Auditory Adaptation and Its Relationship to Clinical Tests of Auditory Function

By J. D. Hood, Ph.D.

It has been known for many years that fatigue or loss of sensitivity results from prolonged auditory stimulation. The study of this phenomenon has been confined for the most part to the measurement of the elevation of the threshold of hearing *following* the application of a stimulus, and for this reason we have found it convenient to term it Post-stimulatory Fatigue.

Fig. 1 illustrates the method which we have used for studying the phenomenon. It consists essentially of an audiometer and recording mechanism.

The apparatus was devised by Dr. Hallpike and Dr. Schuster in 1942 for studying the effects of blast waves upon the cochlea, and we have found it very useful.

The attenuator control of the audiometer is coupled directly by means of a rack and pinion mechanism to an ink recorder. The attenuation in decibels is proportioned to the angle of rotation of the control and the amplitude of the resulting trace is thus proportional to the intensity change in decibels of the sound.

The apparatus has been applied in our fatigue tests and in Fig. 2 is shown a typical test result.

The subject first executes the threshold tracing seen on the left of the figure. This he does by rotating the attenuator control in a rhythmical manner in the neighbourhood of his threshold of hearing. The amplitude of the excursions is normally some 2 to 6 decibels with a time interval between successive peaks of about 2 to 3 seconds. The peaks of the tracing give the just heard level.

In the case illustrated the intensity is raised at the end of one minute to 100 db. above threshold for a period of one minute. The subject then again traces his threshold. It will be seen that fatigue, as measured by the displacement of the threshold level, is still present two minutes after the cessation of the stimulus.

This brings us to the consideration of the measurement of a sensitivity loss of a different kind, and one which manifests itself only during the application of the stimulus. We have accordingly termed it Per-stimulatory Fatigue.

The equipment described has lent itself well to the demonstration and study of this phenomenon, and Fig. 3 is intended to show the test procedure.

On the subject's right there is, as before, the audiometer and threshold recorder; on his left, an additional audiometer. Each audiometer supplies a separate ear-piece, and it is possible by means of an appropriate switching arrangement to stimulate either or both ears. The two audiometers are first adjusted to the same frequency, say 1,000 cycles. The intensity at one ear, the subject's left, is kept constant, say at 80 db. above threshold. The intensity at the right ear is then varied using the threshold recorder to give equality of loudness with the constant tone in the left ear.

Fig. 4 shows the result of such a test procedure.

At the start loudness equality is attained with an intensity in the subject's right or control ear, as it may be called, which is the same as that of the left or test ear, i.e. 80 db. The next step is to switch off the variable tone from the right ear and continue the constant stimulus in the left ear. After a period which may be determined at will, the variable tone is reapplied to the right ear, and it is then found that a loudness balance is attained with an intensity in the right ear which is less than 80 db. by an amount which may be considerable and depends within certain limits upon the duration of application of the constant stimulus.

It will be seen, therefore, that during the period of this application a loss of sensitivity or fatigue of the left or test ear has occurred which is measured by this change, 30 db. in the level at the control ear required to give this final loudness balance.

It will be seen from Fig. 5 that the amount of the fatigue varies with the intensity of the fatiguing tone.

This also shows that irrespective of its amount, the fatigue attains a maximum after a period which has a constant value of about three and a half minutes.

The next point of importance is the recovery process of this fatigue, and this is depicted in Fig. 6.

As before, the first operation is to make the usual loudness balance, in this case at 80 db. at 1,000 cycles. The control ear is then rested while the test ear is fatigued for at least three minutes. At the end of this period the fatigue has reached a level of 30 db. At this point both ears are rested for periods varying from a few seconds to one minute. At the end of each rest period, the fatiguing tone is applied at 80 db. as before, to the test ear, while simultaneously the variable tone is reapplied to the control ear with resumption of the balancing procedure. The diagram shows the different stages of recovery after four different rest periods 0, 10, 30 and 60 seconds.

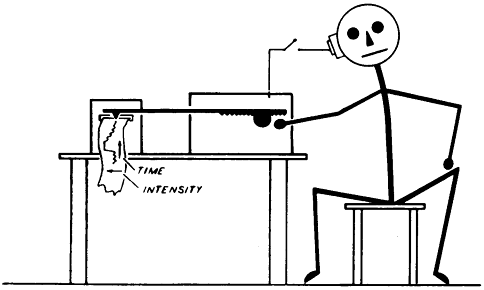

FIG. 1.

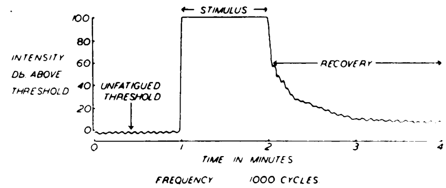

FIG. 2.—Post-stimulatory fatigue.

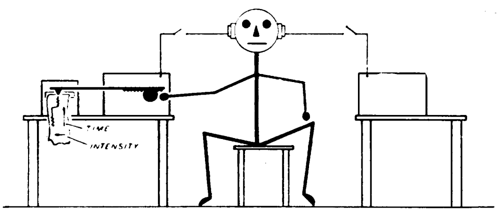

FIG. 3.

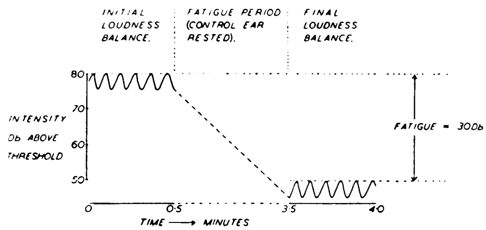

FIG. 4.—Per-stimulatory fatigue. Stimulus intensity 80 db. Frequency 1,000 cycles.

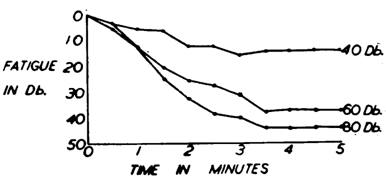

FIG. 5.—Per-stimulatory fatigue: Development. Stimulus frequency 1,000 cycles.

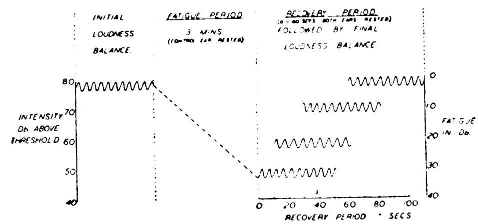

FIG. 6.—Per-stimulatory fatigue: Recovery. Stimulus intensity 80 db. Frequency 1,000 cycles.

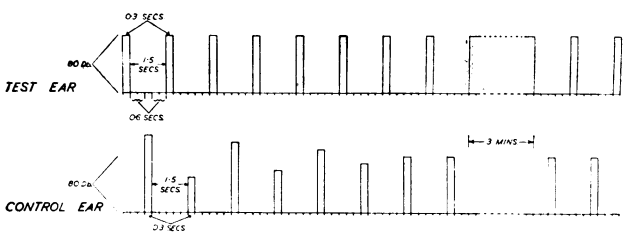

FIG. 7.

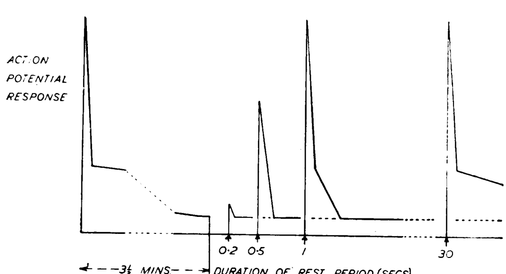

FIG. 8.

It will be seen that recovery is most rapid during the first ten seconds, but that fatigue is still present but much reduced up to one minute after the cessation of the fatiguing tone.

We come now to the consideration of another and better known binaural loudness balancing procedure, known as the alternate balance procedure, and one which is in common use in the investigation of auditory function. Here a balance is made by listening to tones presented to each ear alternately, a procedure which would seem well suited to the measurement of fatigue. We have attempted to use it for this purpose, and a diagrammatic representation of the test procedure is shown in Fig. 7.

The subject wears a pair of telephone receivers with which short-tone impulses are delivered alternately to the test ear and the control ear. The frequency used in this case was 1,000 cycles. The intensity at the test ear is 80 db. with a final loudness matching at 80 db. at the control ear.

The transfer of the stimulus from one ear to the other is carried out with a change-over switch which is operated in a rhythmical manner, and is found by measurement to give the time relations shown in the diagram. The duration of each impulse was about 0·3 second. The switch was in the off position for about 0·6 second, giving an interval between successive stimuli to the same ear of 1·5 seconds.

Following the attainment of the loudness balance, the test ear is fatigued continuously for three minutes. Thereafter further loudness comparisons are made and the balance at 80 db. in each ear is found to be unchanged. In fact, no fatigue is demonstrable.

Now it is the particular purpose of this communication to draw attention to the striking difference between the results obtained with these two procedures, the simultaneous and alternate balance.

In both, the same fatiguing stimulus has been applied. While, however, considerable fatigue can be readily demonstrated with the simultaneous balance test, the alternate balance test reveals none at all. This striking difference appears to depend upon certain important time constants of the nervous apparatus of the cochlea, in particular upon the difference in the manner of their involvement under the conditions of the two test procedures. Here, Matthew's investigation of adaptation of single muscle end-organs appears (1931) to be particularly significant.

His results are represented diagrammatically in Fig. 8. When a stimulus is applied to an end-organ the action potential response consists of an initial high frequency discharge known as the on-effect. The duration of this initial burst of impulses is brief, being of the order of 0·2 second, and is followed by a slow decline in the discharge frequency with time. This decline is termed adaptation.

If, following adaptation, the stimulus is removed and then reapplied after a rest period greater than about one second, the on-effect is present and indeed undiminished, but continued stimulation results in a rapid relapse of the response, i.e. an accelerated, adaptation to a level which is determined by the duration of the rest period. If, however, the rest period is less than 0·2 second no on-effect is present, while for durations of rest period between 0·2 and 1 second the on-effect is present but diminished.

Let us consider how these time constants can be applied to the interpretation of our observations. It would seem likely that, following the application of the fatiguing tone and its momentary interruption, the loudness level attained on reapplication might temporarily relapse with abnormal rapidity, as shown in Fig. 8, to the fatigued level. Nevertheless, the subjective measure of the loudness for the short-tone stimuli used in the alternate balance technique might depend upon the on-effects alone. The magnitude of these is unreduced, and thus no fatigue would be manifest.

This interpretation has been applied to the results obtained with both the simultaneous and alternate balancing techniques, and the results are embodied in Fig. 9.

The upper two diagrams explain the apparent absence of fatigue when investigated by the alternate balance procedure. The lower two explain the presence of per-stimulatory fatigue demonstrable by the simultaneous balancing technique.

The tones are of equal intensity and are applied to the ears of a normal subject. The diagrams show the supposed variations in magnitude of the total action potential responses which constitute the physiological basis of our subjective observations.

In the initial balance period A is shown a series of pulses in the two ears, all of the same magnitude corresponding to equality of loudness. In the second period B, a continuous fatiguing tone is applied to the test ear, and its response declines in the manner shown. In the third period C, we revert to the alternating pulses and, since the on-effect in the fatigued ear is unimpaired, the magnitude of the pulses is equal in the two ears corresponding again to equality of loudness. Below is shown the course of events with the simultaneous balancing procedure. In the initial balancing period A, the responses from the two ears decline in exactly the same way. In periods B and C we see how the continued application of the test tone causes a progressive decline in the response. Meanwhile, during period B the control ear is rested.

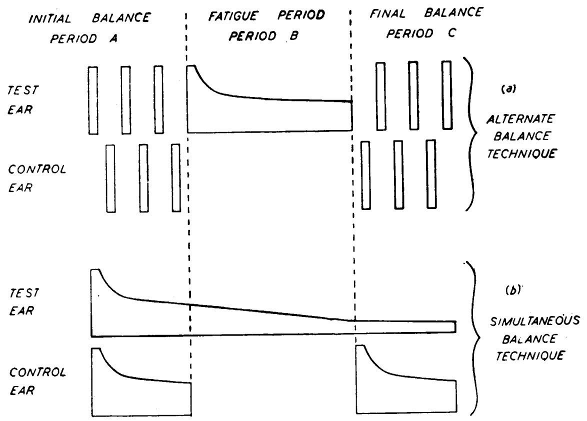

FIG. 9.

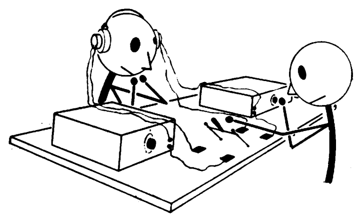

FIG. 10.

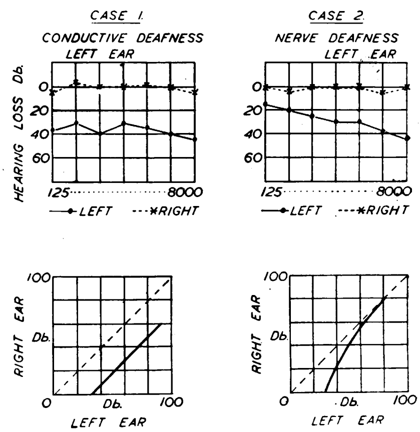

FIG. 11.

The tone is reapplied to the control ear in the final balancing period C and the response, being that of a normal unadapted set of sense organs, is of correspondingly high magnitude, and exceeds that of the test ear.

The subjective response from the test ear at this stage of the procedure is therefore one of diminished loudness, as exhibited in our experiments.

It would seem possible in this way to give a satisfactory explanation of the striking difference in the results obtained by the two balancing techniques, the alternate balance and the simultaneous balance. This difference is an important one for the illustration it gives of the need for designing and interpreting subjective tests of cochlear function in the light of the fundamental physiological factors concerned.

This point arises with particular force in connexion with another and particularly useful clinical test of cochlear function, namely the Loudness Recruitment test. This test was first described by E. P. Fowler, and it formed the basis of a communication given by Dix, Hallpike, and Hood to the Royal Society of Medicine (1948).

Our own investigations on so-called per-stimulatory fatigue seem to throw some light upon this phenomenon, and it is necessary to digress a little at this point to review very briefly the characteristics of the phenomenon and the usual test procedure used for its demonstration. This is shown in Fig. 10.

The subject wears a pair of telephone receivers, each supplied by a separate pure tone audiometer, or preferably by a single audiometer with arrangements for independent adjustment of the intensity in the two receivers. The frequency of the sound stimulus is the same in each receiver, and the tester switches it alternately from right to left.

The audiograms of two typical cases of unilateral deafness are shown in Fig. 11. In Case 1 the deafness is due to a lesion of the conducting mechanism of the left middle ear, and in Case 2 to Ménière's disease affecting the left labyrinth.

The purpose of the test is to equate a tone of variable intensity in the impaired ear with a tone of constant intensity in the normal ear. The constant tone is altered in increasing steps of 20 decibels after each loudness balance has been achieved and the results are plotted conventionally on a graph of the form shown (Fig. 11).

The ordinates represent the intensity of the constant tone in the normal ear and the abscissa, the sound intensities in the impaired ear, giving equality of loudness. In the case of a normal subject, loudness equality is, of course, attained with equal intensities in the two ears giving the dotted 45 degree line shown in the diagram. In both cases shown, the test frequency was 1,000 cycles, at which point the audiogram shows a threshold shift for the affected ear of 30 db., and this is denoted on the chart by the lowest point of the curve in each case. In the case of conductive deafness the obstruction caused by the middle-ear disease to the sound waves on their way to the inner ear introduces an attenuation factor, in this case 30 db., which is constant at all intensities. The result, therefore, is a curve inclined at the same angle as that of the normal, but displaced to the right by 30 decibels.

In Case 2 the audiogram is essentially the same as in Case 1, with a threshold shift of 30 db. at 1,000 cycles per sec.

On ascending the intensity scale, however, it is found that the sensitivity loss or deafness of the left ear, 30 db. at threshold, becomes progressively less until at 80 db. equal intensities at the two ears evoke equal loudness responses.

In other words, the deafness of the affected ear present at threshold disappears at higher intensities, and this in its simplest terms constitutes the phenomenon of loudness recruitment.

One further point arises. It will be seen that in Case 2, the whole loudness range of the test is, in the normal ear, covered by an intensity range of 80 db., while the same loudness range in the impaired ear is covered by only 50 db. Thus equal *intensity* increments are attended by much greater *loudness* increments in the impaired than in the normal ear. Conversely, for equal increment of *loudness* much smaller increments of *intensity* are needed in the impaired than in the normal ear. It follows from this that diminution of the difference limen, which Lüscher (1950) has studied in such detail, is a natural and indeed inevitable corollary of loudness recruitment as it is assessed by the balancing technique which Fowler (1936) originally described and which we have used. It can in fact be said that loudness recruitment and diminution of the difference limen are both manifestations of the same essential disorder of cochlear function.

It will be observed that we have arrived at this result using the second of the two loudness balancing techniques described earlier, namely the alternate binaural loudness balancing technique. From this we are led to certain conclusions of very great importance. We see in the first place that under the conditions of this test the loudness comparisons are dependent only on the on-effects in the two ears.

Now if the conclusions of Hallpike (1948, 1938) on the pathology of Ménière's disease be accepted, namely that the endolymph distension is accompanied by disease of the hair cells of Corti's organ, then it follows from our own findings that these diseased hair cells are capable of exhibiting on-effects of normal magnitude.

Now, as explained earlier, the first of the loudness balancing techniques, namely the simultaneous balancing technique, involves a comparison not of the initial responses, that is, the on-effects, from the two ears, but of their sustained responses to continued stimuli, in fact the adapted responses. It was therefore thought worth while to investigate these adapted responses in monaural deafness due to Ménière's disease and conductive lesions by means of the simultaneous balancing technique and, in particular, to ascertain whether or not the loudness recruitment phenomenon, present in the on-effect with Ménière's disease could also be demonstrated in the adapted response.

Let us consider again and in rather greater detail the simultaneous balancing procedure in the case of normal subjects. In Fig. 12 are two tracings taken in this way.

They represent the intensity variations in one ear, the control ear, required for equality of loudness with a constant tone, in this case 80 db., at 1,000 cycles; in the other ear, shown on the right; in each case taken over a period of five minutes. As would be expected, the 80 db. test tone is matched by a tone of equal intensity in the control ear. The point of importance is that the level of the tracings remains very constant over the five minutes. In other words, any fatigue brought about by the constant 80 db. stimulus in the test ear is matched by equal fatigue brought about by the varying stimulus in the control ear.

In Fig. 13 is shown the course of events with the same balancing procedure at 1,000 cycles applied to unilateral *conductive* deafness.

The deafness at threshold is 30 db. The diagrams on the right represent the constant intensities applied to the impaired or test ear, i.e. 40, 60 and 80 db. above normal threshold. Those on the left show the actual balance tracings obtained from the normal ear at each of these three levels.

It will be seen that for a constant tone of 40 db. in the impaired ear, equality of loudness is obtained as would be expected with a tone of 10 db. in the normal ear. Similarly with a tone of 60 db. in the impaired ear, loudness equality is obtained with a tone of 30 db. in the normal ear, and with 80 db. in the impaired ear 50 db. in the normal ear. In other words, as in the case of the alternate balancing technique applied to unilateral conductive deafness, so with the simultaneous balancing technique, the loudness of the sound in the impaired ear is reduced at each of the three intensity levels by the same attenuation factor, 30 db. Apart from this fact the tracings are identical with those obtained from normal subjects.

The results obtained in a case of unilateral end-organ deafness (Ménière's disease) are shown in Fig. 14.

As before, the threshold loss was 30 db. and on the right will be seen once again the same constant intensities applied to the impaired ear. We will consider first the balance tracing from the normal ear with a constant tone of 40 db. applied to the impaired ear.

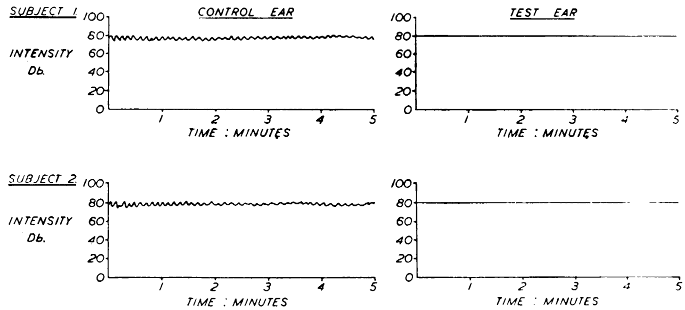

FIG. 12.

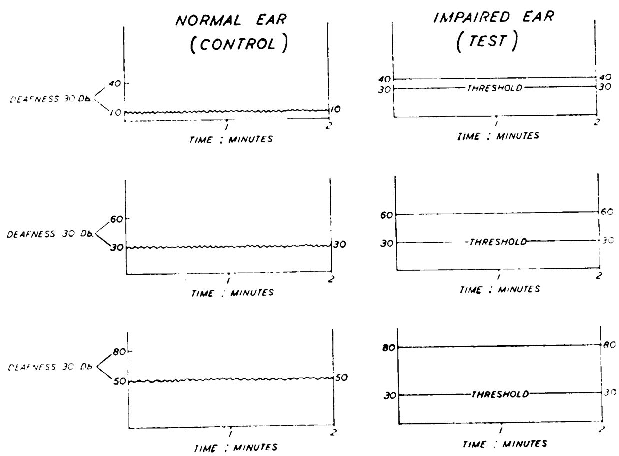

FIG. 13.

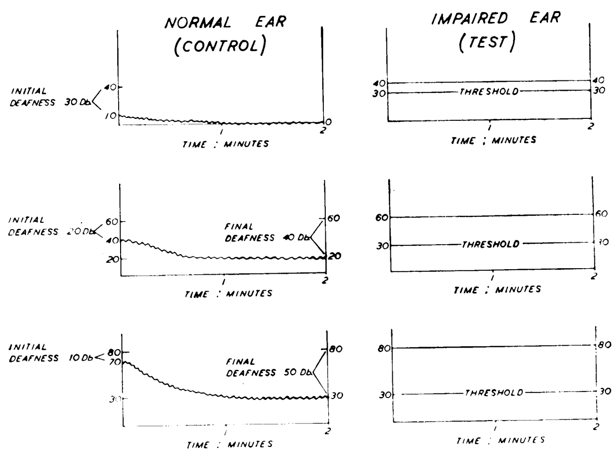

FIG. 14.

As can be seen, equality of loudness is first obtained with a tone of 10 db. in the control ear. As the test proceeds, however, this intensity falls until eventually it approaches the threshold level. Now since this tracing from the control ear is a measure of the loudness of the tone in the impaired ear, it would seem that the constant 40 db. stimulus, although still being applied to the impaired ear, was no longer being heard.

When we consider the second pair of diagrams, we see that with a stimulus intensity of 60 db. applied to the impaired ear, loudness equality is initially obtained with an intensity of 40 db. in the control ear. That is to say, the 30 db. loss at threshold has been reduced on account of recruitment to one of 20 db. With continued stimulation, however, the tracing falls very rapidly, and the final balancing intensity is only 20 db. In other words, the loudness level of the constant tone in the impaired ear was at first high, 40 db., on account of recruitment; but it soon falls and reaches this new level of 20 db. This means that the deafness of 30 db. is first temporarily reduced by recruitment. Thereafter the recruitment seems to disappear and we are left instead with an actual increase of the deafness to 40 db.

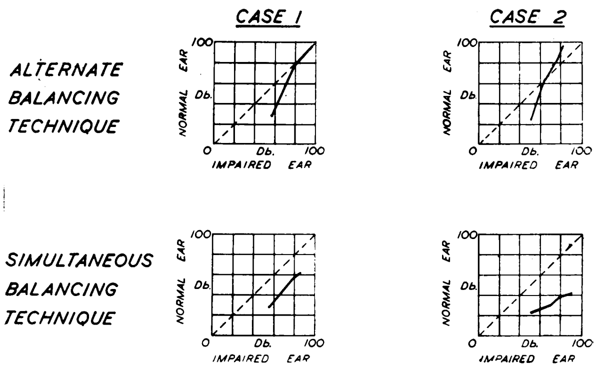

FIG. 15.

In the case of the third pair of diagrams, the stimulus intensity applied to the impaired ear is 80 db. and the initial balancing intensity 70 db. There is thus almost complete recruitment of loudness. The final balancing level, however, is 30 db. so that the deafness of the impaired ear, after being temporarily reduced to 10 db. by recruitment, is finally increased to 50 db.

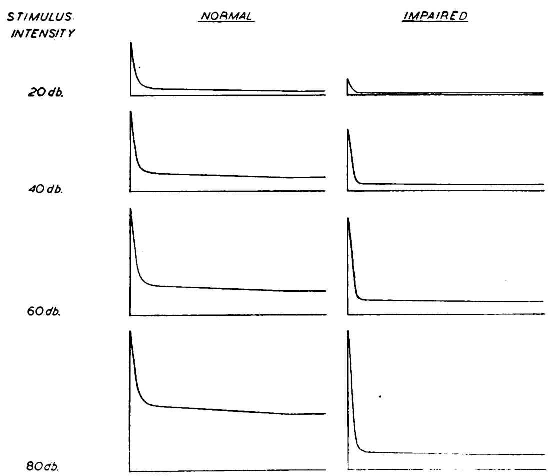

FIG. 16.

We have examined 20 cases of unilateral Ménière's disease, and obtained similar results in all. The final balancing intensity, as can be seen, is not so precise and definite as in the case of the conventional alternate balancing procedure, but falls progressively with time. In general, nevertheless, the fall does reach a maximal decline and thereafter remains constant, and it is this final intensity that we have established in all cases and used as a measure of the loudness loss.

The results for two characteristic subjects are shown in Fig. 15 together with the results obtained with the alternate balancing procedure.

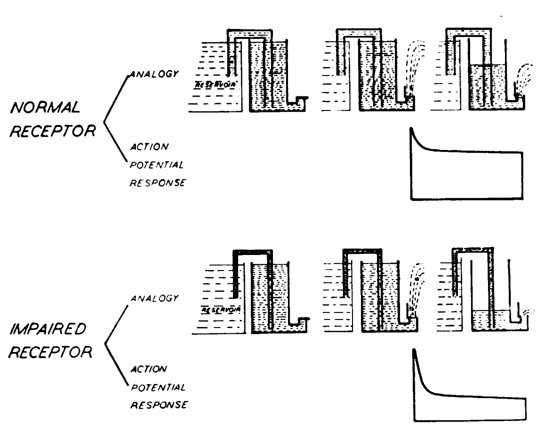

FIG. 17.

It will be seen, that whereas recruitment *is* present with the one, it is *not* with the other. Instead, in Case 2, we obtain a state of affairs which is, perhaps, best described as recruitment reversion.

Clearly the phenomenon of loudness recruitment is a transient one and in some ways a false indication of cochlear function.

We have applied once more our interpretation of what we suppose to be the neural response from both normal and impaired ears, and the results are shown in Fig. 16.

Here are shown the supposed action potential responses from the normal and impaired ears, corresponding to different stimulus intensities.

For a 20 db. stimulus the on-effect in the normal ear is small, and in the impaired ear it is still smaller, corresponding to the deafness at low stimulus intensities. As the intensities are raised the on-effects in the impaired ear approach the size of the corresponding on-effects from the normal ear. At 80 db. they are equal, corresponding to complete recruitment.

The responses from the impaired ear to sustained stimuli, however, are shown to be much reduced from those of the normal ear, corresponding to the results obtained with the simultaneous balancing procedure, namely recruitment reversion.

To sum up then, we can say that recruitment of loudness in a case of end-organ deafness is mediated by a recruitment in the magnitude of the on-effects. The neural response, however, to a sustained stimulus is marked by an abnormally great adaptation, and it is this to which we must attribute the abnormally great decline of loudness which is demonstrable with the simultaneous loudness balancing technique.

Adaptation is generally regarded as a process of equilibration whereby the energy dissipated by the end-organ is matched by an equal restoration of energy. The capacity of a receptor to respond to a sustained stimulus is dictated therefore by the rate at which fresh energy can be supplied to it.

It would seem that in the case of end-organ deafness this capacity of the receptors is grossly impaired and the response consequently falls considerably below that of the normal.

This process has a simple analogy in the discharge and replenishment of a water tank, as shown in Fig. 17.

The upper set of tanks represents a normal receptor; the lower set an impaired receptor. The capacity of each is the same, but the supply pipe to the lower tank is of much smaller diameter than that to the upper tank. The first tank in each case represents the quiescent condition of the two receptors, and it will be seen that they are identical, i.e. the height of the water level in each is the same.

When the taps are opened, corresponding to the response of the respective receptor to a stimulus, the initial fountains are of equal height as in the case of the two on-effects. In time, the water level in the two tanks falls to a level at which a state of equilibrium exists between the in-flow and the out-flow of the water. This is the condition of the adapted receptor when the energy supplied just balances the energy dissipated. Since the supply to the lower tank is reduced, the equilibrium water level is low and the height of the fountain much reduced, corresponding to the adapted level of the action potential response of the impaired receptor. In other words, the energy reserve is deficient.

We consider this finding to be an important one. In the first place because the measurement of the degree of adaptation may prove of some diagnostic value as an assessment of the true physiological impairment of function of the cochlear end-organs and in the second place because it would seem likely to be, at any rate, one of the reasons why recruitment of loudness is not accompanied by recruitment of intelligibility.

In recapitulation it may be said that our own investigations and those of Lüscher and Zwislocki (1948) have now made it clear that the loudness recruitment phenomenon depends upon disordered function of the hair cells resulting from disease or injury. Although their response is absent or reduced when the stimulus level is low, nevertheless their initial response (on-effect) may approximate to or even exceed the normal if the stimulus level is high. But this response is not sustained if the stimulus is continued, and indeed it may show an abnormal tendency to relapse, a characteristic which again seems likely to be the result of hair cell disease. These facts must be taken into account in the design of test procedures for the investigation of the phenomenon. This means, in essence, that the duration and spacing of the stimuli should be so arranged as to involve only the on-effects. Thus, the duration of the interval between successive stimuli to one ear should in all probability have a value not less than one second, while the duration of each stimulus should be sufficient to produce a sensation of tone. It need not, in all probability, much exceed this.

Within these limits the phenomenon can as well be investigated by the alternate binaural balancing procedure described by Fowler as by the differential threshold method of Lüscher and Zwislocki. But any technique which involves sustained stimulation is likely to bring into play the pathological adaptation of the sustained response, which as we have shown, is also a characteristic of hair cell disease and may lead, as we have described, to elimination or even reversal of the recruitment.

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