suppose that the light intensity affects anything but the photochemical part of the process. The amount of chlorophyll must also affect this part, and in the same way. However, since the characteristics of the process (sensitivity to temperature and to prussic acid) cannot be similarly altered by changing chlorophyll content and light intensity, it must be supposed that chlorophyll plays some other part in the process, besides its rôle in the photochemical reaction.

TABLE 1

THE EFFECT OF PRUSSIC ACID ON PHOTOSYNTHESIS AT THREE DIFFERENT CONCENTRATIONS OF CHLOROPHYLL

ϵ	HCN CONCENTRATION	MM.³ O_2 PRODUCED	INHIBITION BY HCN
	O		
0.037	9×10^{-6} N	93.1	40%
		56.2	
	O		
0.060	9×10^{-6} N	122.0	32%
		82.7	
	O		
0.083	9×10^{-6} N	171.5	25%
		129.5	

A more detailed presentation of this work is in preparation, and will appear in the *Journal of General Physiology.*

* NATIONAL RESEARCH COUNCIL FELLOW.

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FUNCTIONAL DISTURBANCES OF HEARING IN GUINEA PIGS AFTER LONG EXPOSURE TO AN INTENSE TONE

By MORGAN UPTON*

PSYCHOLOGICAL LABORATORY, HARVARD UNIVERSITY

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I.—Present controversy regarding theories of the perception of sound seems to be mainly concerned with two sharply defined views. One, the "frequency" theory, regards the basilar membrane as a vibrating unit, which responds in whole or in part in a way depending upon the energy of the stimulating force. A stimulus of great energy would disturb a relatively large part of the basilar membrane and a stimulus of less energy would disturb a relatively shorter section beginning at the base of the cochlea and extending upward. Under this theory pitch is correlated with frequency of nerve impulse and intensity with the number of basilar units set into motion by a stimulus. The other, the "place" theory, regards the transverse fibers of the basilar membrane as resonators which are set into motion by the sound waves which correspond to their natural periods of vibration, thus correlating pitch with the place of disturbance on the basilar membrane. The "place" theory in its modern form is derived from the theory of Helmholtz, and includes certain considerations made necessary by the establishment of the "all or none" law of nervous conduction. Helmholtz assumed that the experience of intensity was correlated with the energy of the nerve impulse, but it now appears that such an assumption is untenable.

The results of an experiment by Yoshii,[1] published in 1909, were widely accepted as clear evidence for the Helmholtz theory. In this experiment guinea pigs were exposed to tones of different pitch for extended periods. Histological examination of the cochleas of the animals so exposed revealed definite structural changes which were limited to transverse strips in the organ of Corti and occurring in the order of the frequencies of the tones to which the animals were exposed, with the highest frequency nearest the base of the cochlea. It has been shown clearly (Boring, 1926),[2] that the data obtained in Yoshii's experiment stand just as firmly in support of a "frequency" theory of hearing. Both the amplitude and the frequency of the stimuli used by Yoshii varied and either one might have determined the locus of degeneration.

Although Yoshii's work demonstrates that certain definite structural changes in the auditory mechanism accompany long exposure to intense tones, without *functional* differentiation his results must occupy an equivocal position as regards the two types of theories of hearing. The present experiment was designed with a view to the determination of the functional changes correlated with extended exposure to intense tonal stimuli.

II.—The effectiveness of relatively pure tones as stimuli in the environment of guinea pigs was demonstrated in a preliminary experiment by the establishment of a specific change in the breathing rhythm as a conditioned response to the sounding of a tone. The unconditional stimulus was an electric shock applied to the rear legs of the animals. A tuning-fork oscillator of 600 cycles driving a loud speaker was the source of the tone. The tone presentation lasted through six respiration cycles and the shock was applied at the cessation of the tone. After 250 presentations of the tone and shock in combination, evidence of conditioning was observable in the breathing curve as recorded on a kymograph. The respiration cycles coincidental with the tone and preceding the shock were equal in amplitude, whereas the breathing curve not coincidental with the tone was characterized by wide and constant variation of amplitude. After approximately 500 presentations of the tone-shock combination a respiration cycle of very wide amplitude occurred in the breathing curve coincidental with or slightly later than the end of the tone when the tone was presented without application of the shock. These changes were regarded as clear evidence of the existence in the guinea pig of a mechanism which mediates the reception of pure tones. Tonal differentiation in the guinea pig was demonstrated for tones whose vibration rates differed by 400 cycles. Finer differentiation is very likely possible, but this was close enough for the purpose of the present experiment.

Upon completion of the preliminary experiment two groups of animals were exposed to a very intense tone with a frequency of 600 cycles, for a period of seventy days. Tuning-fork oscillators and a loud speaker served as the source of the tones employed in this experiment. Distances of 24 inches and 96 inches, respectively, separated the two groups from the source of the tone so that each group would be affected by a different intensity.

At the termination of the exposure period the animals were tested for direct responses (i.e., change in respiratory rhythm) to three intensities (low, intermediate and high) of two frequencies (600 cycles and 1000 cycles). Corresponding intensities of the two frequencies were equal.

The low test tone with a frequency of 600 cycles had been used as the original conditioning tone while the high test tone of the same frequency was identical with the tone to which the animals had been exposed. A group of normal animals was introduced as a control. The responses of the members of this group to corresponding intensities of both frequencies were uniformly similar.

A comparison of the responses of the exposed groups with the responses of the control group revealed significant deviations from the normal. Group I (exposed with a 96-inch separation from the source of the tone) gave definite responses to all three intensities of the exposure frequency. Group II (exposed with a 24-inch separation from the source of the tone) gave no responses to any of the three intensities of the exposure frequency. Two of the animals of this group had previously been conditioned to respond to the low intensity of the 600 frequency. An attempt to recondition them to the same tone was unsuccessful.

The sensitivity of the animals in group I to tones of the exposure frequency had evidently been increased, while the sensitivity of the animals in group II to the exposure frequency had been practically eliminated. The control group gave no responses to the lowest intensity of both frequencies. The responses of both groups I and II to the three intensities of the 1000 frequency were uniformly similar to the responses of the control group to the corresponding intensities of both frequencies.

These results indicate that exposure to a particular frequency is accompanied by certain specific changes: first, by an increase of sensitivity to the exposure frequency, and then by a practical desensitization to all intensities of the exposure frequency within a very wide range. The similarity of the responses of all groups to the frequency of 1000 cycles indicates that no general change in the auditory mechanism accompanied exposure to a particular frequency.

III.—From the results of the experiment it may be said that: (1) exposure to an intense tone over an extended period of time is accompanied by a total loss of sensitivity to tones of the exposure frequency within a very wide range of intensities; (2) exposure to an intense tone is not, apparently, accompanied by any change in the sensitivity of the exposed animals to other frequencies.

The results stand as evidence for a "place-pitch" or "resonance" theory of hearing. Such a theory would regard the cochlea as an organ of pitch discrimination. The discrimination would depend upon the vibration of specifically localized transverse strips of the organ of Corti which would be set into vibration by the sound waves corresponding to their natural periods of vibration. Yoshii (1909) found that the width of the strips in the organ of Corti which were damaged by exposure to intense tones varied with the amplitude of the tones. This linear spread over the basilar membrane, with its center at the fibre whose natural period of vibration corresponds to the stimulating frequency, offers an explanation of the perception of intensity. Each increment of energy would result in an increase of amplitude of the stimulus and therefore in a wider spread along the basilar membrane, thus including additional nerve fibres. Upon this assumption the perceived intensity would be a direct correlate of the number of fibres involved in the disturbed section of the basilar membrane.

* NATIONAL RESEARCH COUNCIL FELLOW, Laboratory of General Physiology, Harvard University, Cambridge, Massachusetts.

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