SENSITIVITY OF THE AUDITORY SYSTEM TO DIFFERENCES IN INTENSITY

Temporal transfer and difference limen studied in psychophysical experiments. Recording and analysis of evoked potentials.

SENSITIVITY OF THE AUDITORY SYSTEM TO DIFFERENCES IN INTENSITY

Temporal transfer and difference limen studied in psychophysical experiments. Recording and analysis of evoked potentials.

PROEFSCHRIFT

ter verkrijging van de graad van doctor in de geneeskunde aan de Medische Faculteit te Rotterdam, op gezag van de dekaan dr. J. Moll, hoogleraar in de faculteit der geneeskunde, tegen de bedenkingen van het college van dekanen uit de faculteit der geneeskunde te verdedigen op woensdag 19 april 1972 te 16.00 uur

door

MARIUS RODENBURG

geboren te Ter-Aar in 1936

Promotor : Prof. Dr. G. van den Brink

Co-referenten : Prof. Dr. W. H. Struben
Prof. Dr. M. W. van Hof

I CAN NOW REJOICE EVEN IN THE FALSIFICATION OF A CHERISHED THEORY, BECAUSE EVEN THIS IS A SCIENTIFIC SUCCESS.

JOHN C. ECCLES

AAN KEES VERWEY
EDZARD KUIPERS
JAN MEERWALDT
ADRIAAN VAN OLPHEN

CO-PROMOVENDI

CONTENTS.

INTRODUCTION

PART 1.

PSYCHOPHYSICAL EXPERIMENTS WITH AMPLITUDE MODULATED NOISE

Chapter 1.

Chapter 2.

PART 2.

MEASUREMENT OF EVOKED POTENTIALS IN MAN
ELICITED BY AMPLITUDE MODULATED NOISE

Chapter 6.

Chapter 7.

INTRODUCTION.

0.1. Subject and investigation method.

An important property of the auditory system is the way this system processes changes in stimulus intensity. Although this problem has been discussed many times since Weber, it is rather surprising that no generally accepted hypothesis about the underlying mechanism has emerged. In the present study the sensitivity of the ear to intensity differences of noise signals is studied. In general two methods of investigation are used for the study of perception: psychophysics and electrophysiology. Fechner founded psychophysics in 1860 (Boring, 1950, 1966) as a study of the relation between stimulus and sensation. In psychophysical experiments a stimulus is presented, and an observer makes some response (either by saying or by pressing a button). The system to be studied contains the peripheral sense-organ as well as the neural pathways that processes the information elicited in the peripheral organ. Considering the stimulus as the input of the system and the response of the observer as the output, it is possible to measure input-output relations by varying the parameters of the input stimulus. The investigator makes assumptions about how the system functions, and these assumptions have to account for the input-output relations. All the assumptions together constitute a model. Such a model of the system can suggest new experiments, and the results of such experiments lead to refinement or rejection of the model. Psychophysical experiments can never prove, however, that the system works like the model.

Another way of studying input-output relations in sensory systems is with electrophysiological experiments. This method has the restriction that parts of the system must be investigated separately. Unfortunately these experiments are possible only with laboratory animals. This is a disadvantage, because the results of electrophysiological experiments with animals cannot be compared directly with the results of psychophysical experiments on humans. Although subtle electrophysiological data as a rule cannot be obtained from human beings, it is possible to obtain some information about the electrical activity of the brain, from the use of electrodes on the scalp, i.e. the electro-encephalogram (EEG).

0.2. Outline of the investigation.

As has been pointed out in paragraph 1 it is possible to measure sensory input-output relations both with psychophysics (output is a quantified sensation) and with electrophysiology (output is, for humans, an evoked response). In vision research both methods have been applied, using sinusoidally modulated light as the stimulus.
De Lange (1952) carried out extensive psychophysical investigations with temporally sine wave modulated light. He measured the so-called attenuation characteristics, which nowadays are frequently called " de Lange curves". These curves give the relation between modulation frequency and threshold modulation depth under various circumstances. An analysis of evoked responses elicited by temporally sine wave modulated light is given by Clynes, et al (1964), van der Tweel (1964), van der Tweel and Verduyn Lunel (1965), Spekreyse (1966), Regan (1968) and Kamphuisen (1969).

In our study we carried out comparable experiments in the auditory system.

The psychophysical experiments are described in the first part if this study. Analogous to de Lange's experiments sinusoidally modulated white noise was used for stimulation. The threshold modulation depth was determined as a function of the modulation frequency. The result, a curve which we call the " auditory temporal transfer function", is characteristically low-pass with a cut-off frequency between 40 and 80 Hz for different observers. The slope of the curve for high frequencies appears only to be 6 dB per octave. The shape of this transfer function appears to be independent of the absolute intensity. Both white noise and bandpass noise have been used as a carrier. In the bandpass conditions, the influence on the temporal transfer function of the central frequency as well as the bandwidth, are investigated.

In the second part of this study a parallel experiment is reported in which evoked responses were recorded.

By plotting the amplitude of the evoked response as a function of the modulation frequency we obtain a narrow bandpass frequency characteristic centered at about 9.5 Hz. This frequency characteristic is very different from that found in the psychophysical experiments.

In analogy with the results of experiments on the visual system the " filtering" at about 9.5 Hz has been called " cortical filtering" (Spekreyse, 1966).

PART 1.

PSYCHOPHYSICAL EXPERIMENTS WITH AMPLITUDE MODULATED NOISE.

CHAPTER 1.

REVIEW OF EXPERIMENTAL METHODS TO DETERMINE THE DIFFERENCE LIMEN (DL).

There are several possible ways to determine the intensity difference limen. The procedures differ both in way the stimuli are presented and in the psychophysical method. It is possible to distinguish three techniques for presenting the stimuli.

1.1. Difference limen for intensity-memory method.

Two stimuli are presented in succession with intensities I_2 and I_1. $\Delta I = (I_2 - I_1)$ is the just noticeable intensity difference. (Fig.1.).

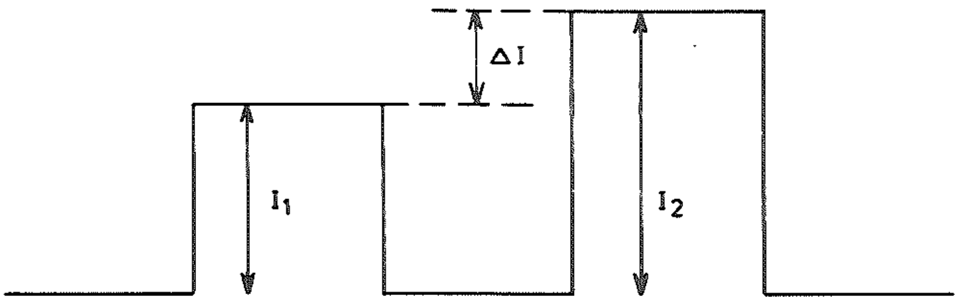

Fig.1. Diagram of stimulus presentation in the loudness-memory experiment.

The difference limen in decibels is defined as

$$DL\ (dB) = 10 \log \left(\frac{I_2}{I_1}\right) .$$

In order to measure the DL, a forced choice method is often used to eliminate the effects of the observer's criterion shifts. In this method the stimuli with intensities I_1 and I_2 are presented in a random order and the observer is required to say which of the stimuli was louder (or softer). Percent correct answers is determined for different values of I_2. The I_2 value corresponding to 75% correct is defined as the just noticeable value.

For a frequency of 1000 Hz the difference limen appears to be 0.5 dB and independent of intensity (I_1) above 20 dB sensation level (Harris, 1963). For white noise the difference limen is also 0.5 dB and independent of intensity (Harris, 1963) (Fig.2.).

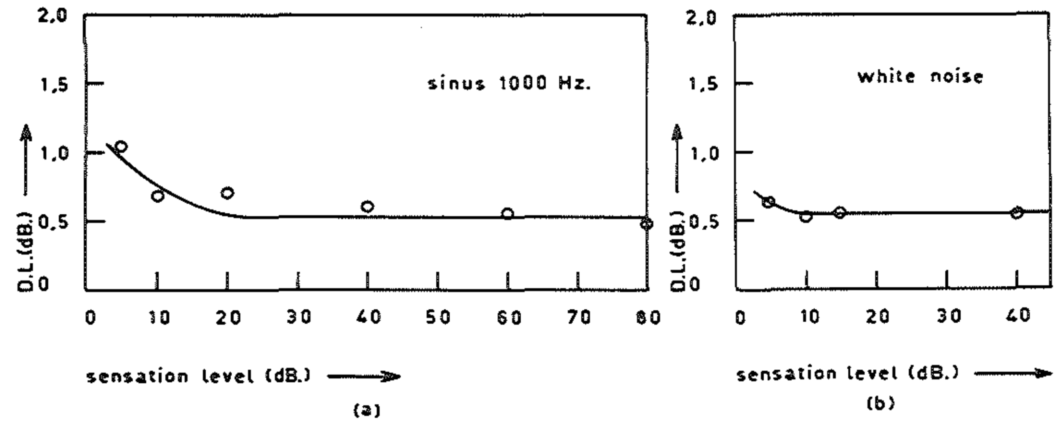

Fig.2. Difference limen as a function of intensity for intensity-memory method

a) for a tone of 1000 Hz (Harris, 1963)
b) for white noise (Harris, 1963).

1.2. Difference limen for intensity modulation (method of Riesz).

On this method the amplitude of the stimulus is modulated. The ratio a/b of the amplitudes of the modulating signal and the carrier is called the modulation depth, m (Fig.3.).

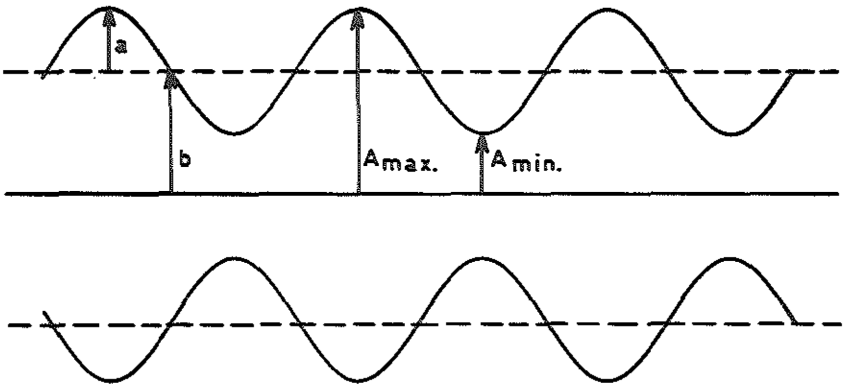

Fig.3. Diagram of an amplitude modulated signal; m= a/b.

The difference limen in dB is defined according to the formula

$$DL\ (dB) = 20 \log \left(\frac{A_{max}}{A_{min}}\right) = 20 \log \left(\frac{1+m}{1-m}\right) .$$

For values of m below 0.3 this formula can be simplified to DL(dB) = 17.5 m. (Zwicker and Feldtkeller, 1967). By combining two simple tones Helmholtz (1863) has found that loudness variations are audible if the beat frequency is less than about 25 Hz. Above this frequency the beating sounds " rough". Helmholtz was able to distinguish 132 beats per second. He assumed that this was near the upper limit.

Terhardt (1968[a]) recently confirmed that the loudness variations by amplitude modulation can be heard up to 25 Hz. This limit appeared to be independent of the carrier frequency. The area within which the amplitude modulated tone gives a sensation of roughness depends strongly upon the carrier frequency (Terhardt, 1968[b], 1970). For modulation frequencies between 75 and 2000 Hz (depending upon the carrier frequency) the roughness disappears. In that case the different spectral components of the modulated signal are audible. Using the modulation method, the difference limen appears to depend upon the intensity (Fig.4.),in contradiction with the memory method with which the difference limen appeared to be independent of the intensity beyond 20 dB sensation level.

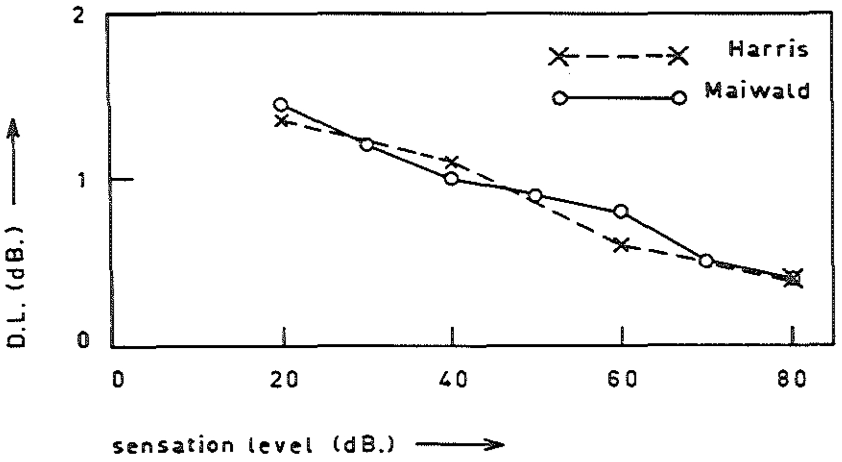

Fig.4. Difference limen as a function of intensity for loudness modulation according to Harris (1963) and Maiwald (1967).

The power spectrum of a modulated signal is white if white noise is used as a carrier instead of a sine wave. Under these circumstances spectral differences between the modulated and the unmodulated signal cannot give a cue for detecting an intensive difference.

We took advantage of this and used white noise as a carrier, to investigate the effects of the modulation frequency.

Zwicker and Feldtkeller (1967, p.98) also using white noise determined the modulation threshold as a function of the modulation frequency. They found a constant threshold for modulation frequencies below 5 Hz. Above this frequency the threshold increases with frequency at a rate of 9 dB per decade.

Dubrovskiĭ and Tumarkina (1967) performed a similar experiment, but obtained different results. They explained their findings with a simple model consisting of a single RC low-pass filter. Their results suggested that the modulation threshold increased at a rate of 6 dB per octave (20 dB per decade), in line with the predictions of their model. The cut-off frequency of their RC-circuit was 18 Hz. When they repeated their experiment they determined a cut-off frequency of 30 Hz.

1.3. Difference limen for intensity-masking.

On a masking experiment a brief increment is made in a continuous signal.

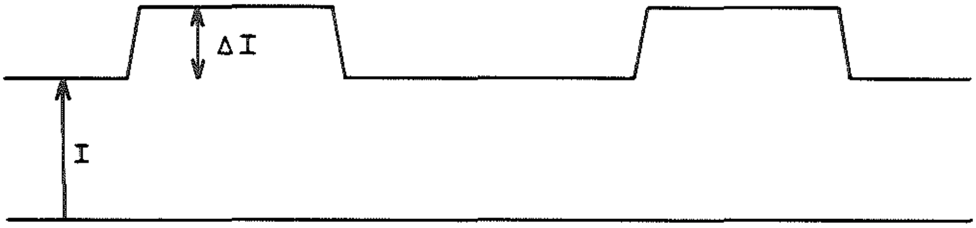

Fig.5. Diagram of stimulus presentation in the loudness-masking experiment.

Defining ΔI as the increment that can just be heard, the difference limen in dB is defined as

$$DL\ (dB) = 10 \log \left(\frac{I+\Delta I}{I} \right) ,$$ with I the

intensity of the continuous signal. A wide variety of different increment durations has been used, ranging from only a few milliseconds to one second.
When a sine wave is used as the continuous signal a rise-decay time is imposed in the increment to limit transient effects. A 10 msec. rise-decay time is typical.

CHAPTER 2.

THE EFFECT OF THE MODULATION FREQUENCY ON THE PERCEPTIBILITY OF AMPLITUDE- MODULATED NOISE.

2.1. Introduction.

Amplitude modulation of optical and acoustical signals has been applied as a means for obtaining information about temporal transfer characteristics of the visual and the auditory systems. Usually a periodic pulse wave or a sine wave is used as the modulation signal. If a periodic pulse is used the modulation frequency as well as the duty- cycle influence the data. De Lange (1952) was able to clarify much of the confusion on flicker perception by using sinusoidally modulated light as a stimulus.

The use of sinusoidally modulated stimuli provides procedural advantages: if we assume the system to be linear, the response to a sine wave is also a sine wave. The amplitude and phase characteristics of the system, which can be determined by varying the frequency of the input, completely describe the system. Of course using a linear systems approach, other types of stimulation, like pulse- and stepfunctions enable us to describe the system as well. However it appeared to us, that the choice of sinusoidal stimulation makes the interpretation of results easier.

The non-linearity of a system is revealed by the extent of which, given a sine wave input, the output is not sinusoidal. Even in a non-linear system it may be possible to find a restricted range of the system parameters within which the system behaves linearly. De Lange's procedure was aimed as this kind of information. He studied the visual system at a constant adaptation level and with modulation depths around threshold. He assumed that the visual system would respond approximately linearly under these circumstances. At different adaptation levels the visual system responds differently, but when the modulation depth is restricted to levels around the threshold the response is still linear within the experimental limitations.

2.2. Reflections on the investigated system.

On these experiments, the procedure consists of presenting an amplitude modulated input and asking the observer to respond, either " modulation is audible" or " modulation is not audible". We will model the observer's behavior with a system consisting of two components: one linear, the other non-linear. The linear component is simply a filter and the non-linear component a detector. The output of the filter is the input of the detector. The detector is a threshold device; the output is " yes" if the input amplitude exceeds a fixed threshold , or " no" if the input is below the threshold. This type of model is illustrated in Fig.6.

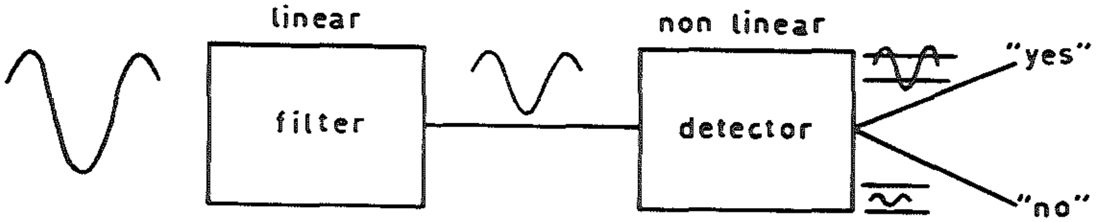

Fig.6. Schematic illustration of our experimental model.

The detector is assumed to be frequency independent so that all effects which depend upon frequency are due to the filter.
The amplitude characterictic of the filter is assumed to be measured by determining the modulation threshold as a function of the modulation frequency.

2.3. Determination of the temporal transfer function with white noise stimuli.

The investigations of de Lange inspired us to undertake an analogous experiment in the auditory system.
White noise was used as a carrier, so that spectral differences between the modulated and the unmodulated signal are eliminated (1.2.).
The block diagram of the experimental setup is given in Fig.7. White noise from the generator N.G. is modulated with a sine wave from generator S.G. Because it is difficult to adjust the modulation depth accurately, the modulator was adjusted to 50% modulation depth and then an unmodulated signal (from the same generator) was added to the modulated signal.

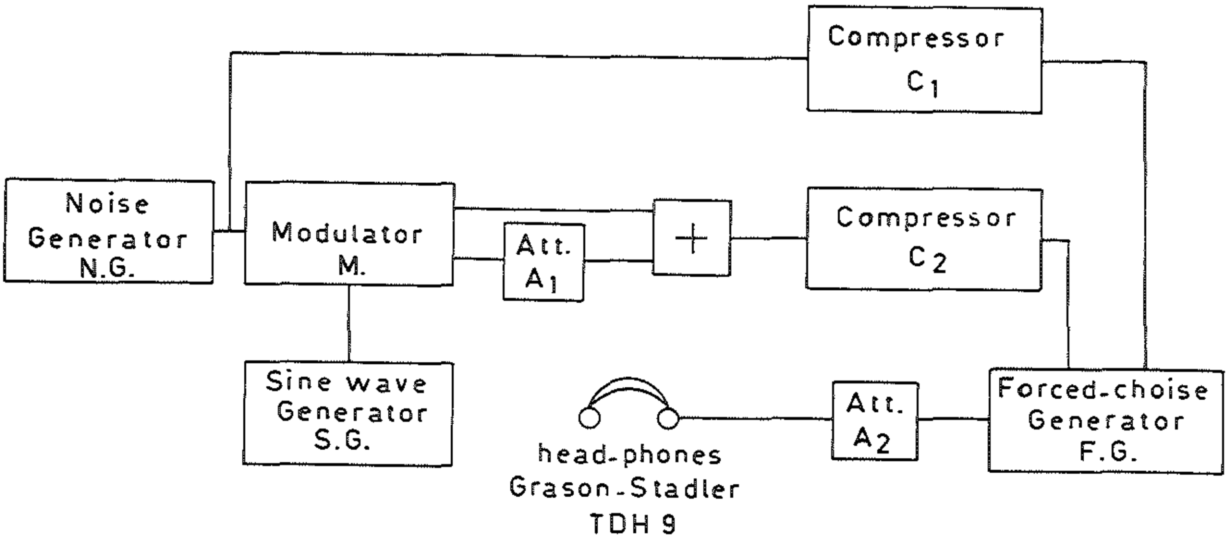

Fig.7. Block diagram of the experimental setup.

The two compressors (C_1 and C_2) provide equal average amplitudes for the modulated and the unmodulated signal. This was necessary because of the forced choice procedure, which was used. Two stimuli with durations of 2 seconds were presented to the observer. One stimulus was modulated and the other was not. The sequence of the stimuli was random and the observer, who had no knowledge of the sequence, had to indicate which of the two stimuli was the modulated one. The percentage of correct responses was determined as a function of the modulation depth. The 75% point on this function was defined as the threshold. With an attenuator (A_2) the overall level was adjusted. The stimuli were presented binaurally.

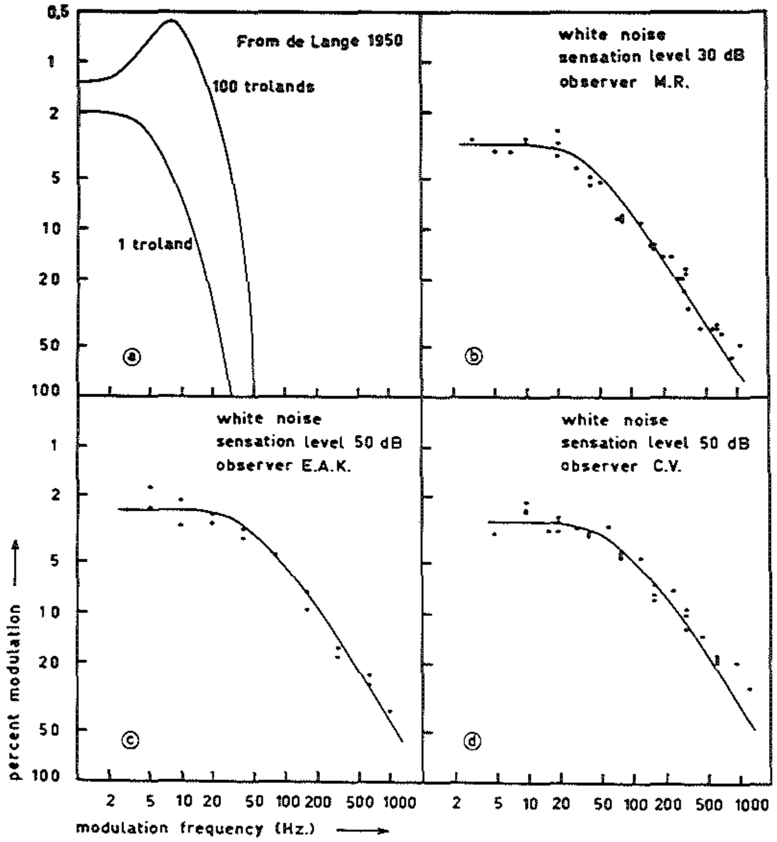

Fig.8. The temporal transfer function: modulation depth (vertically) as a function of the modulation frequency (horizontally)

a) for the visual system according to de Lange (1958);

b) for white noise, sensation level 30 dB obs. M.R. (cut-off frequency 46 Hz);

c) for white noise, sensation level 50 dB obs. E.A.K. (cut-off frequency 54 Hz);

d) for white noise, sensation level 50 dB obs. C.V. (cut-off frequency 80 Hz).

The results are shown in Fig.8. Modulation threshold is plotted as a function of the modulation frequency. This function is called the temporal transfer function. For the purpose of comparing de Lange's results with ours, we also show his curve for the visual system. The frequency characteristic for the visual system shows a cut-off frequency of about 10 Hz. Beyond 10 Hz the curve has a slope of 60 dB per octave. The slopes of his curves appear to depend upon luminance. For high luminances a peak appears at about 10 Hz. An entirely different frequency characteristic is found for the auditory system. From 3 to 20 Hz the modulation threshold is constant and about 0.03. At 20 Hz the threshold begins to increase (curve goes down) slowly. At high frequencies the increase amounts a factor of 2 per doubling in frequency (i.e. 6 dB per octave). Such a characteristic can be explained with an single RC-network, whereas de Lange's data are fit with 10 RC- circuits. The theoretical curves, as shown in Fig.8,are in satisfactory agreement with the measuring data. The curves are characterized by their cut-off frequency (3 dB point), which are given for the different observers in table 1. For low frequencies the threshold is constant at a modulation depth of about 0.03. It is possible to calculate the difference limen from the modulated threshold with the formula $DL = 20 \log(\frac{1+m}{1-m})$. In table 1 the different modulation thresholds and the difference limen are also given, for a modulation frequency of 10 Hz. The difference limen is close to 0.05 dB, which agrees with previous data (Harris, 1963). In an other experiment the difference limen was determined as a function of the intensity. The results are presented in Fig.10. This figure shows that the difference limen is also independent of the intensity, in the range from 20 dB to 60 dB sensation level. It has to be concluded from these data, that Weber's law is valid for white noise and in this intensity range. This result is consistent with previous data (Harris,1963).

Table 1. Cut-off frequency, modulation threshold and difference limen for different observers.

observer	M.R.	C.V.	E.A.K.
cut-off frequency	46 Hz	80 Hz	54 Hz
modulation threshold	3.2%	2.9%	2.5%
difference limen	0.56 dB	0.51 dB	0.44 dB

2.4. Influence of the overall intensity on the temporal transfer function.

Modulation thresholds were determined for modulation frequencies from 10 Hz to 640 Hz and intensities from 20 dB up to 60 dB sensation level. The measured data are presented in Fig.9. At 30 dB sensation level the modulation thresholds were determined 4 times. The average values along with indications of 3 times the standard deviations are presented in Fig.9. The solid line is a calculated characteristic with a cut-off frequency of 43 Hz. The figure shows that the modulation threshold is independent of the sensation level within the experimental error. So we may conclude that the temporal transfer function for the auditory system is independent of intensity. This result is quite different from that obtained in the visual system.

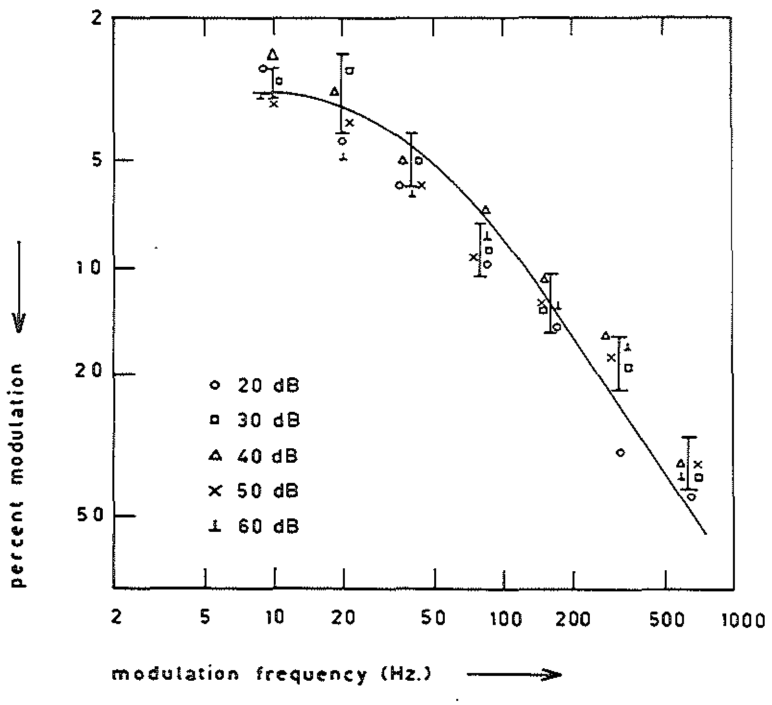

Fig.9. Modulation threshold as a function of overall level.

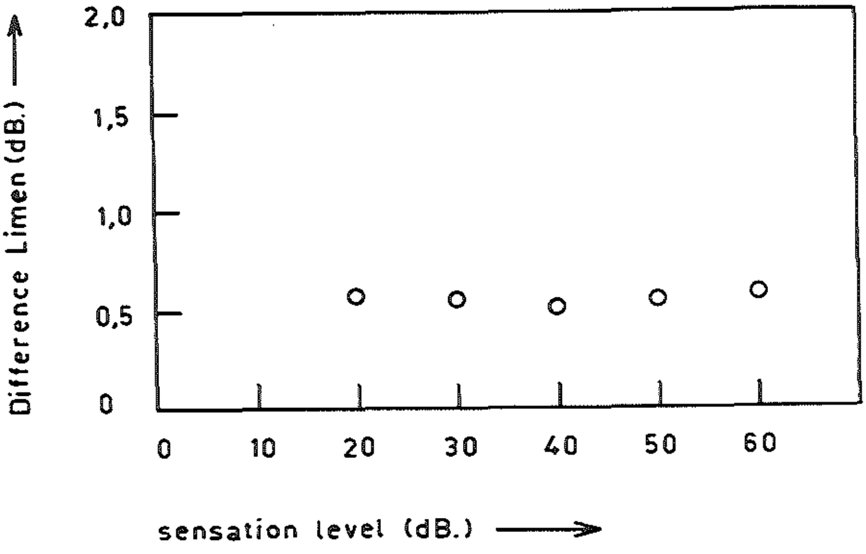

Fig.10. Difference limen of white noise as a function of overall level at a modulation frequency of 10 Hz.

2.5. Modulation of white noise with a periodic pulse wave.

It is possible to predict the output of a system for any input if we know the transfer characteristic completely.
In our case, we have an estimate only of the amplitude characteristic, but this is still possible with certain limitations.
The perceptibility of the modulation is determined only by the first harmonic of the modulating signal if:
a) the first harmonic is relatively strong compared with higher harmonics and/or
b) the modulation frequency is relatively high so that higher harmonics are attenuated.

In the present experiments we used a periodic pulse wave with a duty-cycle between 0.2 and 0.8 as the modulation signal. A modulation frequency of 160 Hz was used. In that case the restrictions a and b are satisfied. The amplitude of the first harmonic varies with the duty-cycle of the modulating pulse waveform.. Consequently, the modulation threshold will change with variation of the duty- cycle. The modulation threshold for a sine wave at 160 Hz was 0.11. The relation between duty- cycle and modulation threshold for the periodic pulse wave modulation was predicted using this value.

In Fig.11 it is shown that the agreement between the results and the prediction is satisfactory. The calculated curve seems to be somewhat more bent than the positions of the measured points suggest. This may be a result of the presence of the second harmonic. This component is absent for a duty-cycle of 0.5 but increases in amplitude when the duty-cycle increases or decreases.

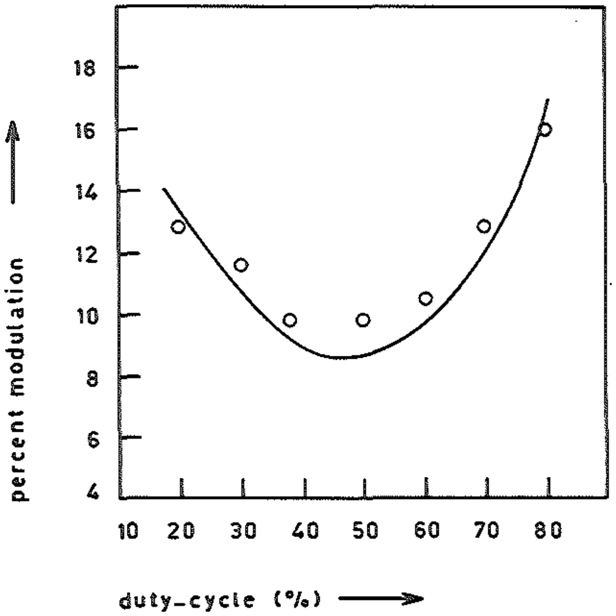

Fig.11. The experimental data are indicated with open circles; the solid curve represents the result of the calculation.

2.6. Determination of the temporal transfer function for noise bands with different center frequencies.

In 2.2 we showed that the temporal transfer function does not depend on overall intensity in a range from 20 to 60 dB sensation level. The question now is, whether it depends upon the carrier frequency. Noise bands had to be used, since it is not possible to determine the transfer function with a sine wave as a carrier, due to the confounding of spectral changes with changes in modulation frequency. When the bandwidth of a noise band was rather wide, it appeared possible to determine the temporal transfer function for modulation frequencies up to about 200 Hz. For higher modulation frequencies it became obvious that the discrimination between the modulated and the unmodulated signal was based strictly on spectral cues.

For this experiment we used the same experimental setup as shown in Fig.7. A filter (Krohn Hite type 3342) was placed between the noise generator and the modulator. A bandwidth of 400 Hz was chosen; the slopes of the filtered bands were 48 Hz per octave. Temporal transfer functions were determined for three center frequencies (500, 2000 and 8000 Hz) at a sensation level of 50 dB. The experimental results are presented in Fig.12.

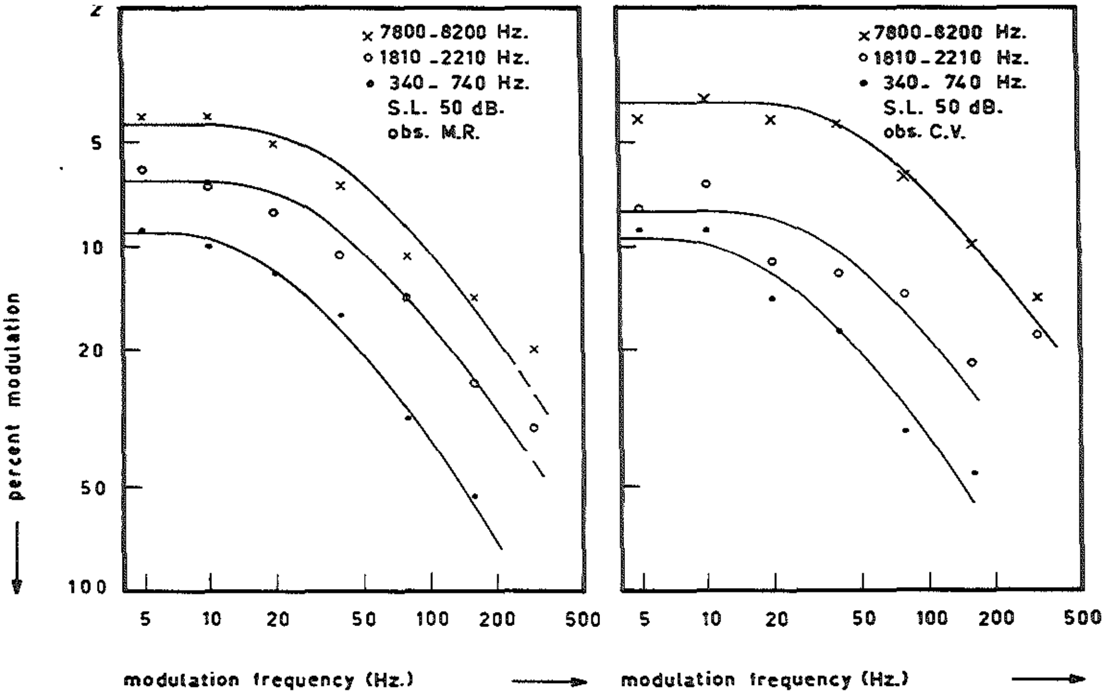

Fig.12. Temporal transfer function for noise bands with different center frequencies; 50 dB sensation level; center frequencies 500Hz, 2000 Hz and 8000 Hz.

Center frequency is obviously important. The temporal transfer function shifts markedly upward with higher frequency bands, and to a less extent horizontally as well.

The horizontal shift results in a change of estimated cut-off frequency. As is shown in Table 2, the estimated cut-off frequency increases with increasing of the center frequency for both subjects, although the effect is much more pronounced for one subject than it is for the other.

Table 2: cut-off frequencies of the temporal transfer function for noise bands of different center frequencies.

observer	center frequency		
	500 Hz	2000 Hz	8000 Hz
C.V.	27 Hz	50 Hz	70 Hz
M.R.	30 Hz	40 Hz	48 Hz

As will be discussed in the next chapter, the vertical shift of the curves must be due to the influence of the bandwidth of the carrier signal.

CHAPTER 3.

INTENSITY DISCRIMINATION OF NOISE BANDS AS A FUNCTION OF BANDWIDTH AND DURATION.

Frequency resolution, as revealed by studies of the critical band mechanism and temporal resolution, two important characteristics of the auditory system, are undoubtedly results of different processes (Zwislocki, 1965). It is not yet clear how these two processes participate in the intensity discrimination of noise bands.

3.1. Possible influence of the critical band upon intensity discrimination of wide band noise.

The critical band mechanism of the auditory system has been investigated, using a wide variety of procedures:
a) masking (Greenwood, 1961, Zwicker, 1961),
b) phase sensitivity (Zwicker, 1952),
c) loudness summation (Zwicker and Feldtkeller, 1955, Scharf, 1959),
d) threshold measurements of complex sounds (Gässler, 1954).
In loudness experiments (Zwicker and Feldtkeller, 1955) it has been reported that the loudness of a band of noise at a constant sound pressure level remains constant as the bandwidth is increased up to the critical bandwidth; beyond that limit the loudness increases. In two tone masking experiments (Zwicker, 1954), the threshold of a narrow band of noise between two masking tones has been determined. Increasing the frequency separation

of the two tones caused no decrease in the masked threshold of the noise band, until a critical frequency separation; beyond that the threshold decreased rapidly. In a large variety of experiments the estimated critical bandwidths were similar. For frequencies below 500 Hz the critical bandwidth is about 70 - 100.Hz and for higher frequencies 15% to 20% of the center frequency (Scharf, 1961). The critical band can be interpreted as reflecting a kind of filtering process that takes place within the auditory system. Whether this filtering takes place in the case of intensity discrimination of wide band noise or not is not yet established (De Boer, 1966, Zwicker and Feldtkeller, 1967. p.100, Maiwald ,1967). Experimental data (Bos and de Boer, 1966, Maiwald,1967) show that the difference limen for noise bands depends upon the bandwidth. This may suggest that the intensity fluctuations of the noise (in other words, the temporal structure of the envelope) is the determining factor in intensity discrimination.

The probability density function of the amplitude of the envelope of a noise band is a Rayleigh distribution. This can be written: $f(a)= \frac{a}{\sigma^2} \exp\left(\frac{-a^2}{2\sigma^2}\right)$, σ is the rms voltage of the noise. The expected number of maxima of the envelope per second is 0.641 (f_b-f_a), (f_b and f_a are respectively the upper and lower cut-off frequencies) of an ideal rectangular filter (Rice,1954). For small bandwidths these fluctuations may influence intensity discriminations. For large bandwidths the fluctuations are rapid and may be smoothed out by the temporal transfer function. In that case the difference limen is smaller for wide bands than for narrow bands. However, if the signal has a bandwidth which exceeds the critical bandwidth of the ear, the decrease of the difference limen will not be continued beyond the critical bandwidth. Thus we would expect that the relation between the difference limen (or the modulation threshold) and the bandwidth of the carrier will be a decreasing function up to a bandwidth corresponding to the critical bandwidth. Beyond that bandwidth the difference limen will be independent of the carrier bandwidth. This transition should occur at a smaller bandwidth for noise bands with a low center frequency than for noise bands with a high center frequency, since the critical bandwidth increases with frequency.

3.2. Determination of the difference limen as function of carrier bandwidth.

The modulation threshold was determined for noise bands of several bandwidths, at three center frequencies (500 Hz, 2000 Hz and 8000 Hz) and with a modulation frequency of 10 Hz.
The experimental method was the same as described in 2.2 for determination of the temporal transfer function. The experimental setup of Fig.7. was used. A Sine Random Generator (Bruel and Kjaer type 1024) was used for bandwidths of 10 Hz, 30 Hz, 100 Hz and 300 Hz. For larger bandwidths a multifilter (General Radio, type 1925) was used to filter wide-band noise. The bandwidth was varied by combining adjacent 1/3 octave filters.
Two students participated as observers in this experiment.
The experimental results are given in Fig.13 and 14. The results of the two observers are similar. In agreement with our predictions, the modulation threshold decreases with increasing bandwidth up to a certain value, and is

constant beyond it. This value is 200 Hz for a center frequency of 500 Hz, 600 Hz for a center frequency of 2000 Hz, and 2500 Hz for a center frequency of 8000 Hz, as indicated with arrows. These values are about twice as large as the critical bandwidths at the same frequencies. However, the rate of increase with increasing center frequency is comparable with that of the critical bandwodth. From these findings we may conclude that it is very likely that the critical band mechanism plays a role in the detection of amplitude modulation of wide band noise.

Earlier we showed that the temporal transfer function for noise bands appears to shift upwards with increasing center frequency (2.6.) Although in this experiment the same bandwidth (400 Hz) has been used at the different center frequencies, the results are quite different. We must conclude from the present data that the " effective" bandwidths are not equal at the different center frequencies. The effective bandwidth at the lowest center frequency is limited by the critical band mechanism. Consequently the modulation threshold is highest at the lowest center frequency.

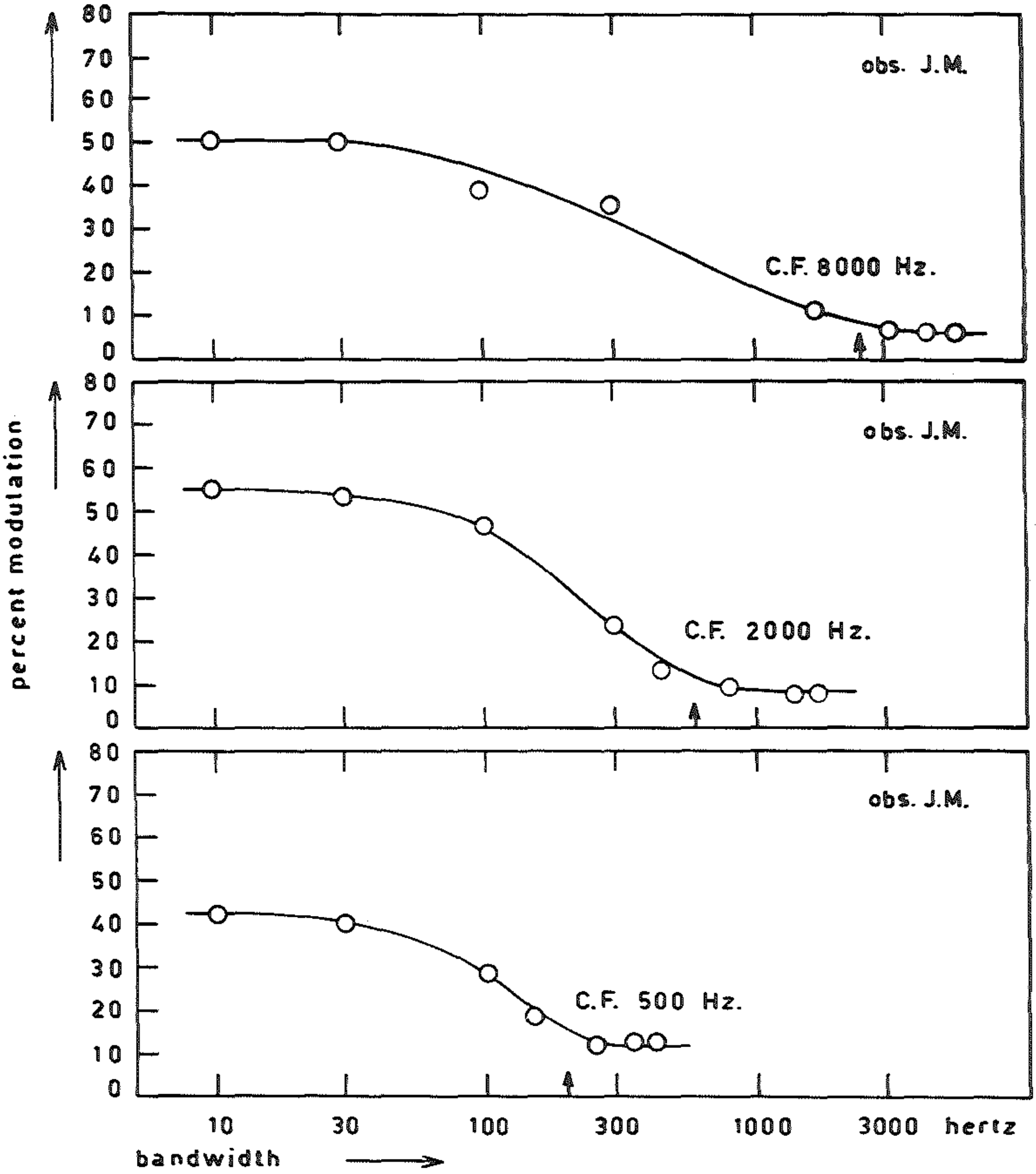

Fig.13. Threshold modulation depth as function of the bandwidth of the noise at three center frequencies. obs. J.M.

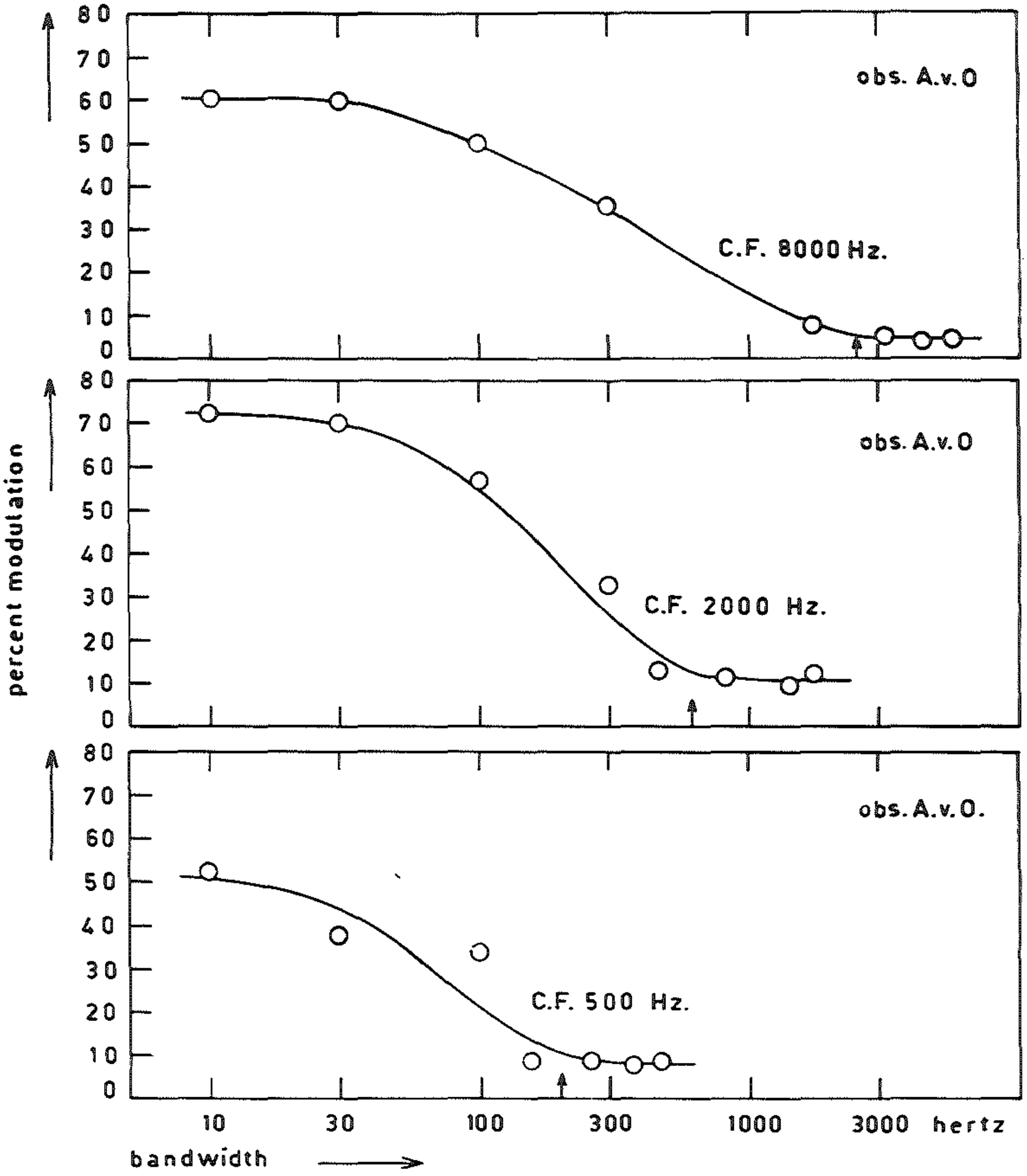

Fig.14. Like Fig.13, obs. A.v.O.

3.3. Temporal integration and the difference limen of noise pulses with different duration.

The relation between the threshold of a tone pulse and its duration can be described with the equation (Plomp and Bouman, 1959):

$$10 \log \frac{I_T}{I_\infty} = - 10 \log (1 - e^{-T/\tau})$$

I_T being the threshold intensity of the tone pulse with a duration T and T_∞ the threshold of a continuous tone. The equation describes a simple energy integrator with a time constant τ . Most authors assume that τ is about 200 msec. and that it is independent of the frequency of the tone (Zwicker and Feldtkeller 1967 p.163, Zwislocki, 1960, 1965). Plomp and Bouman (1959) measured the threshold versus duration relation for tone pulses at frequencies of 250, 500, 1000, 2000, 4000 and 8000 Hz and found that their results were in good agreement with the above mentioned formula. However the estimated time constant appeared to vary from 375 msec. at 250 Hz to 150 msec. at 8000 Hz. With noise pulses, the energy of a single noise pulse fluctuates. The standard deviation σ_T of the energy distribution decreases with increasing duration. Rice (1954) derived an equation which gives the ratio of the standard deviation and the mean of the energy distribution for relatively narrow bands of noise:

$$\frac{\sigma_T}{\bar{E}} \sim \frac{1}{T(f_b-f_a)} \qquad (T(f_b-f_a) \gg 1)$$

(Rice, 1954)

In this formula $\bar{E}$ is the mean energy of the noise pulse with duration T, σ_T the standard deviation, f_b and f_a the upper and lower cut-off frequencies.

Both the ratio $\frac{T}{\bar{E}}$ and the difference limen decrease with increasing T. When the duarion of the noise pulses is longer than the integration time of the ear, it is the integration time, rather than the duration of the noise pulse which determines the threshold. The difference limen of the noise pulses as a function of the duration should thus decrease with increasing T only up to the integration time. For longer durations the difference limen should be constant. This provides another possible estimate of the integration time of the auditory system; we measure the difference limen of noise pulses as a function of the duration.

3.4. Determination of the difference limen of noise pulses as a function of the duration.

The difference limen for intensity ("memory" method) of noise pulses has been determined as a function of the duration. The duration was varied from 25 msec to 1 sec. White noise or bandpass filtered noise (300 Hz wide) at the center frequencies of 500 Hz, 2000 Hz and 8000 Hz was used.

A blockdiagram of the experimental set-up is given in Fig.15. The noise generator was a Sine Random Generator (Brüel and Kjaer, type 1024). Two noise signals of the same amplitude were added. The sum-signal could be attenuated up to 6 dB by attenuation in one of the separate channels (A_1). In this way very small

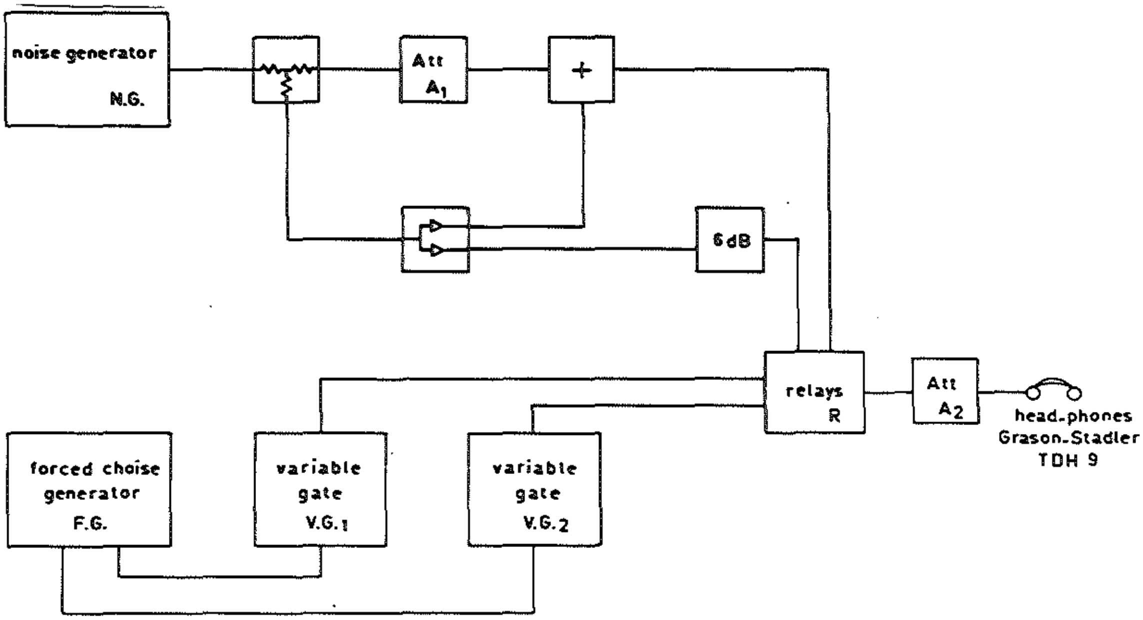

Fig.15. Blockdiagram of the experimental set-up.

intensity differences could be obtained reliably.
The duration of the noise pulses was varied with an adjustable gate. The sequence of the noise pulses was determined by a forced-choice generator. The experiments were carried out at 30 dB sensation level. Two subjects participated in this experiment. The experimental results are given in Fig.16.

For white noise with a duration longer than 100 msec, the two subjects show difference limens of 0.5 and 0.9 dB. For shorter durations the difference limen increases. The difference limen is higher for band-limited noise than for white noise. For a center frequency of 8000 Hz our estimate of integration time (inflection point in the curves) is the same as for white noise.

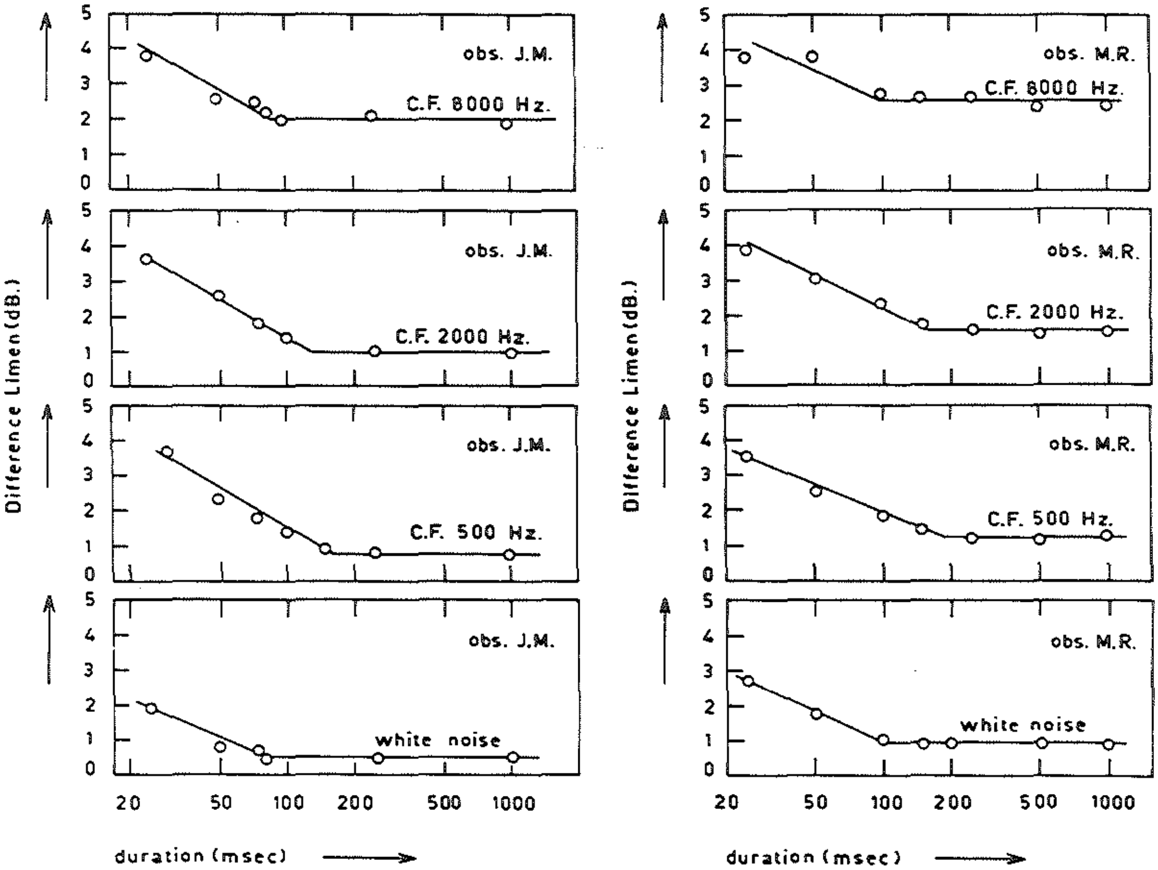

Fig.16. Difference limen of noise pulses as a function of the duration. As stimulus was used white noise, noise bands with 300 Hz bandwidth and with center frequencies of 500 Hz, 2000 Hz and 8000 Hz, respectively; observers J.M. and M.R.

The integration time estimates increase with decreasing center frequency . This corroborates the findings of Plomp and Bouman (1959).

CHAPTER 4.

DISCUSSION OF THE PSYCHOPHYSICAL RESULTS.

In the experiments described above, we attempted to measure the temporal transfer function of the auditory system using random noise stimuli. The transfer function we obtained is essentially low-pass in character with a cut-off frequency between 40 Hz and 80 Hz. The asymptotic slope of this transfer function is about 6 dB per octave. Modulation above 1000 Hz is inaudible.

4.1. Relation between the temporal transfer function and the critical band.

One question that arises is how the temporal transfer function is related to other characteristics of the auditory system (e.g. the critical band and the integration time). It is reasonable to think that the critical band mechanism may reduce the effective modulation depth. An amplitude modulated sine wave consists of the carrier with two side bands at frequencies $f_0 \pm f$ (f_0 the carrier frequency and f the modulation frequency). The frequency difference between the two side bands is 2f. If this frequency difference is larger than the critical bandwidth, the side bands will be attenuated, thus reducing the modulation depth.
It is unlikely that the critical band has any influence on the cut-off frequency of the temporal

transfer function. With a band of noise centered at 8000 Hz as a carrier,we obtained the same cut-off frequency as we did with white noise. The width of the critical band at 8000 Hz is certainly greater than two times the cut-off frequency. At a center frequency of 500 Hz the same result was obtained; the critical band is certainly larger than twice the cut-off frequency (30 Hz). The cut-off frequency at 8000 Hz is about twice what it is at 500 Hz, the critical bandwidth at 8000 Hz is 20 x larger than at 500 Hz. This makes a relation between the cut-off frequency and the critical band unlikely.

4.2. The temporal transfer function and the temporal integration.

Another characteristic of the auditory system that has obviously a close connection with our temporal transfer function is the temporal integration. This property is conveniently discussed in the context of the energy detection model of signal detection described extensively by Green and Swets (1966, chapter 8). This model consists of a filtering process (critical band), a square-law device, an integrator and a decision mechanism (Fig.17). The model proposes that an observer bases his decision about the presence or absence of a signal on the statistics of the process at the input of the detector.

The filtering process is rather well established as having a close connection to the so-called critical band. The square-law device, then, simply computes the power of the filter output [*].

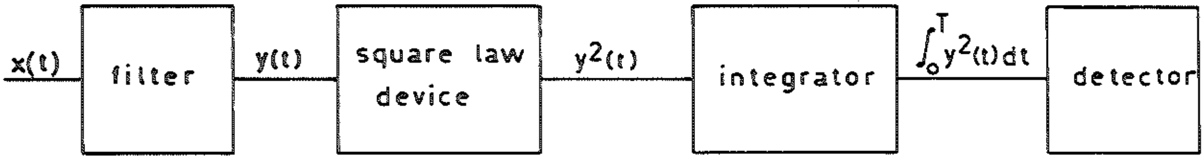

Fig.17. Flow diagram of the energy-model.

The integrator simply computes the energy of the signal in a time T. It is reasonable to assume that this integrator is not perfect - that it can be modeled with a low-pass filter. The cut-off frequency of the low-pass filter is roughly the inverse of the time constant of the integrator. Thus, if we assume that the human integration time is of the order of 200 msec. (Zwislocki, 1960, 1965), this implies a low-pass cut-off of the order of 5 Hz. Thus rapid variations in amplitude cannot be presented at the output of the energy detector. Therefore we must suppose that the auditory system processes information with a parallel channel system, in which separate channels have markedly different temporal characteristics. This was suggested also by Chistovich (1971) to account for the psychophysical data (Kozhevnikov et al, 1971) and electrophysiological data from Radionova (1971) and Gersuni et al (1971).

---

[*] A half-wave rectifier instead of a square-law device might be more realistic from the physiological point of view. Jeffreys (1964, 1970) has proposed such a model.

These latter researches corroborate our position with two types of neurons in the colliculus inferior as well as in the nucleus chochlearis. The first group of neurons is characterized by:

1. a short latency time at the threshold intensity,
2. little change in the threshold with an increase of the duration of the stimulus from 1 to 100 msec.,
3. a slight dependence of the number of spikes in the response on the intensity and the duration of the stimulus.

The second group of neurons is characterized by:

1. a long latency time at threshold,
2. a substantial decrease of the threshold with an increase of the stimulus from 1 to 100 msec.,
3. a pronounced dependence of the number of spikes in the response on the intensity and duration of the sound.

Both groups of neurons show a frequency selectivity. Gersuni et al concluded that the auditory system consists of a multichannel system of neurons tuned to several frequency bands simultaneously. Thus, a frequency analysis is made simultaneously in several channels, each of which processes information with different temporal characteristics.

The short latency system processes the fast variations of the stimulus and the long latency system provides the integration. The systems are parallel, so that these processes take place simultaneously; the output of the separate channels are added as is, among others, evident from our experimental data.

4.3. Influence of the frequency of the carrier.

The influence of the frequency of the carrier was investigated by using bands of modulated noise of diffetent center frequencies. For high center frequencies the cut-off frequency of the temporal transfer function was the same as for white noise. For a low center frequency the cut-off frequency was about a factor 2 smaller. In addition to the decrease of the cut-off frequency a vertical shift of the curves was found (Fig.12). The vertical shift of the curves appeared to be due to the bandwidth of the noise. The effect of the bandwidth was investigated at a modulation frequency of 10 Hz. (Fig.13 and Fig.14). Noise with a small bandwidth has slow amplitude variations, thus resulting in a higher modulation threshold. For large bandwidths the amplitude variations of the noise are rapid and attenuated by the temporal transfer function, so the modulation threshold is decreased. Thus the modulation threshold will decrease by increasing the bandwidth of the noise. In 3.2. it is shown that this occurs only up to a certain bandwidth. This value depends on the center frequency of the noise band. For center frequencies of 500 Hz, 2000 Hz and 8000 Hz we found that the values are about twice the normal critical bandwidths at these frequencies.

This experiment indicates that in tests of intensity discrimination with wide band noise a filtering process is involved. The vertical shift of the temporal transfer function in Fig.12 is probably due to this filtering process. Although the bandwidths of the noises were the same, the effective bandwidths were not. In Fig.18 the modulation threshold for a modulation frequency of 10 Hz (derived from Fig.12) are compared with the asymptotic modulation thresholds from Fig.13 and Fig.14.

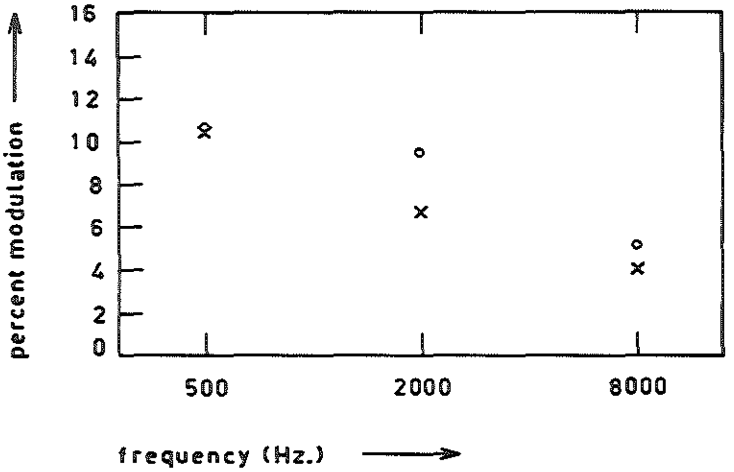

Fig.18. o: modulation threshold for a modulation frequency of 10 Hz from Fig.12;
x: the asymptotic modulation thresholds from Fig.13 and Fig.14.

The agreement between the two results is not excellent but the data show the same general trend. So we conclude that the horizontal shift of the temporal transfer function is due to an internal filtering process.

4.4. Difference limen and the integration time.

It is clear that some internal filtering process is involved in the intensity discrimination of bands of noise. It is also clear that temporal integration (another kind of filtering) is involved. This result comes from experiments on intensity discrimination of noise pulses of various durations. Several researchers have estimated the integration time by measuring the threshold of tone pulses as a function of the duration (Plomp and Bouman, 1959, Zwicker and Feldtkeller, 1967 p.163, Zwislocki, 1960, 1965). Generally, it has been assumed that integration time is independent of frequency. Our results, however, agree with those of Plomp and Bouman who found the integration time being longer at low frequencies. In our data the integration time is about a factor 2 longer for low frequencies than for high frequencies (Fig.16.). For white noise the integration time is the same as for high frequencies. Evidently, the system uses the smallest integration time available given the frequency content of the stimulus.

PART 2.

MEASUREMENTS OF EVOKED POTENTIALS IN MAN ELICITED BY AMPLITUDE MODULATED NOISE.

CHAPTER 5.

INTRODUCTION.

5.1. History of the measurement of the electrical activity of the brain.

Since the discovery of spontaneous electrical brain activity by Richard Caton in 1875, there has been a growing awareness of their importance for experimental use.

In the fifty years after Caton's work, the experiments were continued by Adolf Beck in Poland, Fleischl von Marxow in Vienna, Bechterev and Pravdich- Neminski in Russia and many others (see Brazier, 1961). During all of this time the electrical activity of the human brain was still not studied. It was Hans Berger (1929), who recorded the first human electroencephalogram (EEG) with electrodes on the scalp. His discovery of the alpha waves and their modification by sensory stimulation was a real breakthrough.

Nowadays the clinical application of electroencephalography is so universally accepted that it is surprising that Berger's publications were received with scepticism. Physiologists objected to Berger's work on purely technical grounds. Berger had used a double-coil galvanometer to record the electroencephalogram. No electrical amplification has been used and the optical system that had been used to record the oscillations of a mirror galvanometer on moving film might have allowed contamination from mechanical vibrations. The relatively smooth brain potentials which Berger reported and their periodicity contrasted with the form of action potentials from peripheral nerves. In addition the action potentials grew larger with increased physiological activity, while the brain activity, reported by Berger appeared to be greater during mental relaxation. These considerations led to the view that Berger's recordings were artifactual. Five years later, in 1934, Berger's work was corroborated by Adrian and Matthews, who used a valve amplifier and a pen recording apparatus. Since then the possibilities of the new technique have been appreciated and several workers have applied it to the study of cerebral disorders. Nowadays the electroencephalogram is a popular diagnostic tool.

In addition to corroborating Berger's work Adrian and Matthews (1934) reported an important new discovery that the alpha wave activity could be controlled to some extent by visual stimuli. They were able to phase-lock the alpha waves to a flickering visual stimulus up to 25 Hz flicker frequency. The amplitude of the alpha waves was maximal for flicker frequencies of about 10 Hz. Although it is possible to record the brain potentials that are elicited by sensory stimuli, these potentials are so small and variable that it is impossible to make quantitative measurements without using averaging techniques.

Thus a new era in the investigation of evoked potentials began with the introduction of the summation method (Dawson, 1954) and the development of special-purpose computers for measurement of averaged transient (Barlow, 1957, Clark, 1958).

5.2. Characteristics of visual and auditory evoked potentials.

Evoked potentials are influenced both by the condition of the observer and by physical parameters of the stimulus.
Several investigators have studied the influence of attention on evoked potentials (van Balen, 1960, van Hof et al, 1962, Garcia Austt et al for the visual system, Satterfield, 1965, Smith et al, 1970, Wilkinson and Morlock, 1967 for the auditory system).
In addition Weitzman and Kremen (1965) studied the evoked potentials during different stages of sleep.
One of the more intriguing findings has been the contingent negative variations (CNV) discovered by Grey Walter et al (1964). This potential is a slow negative drift which appears to be jointly correlated with a subject's expectation of the arrival of a stimulus and the requirement that he makes a discrimination response.
Two basic types of stimuli are used in evoked potential experiments. These two types might be called a) transient and b) steady state.
a) The transient stimuli are characterized by brief changes in one or more stimulus parameters (for example : luminance, location or shape of a visual stimulus and amplitude or frequency of an auditory one).
b) A steady state stimulus is obtained by periodic temporal modulation of the parameter of interest.
For example the luminance of a visual stimulus

might be sinusoidally modulated or a noise might be amplitude modulated. The modulation is usually prolonged over a sufficiently long period to allow the sensory system to settle into a steady state before data are taken.

5.3. Visual evoked potentials elicited by transient stimuli.

a. Difference between diffuse and patterned stimuli.

Potentials evoked by diffuse visual stimuli are not the same as those evoked by patterned stimuli (Clynes and Kohn, 1967, Harter, 1968). Jeffreys (1969) found some independence of the evoked potentials elicited by a diffuse flash and the evoked potentials elicited by a pattern, if this pattern is presented without any accompaning change in overall luminous flux. The evoked potentials produced by these two forms of stimulation have different spatial distributions over the head.

b. Locus on the retina.

Jeffreys (1971) reported that changing the retinal locus of a patterned stimulus influences the shape of the evoked potentials. He recorded simultaneously from several electrodes placed in a row along the midline. Whole field and upper and lower half-field stimuli (Skeleton checkerboard) were presented binocularly. When the pattern covered the whole retina the shape of the evoked potentials depended upon the electrode location. This was not the case with half-field stimulation. Then the polarity of corresponding components of the evoked potentials was opposite from the upper and lower half-field stimuli. For small stimuli the size of the evoked potentials was found to decrease as the stimuli were moved to the periphery (van Hof et al, 1966).

c. On and off responses.

Potentials evoked by pattern stimuli contain both an " onset" and an "offset" component (Jeffreys, 1969). In general, onset and offset responses have opposite polarities, and the amplitude of the onset response is usually higher than of the offset response.

5.4. Auditory evoked potentials elicited by transient stimuli.

Auditory evoked potentials have been recorded with click and tone burst stimuli. With clicks the responses recorded from the scalp have myogenic components (Bickford et al 1964). These myogenic components are smaller if tone bursts with a trapeziodal envelope are used (Rapin et al, 1966). It has been determined empirically that the best electrode location for measuring auditory evoked potentials is at the vertex (relative to ear or mastoid). This yields a response with a negative peak at a latency between 70 and 110 msec.(N_2), a positive peak between 180 and 220 msec. (P_2) and another negative peak at about 300 msec. (N_3).
With tone burst stimuli there are clear relations between tone frequency or intensity and the amplitude

of the N_2 - P_2 peak. Using these relations it is even possible to map out a sort of hearing threshold by measuring the evoked potentials.

The effects of some of the stimulus parameters on the evoked responses are briefly summarized below.

a. Frequency and intensity.

By varying the frequency and intensity of a tone burst a change in the amplitude of the N_2 - P_2 peak from 2 μV to 9μV was observerd (Autinoro et al, 1970). With a decrease in the frequency of the tone bursts, the amplitude of the N_2 - P_2 peak increases down to 125 Hz. The amplitude of the N_2 - P_2 peak generally increases monotonically with intensity except at 8000 Hz, where the amplitude asymptoted at high intensities.

b. Effect of repetition rate.

The amplitude of an evoked potential is strongly influenced by previous stimulation. For maximal amplitude the intervals between successive stimuli must be more than 6 sec.(Davis et al, 1966). Milner (1969) found that N_2 -P_2 potential difference increases with decreasing repetition rate down to 1 stimulus per 8 sec.

c. On and off responses.

The amplitude of the offset response is nearly always smaller than that of the onset response, but otherwise similar. A polarity change, as is observed with visual stimuli, does not occur. The ratio between the off response and the on response is about 0.7 at a duty-cycle of 0.5 (Milner, 1969).

5.5. Visual evoked potentials elicited by steady state stimuli.

The use of sinusoidally modulated light (modulation in time) as stimulus has many advantages:

a) the responses are highly reliable,
b) the subject is in a steady state of light adaptation,
c) the intensity of stimulation can be precisely controled by varying the modulation depth,
d) the presence of other frequencies in the evoked potentials gives information about non-linearities of the system.

Evoked potentials elicited by sinusoidally modulated light are very often distorted (i.e.,the EP is not sinusoid). Second or third harmonic components have been reported (Spekreyse, 1966, Kamphuisen, 1969). The second harmonic is very strong for modulation frequencies below 8 Hz; above 10 Hz the second harmonic is weak. The evoked potentials for sinusoidally modulated visual stimuli can be decomposed into low frequency and high frequency components (Spekreyse, 1966, Regan, 1968). The low frequency component has the frequency characteristic of a narrow band filter at 10 Hz. The spontaneous electroencephalogram shows a similar frequency characteristic.

Two types of non-linearities in the visual evoked responses have been reported:

1. amplitude independent rectification,
2. saturation at high modulation depths.

The first non-linearity is very sensitive. Even at a 1% modulation depth, a relatively strong second harmonic is found (Spekreyse, 1966, van der Tweel and Spekreyse, 1969). The second non-linearity is less sensitive. For monocular stimulation the saturation begins at a 40% modulation depth, for binocular stimulation, at 20%. This suggests that it may be not the modulation depth as such, but the size of the response that determines the saturation. In addition, it suggests that the saturation occurs at a stage where the signals from the two eyes are mixed. Using a linearising method, it has appeared possible to determine the characteristic of the linear element which preceeds the rectifier element (Spekreyse, 1966). This element has a frequency characteristic with a maximum at about 10 Hz, a low frequency attenuation of 6 dB per octave and a high frequency attenuation of about 18 dB per octave. In psychophysical experiments a high frequency slope of 60 dB per octave is found.

5.6. Auditory evoked potentials elicited by steady state stimuli.

Measurement of human auditory evoked potentials elicited by steady state stimuli has not yet been attempted. It has been done with animals, however, Tielen et al (1969) measured the evoked potentials elicited by sinusoidally amplitude modulated signals in unanaesthetized dogs. They recorded with electrodes in the inferior colliculus and the auditory cortex. Frequency analysis of these evoked potentials showed that the response included both the first and second harmonic. The frequency characteristics of the responses derived from some of the cortical areas showed a maximum for modulation frequencies between 15 Hz and 30 Hz. Saturation appeared at a modulation depth of 40% in two cortical areas.

CHAPTER 6.

ANALYSIS OF EVOKED POTENTIALS IN MAN ELICITED BY SINUSOIDALLY MODULATED NOISE.

To our knowledge there has not yet been a study of human auditory evoked potentials elicited by steady state acoustic stimuli. We have to perform such an experiment. The stimuli will be amplitude modulated noise, the same stimulus as was used in the psychophysical experiments. The use of this stimulus has the advantage that the spectrum is not changed by amplitude modulation. Futhermore it might be assumed that with a wide-spectrum stimulus the cortex is stimulated maximally, so that the amplitudes of the evoked potentials may be expected to be as great as possible. This was confirmed by an experiment with a sine-wave carrier instead of white noise. The EP elicited by this stimulus was much smaller.

6.1. Experimental method.

Two subjects participated in this experiment. During the recording sessions, the subjects were reading, lying comfortably in a sound proof room. Silver disc electrodes were applied: the active electrode was located at the vertex, the reference electrode at the forehead and the ground at the mastoid.
A block diagram of the experimental set-up is presented in Fig.19.

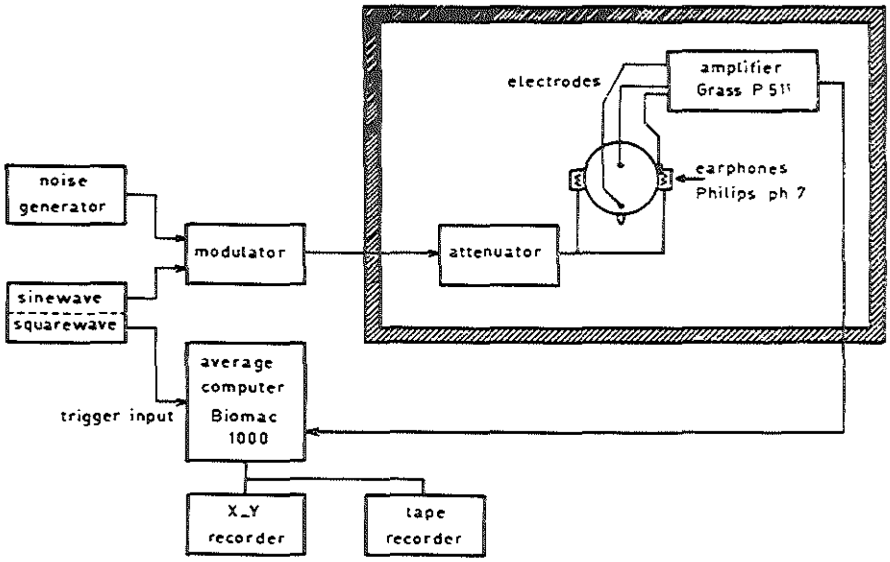

Fig.19. Block diagram of the experimental set-up.

Miniature earphones (Philips PH7) were used with insertable earpieces. The evoked potential between vertex and forehead was amplified (Grass P 511 amplifier) and then fed into the averager (Biomac 1000). The square wave output of the wave form generator, in phase with the modulating sine-wave, was used as the trigger signal for the averager. The evoked potentials from either 1024 or 4096 stimulus-cycles were averaged, and the result was plotted on an X-Y recorder.

In order to measure the spectral content of the evoked potentials, the averaged waveforms were reproduced periodically (Philips Analog 7). This signal was then analysed with a spectral analyser (Textronix 3L5, plug-in unit).

6.2. General results.

The amplitude of the evoked potentials elicited by sinusoidally modulated white noise appeared to be maximal at a modulation frequency between 9 Hz and 9.5 Hz. For one subject the maximal amplitude was 3 µV, and the waveform appeared to be a nearly undistorted sine wave (Fig.20).

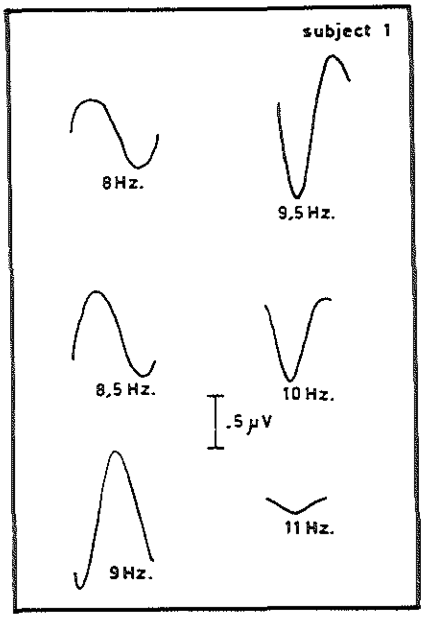

Fig.20. Evoked potentials elicited by amplitude modulated white noise. The results are shown for a number of modulation frequencies; 55 dB sensation level; modulation depth 100%; subject 1.

The results from the second subject were quite different, as is shown in Fig.21. The maximal amplitude was smaller (0.8 µV), and there was a sizeable amount of non-linear distortion.

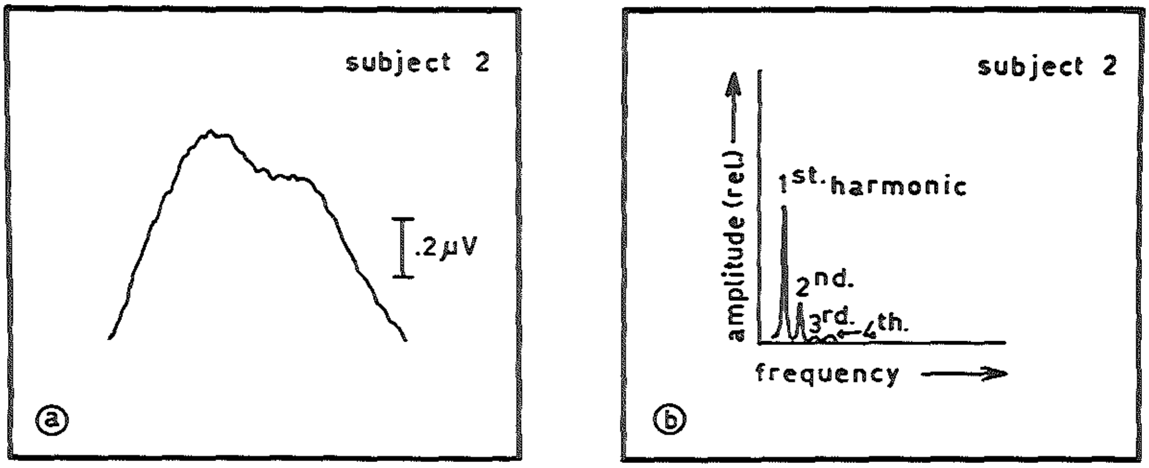

Fig.21. a) Evoked potential elicited by amplitude modulated white noise; modulation frequency 8 Hz; 55 dB sensation level; modulation depth 100%; subject 2.
b) the spectrum of this response.

A spectral analysis showed that the distortion is mainly at the second harmonic (Fig.21b). From Fig.20 we see that the EP amplitude is maximal at a modulation frequency of 9.5 Hz, and is smaller at lower and higher modulation frequencies. Furthermore the phase of the evoked potential appeared to increase steadily with the modulation frequency.
As a function of modulation depth the EP amplitude increases rapidly up to 30% modulation depth (Fig.22). For higher modulation depths the amplitude is constant. The phase of the EP is constant for low modulation depths and changes only at modulation depths above 50%.

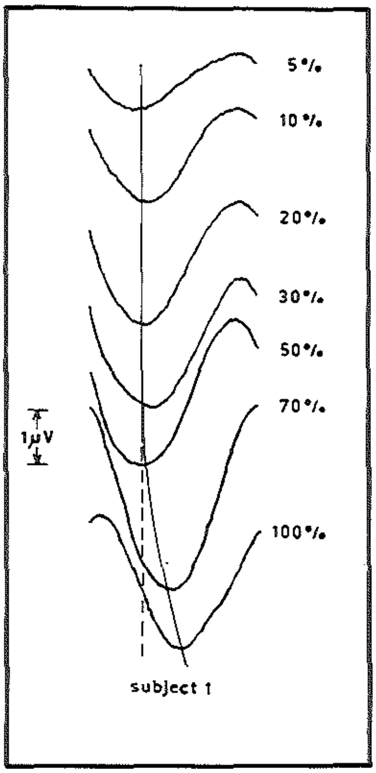

Fig.22. Evoked potential elicited by amplitude modulated white noise as a function of modulation depth; modulation frequency 9 Hz; 55 dB sensation level; subject 1.

6.3. Effect of overall intensity.

The experimental results presented in Fig.20 and Fig.22 were obtained at a stimulus intensity of 55 dB sensation level. In Fig.23 we show the effect of varying the overall intensity. These results were obtained with a modulation frequency of 9.5 Hz and 100% modulation depth.

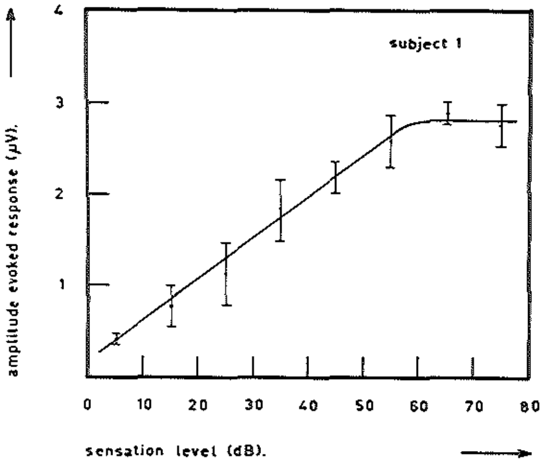

Fig. 23. Amplitude of evoked potentials as function of the intensity; modulation frequency 9.5 Hz; modulation depth 100%; subject 1.

Fig.23 shows the mean and standard deviation of 5 measurements in different sessions. The amplitude of the evoked potential increases with intensity up to about 55 dB sensation level. Above 55 dB sensation level the amplitude appears to be constant.

6.4. Influence of the modulation frequency.

The relation between EP amplitude and modulation frequency was studied at 100% modulation depth. The modulation frequency was varied between 8 Hz and 11 Hz for subject 1 and between 4 Hz and 11 Hz for subject 2. For subject 1, the phase characteristic was also measured. The results are presented in Fig. 24 and Fig. 25.

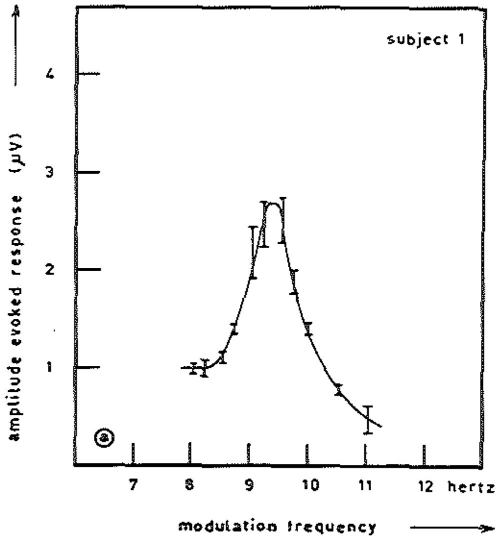

Fig.24. Amplitude characteristic of the evoked potentials elicited by amplitude modulated white noise; 55 dB sensation level; modulation depth 100 %; subject 1.

The EP amplitude is clearly frequency dependent. The amplitude characteristic shows a rather sharp maximum between 9 Hz and 9.5 Hz. The phase of the EP changes rapidly in this frequency region. Between 8.5 Hz and 10 Hz the phase increases about 180°. For subject 2, since the EP appeared to be distorted (Fig.21), the amplitude of only the first harmonic of the EP is plotted as a function of the modulation frequency (Fig.26). This function also shows a maximum at about 9 Hz, although it is not as sharp as for subject 1.

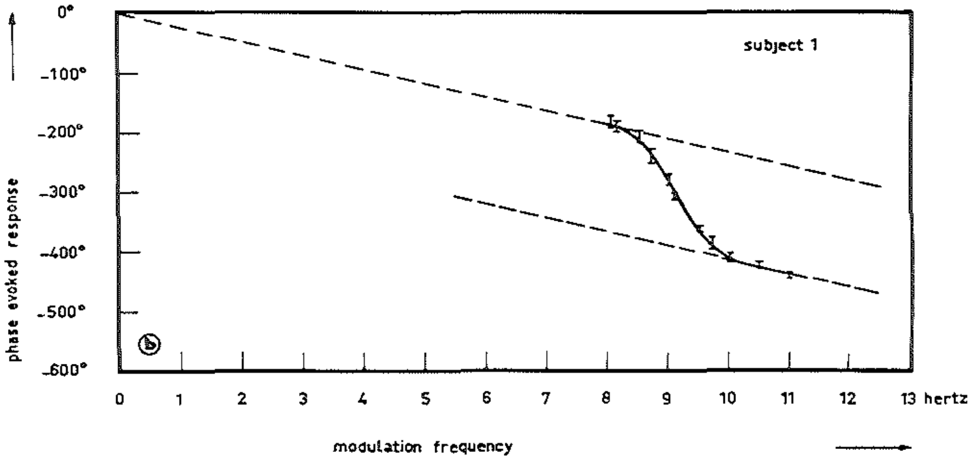

Fig.25.Phase characteristic of the evoked responses elicited by amplitude modulated white noise; 55 dB sensation level; modulation depth 100%; subject 1.

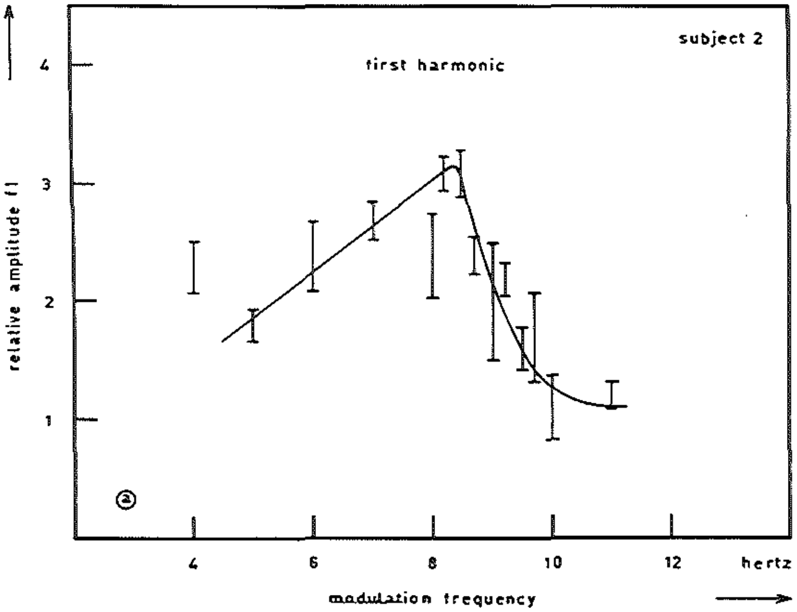

Fig.26.Amplitude characteristic of the first harmonic of the evoked potentials elicited by sinusoidally white noise; 55 dB sensation level; modulation depth 100%; subject 2.

6.5. Influence of the modulation depth.

Evoked potentials from both subjects were measured as a function of the modulation depth, at a modulation frequency of 9 Hz and 55 dB sensation level.

As is shown in Fig.27 and Fig.28 the EP amplitude increases with modulation depth up to 25% for both subjects (first harmonic amplitude for subject 2's data). Above 25% modulation depth the amplitude remains constant.

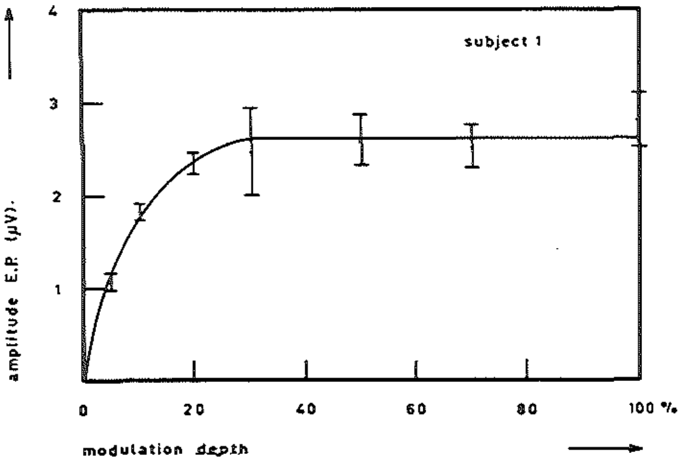

Fig.27. Amplitude of the evoked potentials as a function of the modulation depth. Modulation frequency 9 Hz; 55 dB sensation level; subject 1.

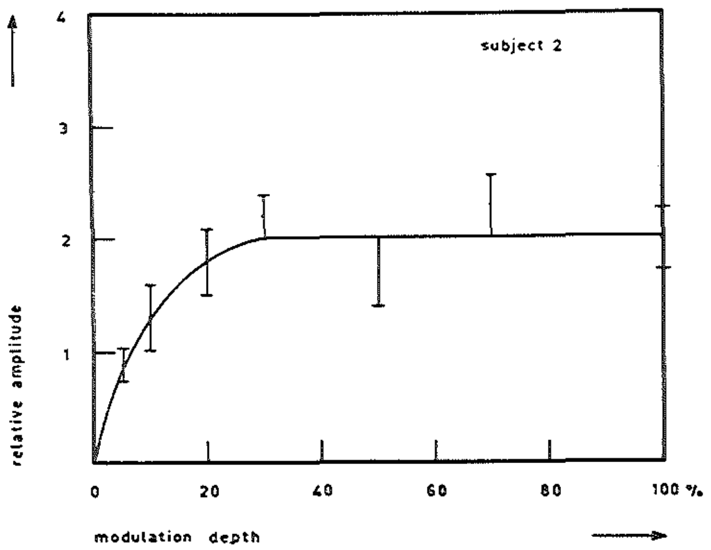

Fig.28. Amplitude of the first harmonic of the evoked potentials as a function of the modulation depth. Modulation frequency 9 Hz; 55 dB sensation level;subject 2. Note that the vertical scale is relative.

6.6. Sequence of the filtering process and the saturation mechanism.

The data from our various experiments on the EP suggest both action of some kind of filter and the presence of a sort of saturation element. The effect of modulation frequency suggests the filtering (a filter with a resonance between 8 Hz and 11 Hz). The effect of modulation depth suggests saturation (no change in EP amplitude above 25% modulation depth).
It might be possible to determine the sequence of

filtering and saturation mechanisms. If saturation occurs after filtering, then it should occur at the lowest modulation depth for a modulation frequency of 9.5 Hz, since the filter response is maximal at this frequency. At frequencies other than 9.5 Hz saturation should occur at higher modulation depths. However, if saturation occurs before the filter, it would always occur at the same modulation depth.

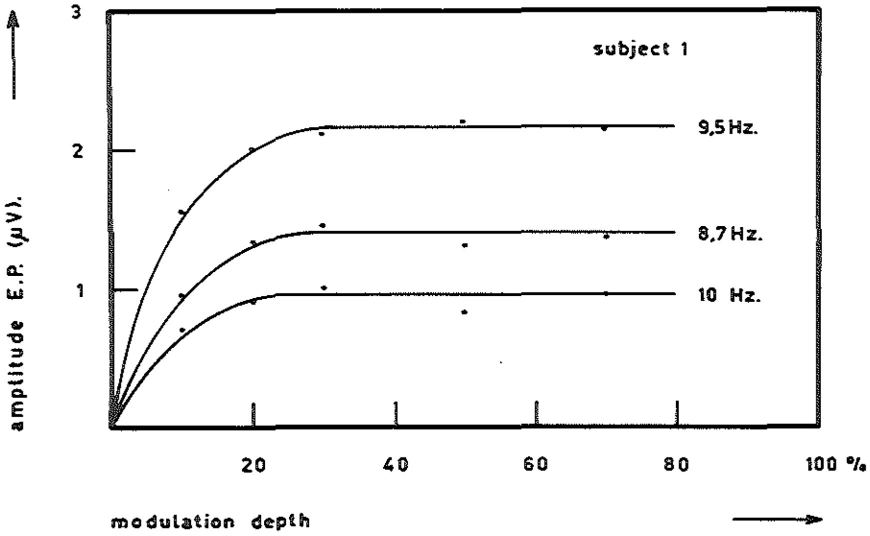

Fig.29. Saturation characteristics for modulation frequencies of 8.7, 9.5 and 10 Hz; 55 dB sensation level; subject 1.

Thus if we measure the saturation characteristic at different modulation frequencies we might be able to determine the sequence of filtering and saturation. To this end we measured saturation characteristics at three modulation frequencies (8.7, 9.5 and 10 Hz). The results are presented in Fig.29. The data show clearly that saturation always occurs at the same modulation depth. From these results we conclude that the saturation mechanism is located before the filtering mechanism.

CHAPTER 7.

DISCUSSION OF THE PHYSIOLOGICAL SIGNIFICANCE OF THE EVOKED POTENTIALS ELICITED BY SINUSOIDALLY MODULATED NOISE AND ITS RELATION TO PSYCHOPHYSICS.

The measurements of the evoked potentials elicited by sinusoidally modulated noise are analogous to the experiments with sinusoidally modulated light. The major difference between the auditory and visual results appears to be that the amplitude of the auditory EP is only 3 μV at most, while the amplitude of the visual EP is of the order of 20 μV (van der Tweel, 1964).

7.1. Amplitude and phase characteristics of the evoked potentials.

The amplitude characteristic (amplitude vs frequency) of the EP system is similar to the transfer function of a bandpass filter. The maximum amplitude is at about 9.5 Hz, and it decreases rapidly at higher and lower modulation frequencies (Fig.24.). The phase characteristic (Fig.25) can be decomposed into two different phase functions. One simply increases linearly with frequency. This implies nothing else than a time delay. The slope of the broken line in Fig.25 gives the time delay for this experiment. This slope implies a delay of about 66 msec. In analogous visual experiments a time delay of about 55 msec has been observed (Spekreyse, 1966, Regan, 1968).

Tielen et al (1969) reported a delay between 34 and 43 msec for auditory evoked potentials recorded from the cortex of a dog. These results agree with ours. The second phase shift of about 180^{o} occurs between 8Hz and 10Hz. This is consistent with the characteristic of the filtering process at these frequencies. The results from both subjects show a profound dependence of the EP on the modulation frequency. The optimal frequency of the EP system is between 9 Hz and 9.5 Hz. It is interesting to speculate that the EP activity might be related in some way to the alpha- activity, since the frequency composition of the latter is quite similar.

7.2. Relation between evoked potentials and spontaneous activity.

The possible relation of the evoked potentials to spontaneous activity, in particular to alpha-rhythm has been studied by Walter and Walter (1949), van der Tweel and Verduyn Lunel (1965), Spekreyse (1966) and Regan (1966). Various system theoretical approaches have been applied to analyse the alpha-activity. Filtering (van der Tweel and Verduyn Lunel, 1965, Bekkering et al, 1958, D.O.Walter, 1963) and autocorrelation studies (Weiss, 1959, Barlow, 1959) have shown that the alpha-activity can be described as a narrow band of noise. The amplitude probability density is Gaussian (Saunders, 1963).
The similarity of the spectrum of the spontaneous alpha-activity and the evoked potentials elicited

by sinusoidally modulated light might mean that the visual stimulus somehow synchronizes the alpha-rhythm (Grey Walter, 1959, J.S.Barlow, 1960). Several data conflict with this hypothesis. For example, van der Tweel and Verduyn Lunel (1965) reported that for one subject the alpha-activity with a maximum amplitude at 10.2 Hz was not effected by stimulation with light sinusoidally modulated at 9 Hz and 11 Hz.

Another argument against synchronization is put forward by Spekreyse (1966). He showed that the amplitude of the fundamental frequency was the same if noise was added to the modulation signal. The added noise would be expected to eliminate the possibility of synchronization.

If synchronization plays a role, the amplitude of the evoked potentials elicited by sinusoidally modulated noise should be larger when alpha-activity is present, than when it is not.

The experiments described in Chapter 6 were carried out with the subjects reading during the experiment. There was no alpha-activity under these circumstances. In another experiment we determined the amplitude characteristic of the amplitude potentials elicited by sinusoidally modulated noise, with alpha- activity present (closed eyes). The results are shown in Fig.30. This amplitude characteristic is similar in all respects to the characteristic from Fig.24. With open eyes the maximum amplitude was 2.6 µV and with closed eyes 3.0 µV. The amplitude of the alpha-activity

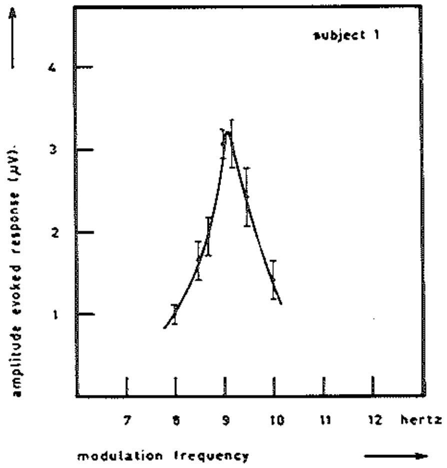

Fig.30. Amplitude characteristic of the evoked potentials elicited by amplitude modulated noise; 55 dB sensation level, modulation depth 20%, eyes closed, subject 1.

was about 40 µV, an order of magnitude larger than the amplitude of the evoked potentials. Thus we conclude that the alpha- activity and EP are independent processes.

7.3. Evoked potentials and psychophysics.

The evoked potential is largest at about 9.5. Hz modulation frequency, and is highly frequency dependent (6.4.). A very different characteristic was reported in our psychophysical experiments with the same stimulus. In these experiments the characteristic was strictly low-pass, with a cut-off frequency between 40 Hz and 80 Hz (2.3.).

We measured auditory evoked potentials with modulation frequencies between 4 Hz and 11 Hz. In this region the auditory temporal transfer function (determined from our psychophysical experiments) is independent of frequency. Because of the small amplitude it is not feasible to measure evoked potentials for frequencies above 11 Hz.

In visual experiments with sinusoidally modulated light, however, it is possible to measure evoked potentials for modulation frequencies beyond flicker-fusion frequency. Comparison of the de Lange curves with the frequency characteristics of the evoked responses led to discrepancies, which could not easily be explained. A breakthrough was made by Spekreyse (1966). He suggested that two frequency dependent mechanisms exist in the visual system, in addition to a rectifying mechanism and a saturation mechanism. One of the frequency dependent mechanisms was a low-pass filter, the other a band-pass filter centered at 9 Hz. Fig.31 gives the block-diagram of the Spekreyse model.

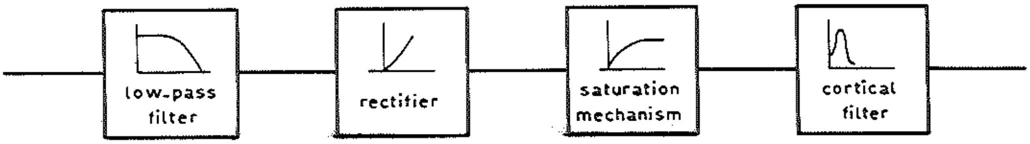

Fig.31. A simplified presentation of Spekreyse's model.

The rectifying mechanism introduces a second harmonic in the EP response, but Spekreyse was still able with a linearizing method to determine the frequency characteristic of the mechanism which was thought to be located before the rectifier.

The second filter is often called the " cortical filter". The operation of the saturation mechanism and the " cortical filter" can also be observerd in the results of our auditory experiments. The sequence of these two processes,which we discussed earlier,is the same as in the visual system (6.6.). It is not certain whether rectification also occurs in the auditory system. For one subject we found a distorted response, but whether this is caused by a specific non-linear device or by background activity is still an open question.

If a specific non-linear device introduces a second harmonic, this harmonic will have its maximal amplitude when the modulation frequency is about 4.5 Hz, because the " cortical filter" has its maximum at 9 Hz. Subject 1, which appeared to have an undistorted reponse for modulation frequencies between 8 Hz and 11 Hz, does show a distorted response for a modulation frequency of 4.5 Hz. However, we are unable to conclude that the second harmonic was due to a rectifying mechanism.

The low-pass filter cannot influence the evoked potentials because the output of this filter is independent of the frequency in the frequency-range between 4 Hz and 11 Hz. The low-pass filtering is clearly involved however in the process that leads finally to sensation. This was shown in the

first part of our study. It is reasonable to assume that these processes occur in an early stage of the processing and also are involved in the process that leads to the occurrance of evoked potentials. The process that leads to sensation is obviously accompanied by electrical activity. Much of this activity may not be detectable in the evoked potentials. Moreover the processes that result in the evoked potentials may produce activity, which does not play a role in the process which leads to sensation (Lopes da Silva, 1970). We showed that the " critical filter" is the last of a serie of processes that leads to the evoked potentials. We assume that this filter is only involved in the process that leads to the occurrance of evoked potentials. Thus it is not unreasonable that a low-pass characteristic is found in the psycho-physical experiments and a band-pass characteristic in the EP experiments.
It must be noted, that while the " cortical filter" may not be relevant with respect to sensation, its characteristics must be known if evoked response techniques are applied in studies of the visual and auditory systems.

Finally it should be stressed that we have made no attempt to describe the neurophysiological mechanisms underlying the generation of the evoked potentials. This issue might be clarified by studying the relations between evoked potentials and single cell recordings. This is obviously beyond the scope of this study.

SUMMARY.

It has been possible to measure input-output relations for the auditory system using as output both a quantified sensation and evoked potentials. In vision research both methods have been applied using sinusoidally modulated light as the stimulus. In the present study comparable experiments were carried out in the auditory system.

The psycho-physical experiments described in the first part of this study were analogous to de Lange's flicker experiments. We measured the relation between the modulation frequency and the modulation depth with sinusoidally amplitude modulated white noise as a stimulus. The result was a low-pass frequency characteristic with a cut-off frequency between 40 Hz and 80 Hz depending upon the observer. The asymptotic slope of the curve was about 6 dB per octave. We have called this curve the auditory temporal transfer function. The shape of the transfer function appeared to be independent of intensity from 20 dB to 60 dB sensation level. We also used bandlimited noise as a carrier. At a center frequency of 8000 Hz the cut-off frequency of the temporal transfer function is the same as for white noise. The cut-off frequency decreases with the center frequency of the noise band. At a center frequency of 500 Hz the cut-off frequency is about ½ what it is at 8000 Hz.

We also studied the effect of the bandwidth of the modulated noise on the temporal transfer function. Center frequencies of 500 Hz, 2000 Hz and 8000 Hz were used. The modulation threshold decreases with increasing bandwidth up to a certain value. At a center frequency of 500 Hz, this value was 200 Hz; at 2000 Hz center frequency it was 600 Hz, and at 8000 Hz center frequency it was 2500 Hz. The increase in this asymptotic value with increasing center frequency is comparable with that of the critical band. Therefore it appears likely that the critical band mechanism plays some role in the perceptibility of amplitude modulation of wide band noise.

The difference limen of noise pulses is a function of the duration of the noise pulses. For short durations the difference limen decreases with increasing duration. For durations longer than the integration time of the ear the difference limen is independent of the duration. Therefore it is possible to estimate the integration time by measuring the difference limen for noise pulses as a function of their duration. An integration time of 100 msec was estimated for white noise stimuli. This value was also found for bandpass noise at a center frequency of 8000 Hz. The integration time appears to increase as the center frequency decreases. This corroborates the findings of Plomp and Bouman (1959), who measured the threshold for tone pulses as a function of their duration.

It is impossible that rapid amplitude variations are presented in a system with a time constant between 100 and 200 msec. Therefore it is reasonable to conclude that the entire auditory system cannot be represented as a serial model, such as is proposed by Green and Swets (1966), but must consist of parallel data processing channels.

In the seond part of this study auditory evoked potentials were recorded from the human scalp. Sinusoidally modulated white noise was used as a stimulus. The influence on the EP of the modulation frequency and the modulation depth were studied. With one subject an undistorted sinusoidal EP was observed for modulation frequencies between 8 Hz and 11 Hz. With the other subject the EP waveform was distorted. The spectrum of this wave consists mainly of the first and second harmonics. The amplitude of the EP from the first subject was heavely dependent on the modulation frequency. The frequency characteristic was that of a sharp bandpass filter with a maximum between 9 Hz and 9.5 Hz. The first harmonic of the evoked potentials obtained from the second subject shows a comparable frequency characteristic, although less sharp.
In visual experiments with sinusoidally modulated light a similar frequency characteristic is found (Spekreyse, 1966, Regan, 1968). The apparent filtering process is often called " cortical filtering".
Evoked potentials were also measured as a function of the modulation depth. The amplitude of the EP increases with modulation depth up to 25%. At

this modulation depth a kind of saturation occurs. By determining the dynamic characteristics of the evoked potentials at different modulation frequencies it is demonstrated that the saturation occurs before the " cortical filter".

The frequency characteristic found with evoked response techniques is very different from the temporal transfer function. The discrepancy can be explained by assuming that the " cortical filter" does not play a role in the process that leads to sensation.

SAMENVATTING.

Input- output relaties zijn gemeten, zowel met gekwantificeerde sensaties als met " evoked potentials" als de output van het zintuig systeem. In het visuele onderzoek worden beide methodes toegepast met sinusvormig gemoduleerd licht als stimulus.

In het eerste deel van deze studie worden de psycho-fysische experimenten beschreven. Analoog met de experimenten van De Lange werd sinusvormig amplitude gemoduleerde witte ruis als stimulus gebruikt. De relatie tussen de modulatie frekwentie en de modulatie diepte, die nodig was om de modulatie juist hoorbaar te maken, werd gemeten. De frekwentie karakteristiek, die aldus gevonden werd, is te beschrijven als een laag doorlaat filter met een afsnijfrekwentie tussen 40 Hz en 80 Hz, afhankelijk van de proefpersoon. De steilheid van de flank van deze karakteristiek voor hoge frekwenties bedraagt slechts 6 dB per octaaf, in tegenstelling met de visuele temporele overdrachtsfunktie, waar een steilheid van 60 dB per octaaf wordt gevonden (De Lange, 1952). Deze karakteristiek wordt de auditieve temporele overdrachtsfunktie genoemd. Deze overdrachtsfunktie is onafhankelijk van de intensiteit in het gebied van 20 dB tot 60 dB sensatie niveau.
Bij gebruik van een ruisband als draaggolf signaal, blijkt de overdrachtsfunktie ook afhankelijk te zijn van de centrale frekwentie van deze ruisband.

Voor ruisbanden met 8000 Hz als centrale frekwentie is de afsnijfrekwentie dezelfde als voor witte ruis. Voor bandruis met 500 Hz als centrale frekwentie is de afsnijfrekwentie bijna een faktor 2 kleiner. De afsnijfrekwentie van de overdrachtsfunktie neemt dus af met afnemende centrale frekwentie van de ruisband.
Voor ruisbanden met 500 Hz, 2000 Hz en 8000 Hz als centrale frekwentie werd het effekt van de bandbreedte op de hoorbaarheid van de modulatie onderzocht. De modulatie drempel neemt af met een toename van de bandbreedte tot een bepaalde waarde. Voor nog grotere bandbreedtes is de modulatie drempel konstant. De modulatie drempel neemt af bij toenemende bandbreedte tot 200 Hz, 600 Hz en 2500 Hz respectievelijk, voor de centrale frekwenties 500 Hz, 2000 Hz en 8000 Hz. Dientengevolge is het zeer waarschijnlijk, dat bij het waarnemen van amplitude modulatie van signalen met een breed spectrum, het kritieke band-mechanisme in werking is.

De difference limen voor ruispulsen is een funktie van de duur van de ruispulsen. Voor korte duur van de ruispulsen neemt de difference limen af bij toename van de duur. Voor duren groter dan de integratie tijd van het oor is de difference limen onafhankelijk van de duur. Het is dus mogelijk de integratie tijd voor het oor te bepalen door de difference limen van ruispulsen te bepalen als funktie van de duur. Voor witte ruis wordt op deze wijze een integratie tijd van 100 msec. gevonden. Deze waarde wordt ook gevonden voor een ruisband met 8000 Hz als centrale frekwentie.De

integratie tijd neemt af als de centrale frekwentie afneemt. Dit is een bevestiging van de resultaten van Plomp en Bouman (1959).
Het is niet mogelijk, dat snelle amplitude variaties verwerkt worden door een systeem met een integratie tijd tussen 100 en 200 msec. Daarom moeten wij wel aannemen, dat het auditieve systeem niet kan worden opgevat als een serie model, zoals is voorgesteld door Green en Swets (1966), maar dat het uit parallelle systemen bestaat: een systeem met een betrekkelijk lange integratie tijd en een systeem met een zeer korte integratie tijd om snelle fluctuaties te kunnen waarnemen.

In het tweede deel van de studie wordt een beschrijving gegeven van de metingen van de " evoked potentials" afgeleid van de vertex van de mens. In analogie met visuele experimenten met continue signalen, werd sinusvormig gemoduleerde witte ruis als stimulus gebruikt. De invloed van de modulatie frekwentie en de modulatie diepte op de " evoked potentials" werd onderzocht voor 2 proefpersonen.
Voor de ene proefpersoon wordt voor modulatie frekwenties tussen 8 Hz en 11 Hz een onvervormde sinusvormige responsie gevonden. Voor de andere proefpersoon wordt een vervormd signaal gevonden.
Het spectrum van dit signaal bestaat hoofdzakelijk uit de eerste en de tweede harmonische. De amplitude van de " evoked potentials" van de eerste proefpersoon als funktie van de modulatie frekwentie uitgezet, levert een frekwentie karakteristiek van een banddoorlaat-filter met een maximum tussen 9 Hz en 9.5 Hz op. De amplitude van de eerste harmonische van de

" evoked potentials" van de andere proefpersoon levert een gelijksoortige karakteristiek op.

In visuele experimenten met sinusvormig gemoduleerd licht wordt een overeenkomstige frekwentie karakteristiek gevonden (Spekreyse, 1966, Regan, 1969). Dit wordt vaak " cortical filter" genoemd.
Voor beide proefpersonen werden de " evoked potentials" bepaald als funktie van de modulatie diepte. De amplitude van de eerst harmonische neemt toe met een toename van de modulatie diepte tot 25%; daarna treedt verzadiging op. Door de dynamische karakteristieken van de " evoked potentials" voor verschillende modulatie frekwenties te bepalen, konden wij aantonen, dat het verzadigings mechanisme vóór het " cortical filter" is gelokaliseerd.

De frekwentie karakteristiek, die wij door middel van metingen van " evoked potentials" hebben gevonden, is totaal verschillend van de temporele overdrachtsfunktie, die met psycho-fysische methodes bepaald werd. Deze discrepantie kan verklaard worden door aan te nemen, dat het " cortical filter" geen rol speelt in het proces dat tot waarneming van de modulatie leidt.

REFERENCES.

E.D.ADRIAN and H.B.C.MATTHEWS, 1934.
The Berger rhythm: potential changes from the occipital lobes in man. Brain 57: 355-385.

F.ANTINORO, P.H.SKINNER and J.J.JONES, 1969.
Relation between sound intensity and amplitude of the AER at different stimulus frequencies.
J.A.S.A. 46: 1433- 1436.

A.TH.M. VAN BALEN, 1960.
De electro- encephalografische reactie op licht prikkeling en zijn betekenis voor de oogheelkundige diagnostiek. Proefschrift , Utrecht, Klomp & Bosman's drukkerijen N.V.

J.S.BARLOW, 1957.
An electronic method for detecting evoked responses of the brain and for reproducing their average waveforms. Electroenceph. clin. Neurophysiol. 9: 340-343.

J.S.BARLOW, 1959.
Autocorrelation and crosscorrelation analysis in electroencephalography. IRE Transac on Med. Electronics ME-6: 179-183.

J.S.BARLOW, 1960.
Rhythmic activity induced by photic stimulation in relation to intrinsic alpha activity of the brain in man. Electroenceph. clin. Neurophysiol. 12: 317-325.

I.D.H.BEKKERING, W.S. VAN LEEUWEN and A.KAMP, 1958.
The EEG- spectrograph. Electroenceph. clin. Neurophysiol. 10: 555-559.

H.BERGER, 1929.
Über das Elektrenkephalogramm des Menschen.
Arch.f. Psychiat. 87: 527-570.

R.G.BICKFORD, J.L.JACOBSON and T.R.CODY, 1964.
Nature of average evoked potentials to sound and other stimuli in man. Ann.N.Y.Acad.Sci. 112: 204-217.

E. DE BOER, 1966.
Intensity discrimination of fluctuating signals.
J.A.S.A. 40: 552-560.

E.G.BORING, 1950.
A history of experimental psychology. Appleton-Century-Crofts.

E.G.BORING, 1966.
Editor's introduction in "Elements of Psychophysics" by Gustav Fechner ed. by Davis H.Howes and Edwin G.Boring. Holt, Rinehart and Winston, Inc, New York

C.E.BOS and E. DE BOER, 1966.
Masking and discrimination. J.A.S.A. 39: 708-715.

M.A.B.BRAZIER, 1961.
A history of the electrical activity of the brain. The first half-century Pitman medical publishing co, Ltd, London.

R.CATON, 1875.
The electric currents of the brain. Brit.med.J. 2: 278.

L.A.CHISTOVICH, 1971.
Auditory processing of speech stimuli- evidences from psychoacoustics and neurophysiology. Proceedings of the 7th International Congress on Acoustics. Vol. 1: 27-41. Akadémiai Kiadó, Budapest.

W.A.CLARK JR., 1958.
Average response computer (ARC-1). Quarterly Progress Report Research Laboratory of Electronics, M.I.T. 114-117.

M.CLYNES and M.KOHN, 1967.
Spatial visual evoked potentials as physiologic language elements for color and field structure. Electroenceph. clin. Neurophysiol. Suppl. 26: 82-96.

M.CLYNES, M.KOHN and K.LIFSHITZ, 1964.
Dynamics and spatial behaviour of light evoked potentials, their modification under hypnosis and on-line correlation in relation to rhythmic components. Ann.N.Y. Acad,Sci. 112: 468-509.

H.DAVIS, T.MAST, N.YOSHIE and S.ZERLIN, 1966.
The slow response of the human cortex to auditory stimuli: recovery process. Electroenceph.clin. Neurophysiol. 21: 105-113.

P.A.DAVIS, 1939.
Effect of acoustic stimuli on the waking human brain. J.Neurophysiol. 2: 494-499.

N.A.DUBROVSKIĬ and L.N. TUMARKINA,1967.
Investigation of the human perception of amplitude-modulated noise. Soviet Physics- acoustics 13: 41-47.

E.GARCIA-AUSTT, J.BOGACZ and A.VANZULLI, 1964.
Effects of attention and inattention upon visual evoked responses. Electroenceph. clin. Neurophysiol. 17: 136-143.

G.GÄSSLER, 1954.
Über die Hörschwelle für Schallereignisse mit verschieden breitem Frequenzspektrum. Acustica 4: 408-414.

G.V.GERSUNI, J.A.ALTMAN, A.M. MARUSEVA, E.A. RADIONOVA, G.I.RATNIKOVA and I.A. VARTANIAN, 1971.
Functional classification of neurons in the inferior colliculus of the cat according to their temporal characteristics. Chapter 10 in "Sensory processes at the neuronal and behavioral levels" G.V.Gersuni, ed. Academic Press, New-York- London.

D.M.GREEN and J.A.SWETS, 1966.
Signal detection theory and psychophysics.
John Wiley and sons, Inc. New York, London, Sydney.

D.D.GREENWOOD, 1961.
Auditory masking and the critical band. J.A.S.A. 33: 484- 502.

J.D.HARRIS, 1963.
Loudness discrimination. J.Speech and Hear. Dis. suppl.11.

M.R.HARTER, 1968.
Effects of contour sharpness and check-size on visual evoked cortical potentials. Vision Res. 8: 701-711.

H.HELMHOLTZ, 1863.
Die Lehre von den Tonempfindungen als physiologische Grundlage für die Theorie der Musik.
F.Vieweg & Sohn, Braunschweig.

M.W.VAN HOF, J.VAN HOF- VAN DUIN, J.VAN DER MARK and W.J.RIETVELD, 1962.
The effect of image formation and that of flash-counting on the occipital response to light-flashes. Acta physiol. and pharmacol. Neerl. 11: 485-493.

M.W.VAN HOF, J.VAN HOF- VAN DUIN, W.J.RIETVELD, 1966.
Enhancement of occipito-cortical responses to light flashes in man during attention. Vision Res. 6: 109-111.

L.A.JEFFRESS, 1964.
Stimulus-oriented approach to detection. J.A.S.A. 36: 766-774.

L.A.JEFFRESS, 1970.
Masking chapter III in "Foundations of modern auditory theory". J.V.Tobias ed. Volume I Academic Press New York and London.

D.A.JEFFREYS, 1969.
Characteristics of visual and auditory EP's in " Evoked potentials as indicators of sensory information processing. D.Mackay ed. Neuro-science Research. Program Bulletin 7: 181-276.

D.A.JEFFREYS, 1971.
Source of cortical evoked potentials components located by recording from the human scalp. Nature 229: 502-504.

H.A.C.KAMPHUISEN., 1969.
Average EEG response to sinusoidally modulated light in normal subjects and patients. Thesis Utrecht.

V.A.KOZHEVNIKOV, J.J.KUZMIN, S.J.ZHUKOV, 1971.
Perception of amplitude modulated vowel-like stimuli. Proceedings of the 7th International Congress on Acoustics. Vol. 3: 21-23. Akadémiai Kiadó Budapest.

H.DE LANGE Dzn.,1952.
Relationship between critical flicker frequency and a set of low frequency characteristics of the eye. J.Opt.Soc.Am. 44: 380-389.

H.DE LANGE Dzn., 1958.
Research into the dynamic nature of the human fovea-cortex systems with intermittent and modulated light I attenuation characteristics with white and colored light. J.Opt.Soc.Am. 48: 777-784.

F.H.LOPES DA SILVA, 1970.
Dynamic characteristics of visual evoked potentials. Schotanus & Jens Utrecht 1970.

D.MAIWALD, 1967a.
Ein Funktionsschema des Gehörs zur Beschreibung der Erkennbarkeit kleiner Frequenz- und Amplitudenänderungen. Acustica 18: 81- 92.

D.MAIWALD, 1967b.
Die Berechnung von Modulationsschwellen mit Hilfe eines Funktionsschema. Acustica 18: 193-207.

G.A.MILLER and W.G.TAYLOR, 1948.
The perception of repeated bursts of noise. J.A.S.A. 20: 171-182.

B.A.MILNER, 1969.
Evaluation of auditory function by computer techniques. International Audiology VIII: 361-370.

R.PLOMP and M.BOUMAN, 1959.
Relation between hearing threshold and duration for tone pulses. J.A.S.A. 31: 749- 758.

E.A.RADIONOVA, 1971.
Two types of neurons in the cat cochlear nuclei and their role in audition Chapter 9 in " Sensory processes at the neuronal and behavioral levels". G.V.Gersuni ed. Academic Press. New York- London.

I.RAPIN, 1965.
Auditory evoked response in normal waking adults. Acta oto-laryng. suppl. 206: 113-122.

I.RAPIN, H.SCHIMMEL, L.M.TOUK, N.A.KRASNEGOR, Ch.POLLAK, 1966.
Evoked responses to clicks and tones of varying intensity in waking adults. Electroenceph.clin. Neurophysiol. 21: 335-344.

D.REGAN, 1966.
An effect of stimulus colour on average steady-state potentials evoked in man. Natue (London) 210: 1056-1057.

D.REGAN, 1968.
A high frequency mechanism which underlies visual evoked potentials. Electroenceph. clin. Neurophysiol. 25: 231-237.

S.O.RICE, 1954.
Mathematical analysis of random noise in "Selected papers on Noise and Stochastic processes" N.Wax ed. Dover- New York.

J.H.SATTERFIELD, 1965.
Evoked cortical responses enhancement and attention in man. A study of responses to auditory and shock stimuli. Electroenceph. clin. Neurophysiol. 19: 470-475.

M.G.SAUNDERS, 1963.
Amplitude probability density studies on alpha and alpha-like patterns. Electroenceph. clin. Neurophysiol. 15: 761-767.

B.SCHARF, 1959.
Loudness of complex sounds as a function of the number of components. J.A.S.A. 31: 783-785.

B.SCHARF, 1961.
Complex sounds and critical bands. Psychol.Bull. 58: 205-217.

R.A.SMIAROWSKI and B.L.KINTZ, 1966.
The auditory fusion frequency of intermittent sounds. J. of Gen.Psychol. 74: 129-143.

D.B.D.SMITH, E.DONCHIN, L.COHEN and A.STARR, 1970.
Auditory averaged evoked potentials in man during selective binaural listening. Electroenceph. clin. Neurophysiol. 28: 146-152.

H.SPEKREYSE, 1966.
Analysis of EEG responses in man evoked by sinewave modulated light. Thesis Amsterdam. Dr.W. Junk publishers,The Hague.

D.SYMMES, L.F.CHAPMAN and W.C.HALSTEAD, 1955.
The fusion of intermittent white noise. J.A.S.A. 27: 470-473.

E.TERHARDT, 1968a.
Über die durch Amplituden modulierte Sinustöne hervorgerufene Hörempfindung. Acustica 20: 210-214.

E.TERHARDT, 1968b.
Über akustische Rauhigkeit und Schwankungsstärke. Acustica 20: 215-224.

E.TERHARDT, 1970.
Frequency analysis and periodicity detection in the sensation of roughness and periodicity pitch, in " Frequency analysis and periodicity detection in hearing". R.Plomp and G.F.Smoorenburg eds. A.W. Sythoff, Leiden.

A.M.TIELEN, A.KAMP, F.H.LOPES DA SILVA, J.P.RENEAU and W.STORM VAN LEEUWEN, 1969.
Evoked responses to sinusoidally modulated sound in unanaesthetized dogs. Electroenceph. clin. Neurophysiol. 26: 381- 394.

L.H.VAN DER TWEEL, 1964.
Relation between psychophysics and electrophysiology of Flicker. Symp. Amsterdam 1963, Doc. Ophtal. 18: 287-304.

L.H.VAN DER TWEEL and H.F.E.VERDUYN LUNEL, 1965.
Human visual responses to sinusoidally modulated light. Electroenceph. clin. Neurophysiol. 18: 587-598.

L.H.VAN DER TWEEL and H.SPEKREYSE, 1969.
Signal transport and rectification in the human evoked-response system. Ann. N.Y. Acad. Sci. 156: 678-695.

D.O.WALTER, 1963.
Spectral analysis of electroencephalograms: mathematical determination of neurophysiological relationships from records of limited duration. Exptl.neurol. 8: 155-181.

W.G.WALTER, 1959.
Intrinsic rhythms of the brain."Handbook of Physiology", vol. I, chapter XI, American Physiological Society, Washington, D.C.

W.G.WALTER, R.COOPER, V.J.ALDRIDGE, W.C.MACCALUM and A.L.WINTER, 1964.
Contingent negatieve variation : an electric sign of sensori-motor association and expectancy in the human brain. Nature (London) 203: 380- 384.

V.J.WALTER and W.G.WALTER, 1949.
The central effects of rhythmic sensory stimulation. Electroenceph. clin. Neurophysiol. 1: 57-86.

R.T.WILKINSON and H.C.MORLOCK, 1967.
Auditory evoked responses and reaction time. Electroenceph. clin. Neurophysiol. 23: 50-56.

T.F.WEISS, 1959.
Some properties of the finite time sample autocorrelation of the electroencephalogram. Thesis M.I.T. Cambridge, Mass.

E.D.WEITZMAN and H.KREMEN, 1965.
Auditory evoked responses during different stages of sleep in man. Electroenceph. clin. Neurophysiol. 18: 65-70.

E.ZWICKER, 1952.
Die Grenzen der Hörbarkeit der Amplitudenmodulation und der Frequenzmodulation eines Tones. Acustica 2: 125-133.

E.ZWICKER, 1954.
Die Verdeckung von Schmalbandgeräuschen durch Sinustöne. Acustica 4: 415- 420.

E.ZWICKER, 1961.
Subdivision of the audible frequency range into critical bands (Frequenzgruppen) J.A.S.A. 33: 248.

E.ZWICKER and R.FELDTKELLER, 1955.
Über die Lautstärke von gleichformigen Geräuschen. Acustica 5: 303- 316.

E.ZWICKER and R.FELDTKELLER, 1967.
Das Ohr als Nachrichtenemphänger. S.Hirzel Verlag, Stuttgart.

J.ZWISLOCKI, 1960.
Theory of temporal auditory summation. J.A.S.A. 32: 1046- 1060.

J.ZWISLOCKI, 1965.
Analysis of some auditory characteristics."Handbook of mathematical psychology". R.D.Luce, R.R.Bush and E.Galanter eds. Vol III, chapter 15. John Wiley and Sons.Inc.

CURRICULUM VITAE

23 april 1936	geboren te Ter-Aar.
1954	Eindexamen HBS-B.
1954-1963	Studie Wiskunde en Natuurkunde, VU Amsterdam; afgestudeerd met experimentele natuurkunde als hoofdvak, wiskunde en filosofie als bijvakken.
1963-1967	Werkzaam op de Keel-, Neus- en Oorafdeling van het Radboudziekenhuis te Nijmegen, waar electrofysiologisch onderzoek aan de cochlea van de kat werd verricht.
vanaf augustus 1967	In dienst van de Medische Faculteit Rotterdam en werkzaam op de afdelingen Biologische en Medische Natuurkunde en Keel-, Neus- en Oorheelkunde.