the cochlea, and (5) electrical changes produced within the sense-organ.

(1) *Induction Effects.*—The entrance of currents into the electrical system through induction need be considered only where electrical or

magnetic sources of sound are employed. While in some of the early experiments audio-oscillators and tuning forks were used, these were discarded in favor of mechanical sources, such as whistles, organ pipes, and the voice, in all the crucial experiments.

(2) *Microphonic Action of the Amplifier Tubes.*—The possibility of microphonic effects due to movements of the vacuum tube elements under the action of the sound was eliminated by placing the amplifier in the soundproof room, with the animal and stimulating sources in another room about 50 feet distant.

(3) *Mechanical Action of the Electrodes.*—Movements of the electrodes in response to the sound might be expected to produce an audible effect in the receiver if these movements were such as to vary the potential between the electrodes, or to alter the inter-electrode resistance in the presence of a constant potential. To check this possibility the following experiments were made:

(*a*) The electrodes were placed on various tissues remote from the nerve: on skin, muscle, the cut surface of the cerebrum, the radial nerve in the foreleg, and the saphenous nerve in the hind-leg; in no case was the response observed.

(*b*) After the death of the animal the response first diminished in intensity, and then ceased.

(*c*) After destruction of one cochlea, the response was noticeably diminished; after destruction of both cochleas the response ceased.

(*d*) The response was more intense if the sound was conducted through a tube into the auditory meatus than if the same sound was made in the region of the electrodes.

(*e*) Holding the vertebral arteries, which, since the carotids had previously been tied, were the only sources of blood supply to the head, produced a rapid reduction in intensity, and in most cases complete cessation of the response. A few seconds after the arteries were released, the response returned.

(*f*) The introduction of a steady direct current into the nerve caused a cessation of the response; removal of the polarizing current restored the response.

(4) *Movements of the Nerve.*—While the above-mentioned experiments would seem effectively to rule out the possibility of mechanical action of the electrodes, they are less effective against the possibility that the cochlea, acting in its recognized rôle as a specially sensitive detector of pressure-variations, was able to transmit these variations mechanically to the nerve, and that the movements of the nerve against the active electrode varied the effective potential of the electrode circuit, and thus gave rise to the phenomena in question. Truly this seems not a very likely possibility, as nerve-substance is hardly an efficient medium for

the transmission of mechanical vibrations, and, moreover, the fibers of the nerve issue from the cochlea not in a single body but in numerous small filaments through their individual foramens in the spiral lamina. But for the sake of conservatism this possibility has been considered as seriously as if it were clearly reasonable.

(*a*) Some evidence against this possibility has already been given in the experiments showing the response to cease on death of the animal, on restriction of circulation, and on introduction of a polarizing current into the nerve. It would seem reasonable to suppose that mechanical action of the cochlea would continue in some measure at least for a short time after death and after shutting off the blood supply, for the tissues should be expected to undergo no very rapid deterioration, and the cochlea is not a highly vascular organ. However, it is conceivable that there is some modification of the cochlea sufficient to impair its sensitivity and thus eliminate the effects. The experiment with the polarizing current is a better check, but here again it is possible to imagine that the current spread to the end-organ and somehow impaired its action, or that the current eliminated the source of inter-electrode potential assumed as necessary for nerve movements to be effective.

(*b*) Non-polarizable electrodes of the silver-chloride type were used as a partial check against the formation of the inter-electrode potential just mentioned. The response continued as before, in unimpaired intensity.

(*c*) The non-polarizable electrodes were both placed on the nerve at a distance of 2 mm. from one another in the further effort to rule out a potential difference between the electrodes by having them on similar and adjacent tissue. Moreover, these electrodes were firmly embedded in an insulating cement, except where they made contact with the nerve, and not only should they be similarly acted upon by movements of the nerve, but they could hardly have been displaced with respect to one another by such movements. Yet in this experiment also the response continued as strongly as before. There was noticed a distortion of speech, however, which may have been due to the reception of diphasic action currents.

(*d*) If the active electrode was in contact with the nerve and the lateral surface of the medulla on one side, and the cochlea on that side was destroyed, there was a noticeable decrease in the intensity of the response; yet the response was still present, and the usual signals received easily; here it could be shown that the effects originated in the cochlea on the opposite side, for they ceased with its destruction. Therefore, the response was transmitted across the medulla, and at an intensity far beyond that reasonable to assume if the transmission were mechanical.

(*e*) The argument of the preceding section is fortified by experiments in which the response was obtained from the anterior surface of the brain stem where it was cut across in decerebration. The response from this region was of good intensity, though noticeably distorted and weaker than that directly from the nerve.

(*f*) In connection with this section, it should be mentioned that both local and general anesthesia (novocaine, ether) have been used in the attempt to reduce or eliminate the nerve response, but without clear success. However, there is no reason for believing that a general anesthetic should act on the nerve so rapidly as to impair its response before the breathing centers are dangerously affected; or that a local anesthetic, however effective it is known to be on end-organs, should act on peripheral nerve rapidly enough to permit a crucial test. In some of the experiments there was evidence of a slight reduction in the intensity of the response, but the observation, resting as it does on a subjective estimate of intensity, is too uncertain to be considered as of great significance.

(*g*) A final check against any kind of mechanical effect was made possible by the discovery that in some instances the electrical spread of nerve current is extensive enough to permit the response to be obtained from tissues adjacent to the nerve. It was found in certain cases that the response could be obtained if the electrodes were placed on a lump of wet cotton resting on the petrous bone in the vicinity of the nerve. However, if a piece of dry collodion film were first placed on the bone so as to make firm contact with it, and the cotton bearing the electrodes placed on the film so as to be insulated from the tissues, the response was absent. Yet if a small wisp of the cotton were picked up with forceps and carried over the edge of the film to make contact with the underlying tissues, the response appeared. The wisp of cotton acted as an effective and positive switch by which the response could be controlled. And since in its manipulation the position of the electrodes as well as the other mechanical features of the situation was undisturbed, the experiment shows definitely that the transmission in question is electrical and not mechanical.

(5) *Electrical Spread from the Sense Organ.*—The evidence above outlined indicates an electrical response correlated with sound stimulation. The evidence does not, however, point definitely to the source of the electrical effects. Though the presumption is in favor of nerve response under the conditions, it is still conceivable that the source of the currents detected is the sense organ and not the nerve. Experiments were made therefore to test this possibility.

(*a*) It has already been mentioned that the response was obtained across the medulla and from the anterior surface of the brain stem. The intensity of the response from these regions was much greater than would be expected if the effect were due to electrical spread from the cochlea. Moreover, it was found that the response could not be obtained from other tissues equally distant from the cochlea, even though these tissues were thoroughly wet with salt solution, and would presumably be as good or better electrical conductors than nerve substance.

(*b*) The active electrode was placed on the brain stem, and the left cochlea removed. Responses were still obtained. The nerve on the right side was then severed; the responses were no longer obtainable from the brain stem. Yet for a time they could still be observed at normal intensity by placing the electrode on the cut stump of the nerve. The electrical conductivity between cochlea and brain stem could not have been much altered by severing the nerve, especially since the tissues still made contact after the transection, and the whole area was kept saturated with salt solution. The inference is, then, that we are dealing, not with simple electrical spread from the end organ, but with the electrical processes accompanying the conduction of nerve impulses.

Discussion.—In view of the positive nature of the checks made, the results of this investigation may be regarded as definitely establishing a correlation between frequency of sound stimulation and frequency of impulse in the auditory nerve. This finding is of importance not only to auditory theory, but also to fundamental questions of nerve physiology, conflicting as it does with correlations of stimulus intensity and response frequency as previously demonstrated in other sensory nerves. What has been regarded as a general law of sensation is thus brought seriously in question.

In question also is the modern formulation of the Helmholtz theory of hearing, which is the familiar place-resonance theory as modified to accord with accepted physiological principles.[2] And it may now be said that this present version of the Helmholtz theory can no longer be accepted; the theory must be subjected to further emendation or elaboration, or else be finally abandoned.

At the same time, other theories of hearing are brought forward in more favorable light; and the demonstration of a correspondence between stimulus-frequency and frequency of response, together with the discovery of a response-frequency in the nerve as high as 4100 ~/sec. makes more reasonable than ever before the outstanding rival of the Helmholtz hypothesis, the so-called telephone theory of audition.[3]

But here one must proceed with caution. The discovery of impulses in the auditory nerve establishing a frequency above 4000 ~/sec. is indeed beyond the usual predictions, as it represents a rate considerably above that previously found in any nerve; but it must be pointed out that a high rate of impulses in the nerve as a whole does not necessarily define the nature of refractory phase and hence rate of response in the individual fibers; it is possible for a high rate to be established by slowly acting fibers going off in volleys.

An opinion on this question must await evidence regarding the response of the individual fibers. Our investigation is still continuing in the effort to analyze in more detail the nature of the response obtained, and thus to secure evidence which may give an empirical answer to this and other questions concerning the action of the nerve, and which may then decide as well the dependent problem of auditory theory.

[1] *J. Physiol.*, 1926, **61**, 49–72, 151–171, 465–483; **62**, 33–51; 1927, **63**, 378–414.

[2] See A. Forbes and A. Gregg, *Amer. J. Physiol.*, 1915, **39**, 229 ff.; G. Wilkinson and A. A. Gray, *The Mechanism of the Cochlea*, **1924**, 175 ff.

[3] As represented, e. g., by E. G. Boring, *Amer. J. Psychol.*, 1926, **37**, 157–188.

MUTATIONS AND ALLELOMORPHISM IN THE GROUSE LOCUSTS (TETTIGIDAE, ORTHOPTERA)[1]

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Five species of the grouse locusts (*Tettigidae*) have been submitted more or less to breeding analyses, as follows: *Paratettix texanus*, more than twenty-three dominant and three recessive, elementary, color patterns; *Apotettix eurycephalus*, twelve dominant, primary patterns and the "normal recessive," or "wild type;" *Telmatettix aztecus*, four dominant and the one recessive; *Tettigidea parvipennis pennata*, six dominant patterns, and *Acrydium arenosum*, more than twenty-five dominant patterns and the one recessive. Symbols, or letters, have been arbitrarily assigned to the several factors for elementary patterns upon their verification. Example, *B*, *F* and *I* represent the factors for the whiteness, yellow stripe and black spot, respectively, *P. texanus*, and *M*, *O*, *Z*, *G* stand, severally, for the factors for prominent patterns in *A. eurycephalus*.[2,6,7]

The so-called "normal recessive," or "wild type" pattern, $+/+$ is common to, and very much the same, in all the species so far examined. The color patterns considered are on the pronota and posterior femora, and appear to be due mainly to the distribution of various colored pigments in the hypodermal cells. The colors are also probably influenced somewhat by the topography of the surfaces and other features of light absorption and reflection. A much more complete study is needed of the chemical, embryological and morphological features of these marvelous, primary and hybrid emergent patterns.

Twenty-six primary patterns, including the "wild type," $+/+$, and