ADAPTATION OF THE SENSES OF TEMPERATURE AND TOUCH

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ACADEMISCH PROEFSCHRIFT TER VERKRIJGING VAN DE GRAAD VAN DOCTOR IN DE WIS- EN NATUURKUNDE AAN DE R. K. UNIVERSITEIT TE NIJMEGEN OP GEZAG VAN DE RECTOR MAGNIFICUS MR. L.G.A. SCHLICHTING, HOOGLEERAAR IN DE FACULTEIT DER RECHTSGELEERDHEID, VOLGENS HET BESLUIJT VAN DE SENAAT DER UNIVERSITEIT IN HET OPENBAAR TE VERDEDIGEN OP VRIJDAG 4 DECEMBER 1959 DES NAMIDDAGS TE 4 UUR.

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CHAPTER 1

INTRODUCTION

§1. Field of investigation

Adaptation is one of the most remarkable properties of biological systems; it is frequently encountered in investigations of the senses.

The aim of this study is to gain information concerning the adaptation in the senses of the human skin.

It is a well-known phenomenon that if a physical stimulus remains constant during some time the sensation does not have a constant magnitude but often diminishes in time. Such a dynamic behaviour of the sense system is often called adaptation. As the term adaptation is employed in a confusing way it is intended to use it here according to Jenkins 6) for the dynamic behaviour mentioned above. For convenience's sake the sensory system is presented in simplified form in fig. 1. It consists of receptors of which the output reaches the central nervous system via peripheral nerve fibres. Somewhere some change in activity in the nervous system gives rise to a sensation.

![Fig. 1. A simplified block diagram of the system to be investigated.](image)

The methods available for an investigation, as mentioned above, are roughly to be divided into two categories. First under certain experimental conditions a subject can be asked for a description of his sensation (Psychophysics). The obvious disadvantage of this method is the impossibility of isolating the system to be tested. When this method is used, every precaution has to be taken, to prevent other parts of the complex system from interfering.

Secondly the electrical activity in parts of the nervous system
can be measured (Electrophysiology). This requires a more or less destructive preparation, restricting this method to animals. Moreover, the functional meaning of a measured activity cannot always be established. If an increase in temperature e.g. produces some activity in a part of the nervous system this may give rise to a warmth sensation, a sensation of pain or possibly no sensation at all. By the use of both methods in quantitative investigations we may find the functional meaning of the electrical activity and the localisation of certain features of the stimulus sensation relations.

The senses in the skin yield a spectrum of sensations: warmth, heat, cold, pain, touch, pressure, tickle etc. 2) thus providing information concerning the physical conditions of the body surface. This study limits itself to the senses of temperature and touch.

§2. Review of literature

In handbooks of physiology 6,7,16) it is suggested that certain shapes of end-organs in the skin can be functionally identified as being a receptor e.g. for touch, for warmth or for cold. Weddell c.s. 18,19,20) expressed doubt about this classification. They found free nerve endings with accidental graded differences in shape and position. As a consequence of this they rejected the specificity of these nerve endings 13). However, in electrophysiology the activity of nerve fibres which show responses to not too excessive stimulation, is mostly found to be very specific. A small deformation in the skin elicits an activity in other fibres than in those stimulated by a moderate thermal stimulus, such "deformation" fibres being relatively insensitive to thermal stimulation. Some fibres show an activity that is not specific for a certain kind of stimulation, but their sensitivity to both thermal stimulation and deformation are relatively small 9,91,94). Moreover, some mechano-receptors have been extensively investigated recently and there can be no doubt about their specificity 89).

The mechanism which converts in the receptor or specialised nerve ending a physical stimulus into a form of energy suitable to trigger the nerve, is not well known. But a direct relation is often demonstrated between the frequency of impulses in the sensory nerve and the electrical activity of the receptor, the so-called receptor potential 1,89).

Attempts made to explain the mechanism of the temperature receptors 56,59,63) have not been decisive as yet.

From electrophysiological investigations it becomes clear that adaptation is very marked for both the "deformation" and the tempe-
The adaptation of cutaneous nerves after a constant stimulus can be complete or not (fig. 2). It is mostly or perhaps always present.

The deformation fibres can be divided into rapidly and completely adapting touch fibres and the less sensitive slower and incompletely adapting "pressure" fibres. Investigations have been carried out by Keidel 94), by Adrian and Zotterman 73), Catton 80) and others, but quantitative data about time constants are lacking.

Hensel and Zotterman 45) investigated fibres in the cat's tongue signalling cold. These fibres show incomplete adaptation; the time-constant of the decay of activity is in the range 0.3 - 2.2 seconds. The warmth fibres found by Dodt and Zotterman 35) in the tongue of the cat also display incomplete adaptation; they behave, however, more irregular, are much less frequently found and seem to be less sensitive. This, and the fact that they are difficult to find elsewhere in the cat, led Boman 29) to the conclusion that the sensations of warmth and cold are mediated by the same cold fibres. The so-called warmth fibres can be considered to be in fact pain fibres.

A common daily experience learns that slight weights put upon the skin are felt only a short time.

Psychophysical procedures to investigate the sense of touch have been used mainly to gain quantitative data about the sensitivity of the skin to vibration. Békésy 74), Wilska 107) and others 94) showed that sensitivity is greatest at frequencies of about 250 Hz.

Psychophysical studies of the last decennium have revealed that
in order to describe warmth sensations at least three quantities have to be considered: temperature, rate of change of temperature and stimulus area. Hensel reached this conclusion by measuring the change of temperature in different layers in the skin. Vendrik and Vos used microwave radiation to get a uniform temperature rise in the superficial layers of the skin, where the receptors are situated. These experiments suggested that, when slowly rising temperatures are produced in the skin, a central adaptation occurs which prevents their being perceived.

§3. Presentation of the problem

Generally speaking biological sense systems are better suited to perceive changes in environmental physical conditions rather than stationary conditions. Such dynamic properties will here be studied quantitatively in the case of touch and temperature sense in the human skin. For this purpose the output of the sense system has to be measured when a known input is applied to the system. The output is the magnitude of the sensation or the electrical activity in parts of the nervous system.

The measurement of the electrical activity in peripheral nerve fibres raises no essential problems. On the other hand it is difficult if not impossible for a human observer to describe with sufficient reliability his sensations quantitatively as a function of time. Sensation scales as advocated by Stevens can be employed but their usefulness with the relatively rapidly changing sensations as encountered in practice must be doubted. Therefore threshold measurements are used. If threshold values of slowly rising stimuli of long duration are compared with rapidly increasing brief stimuli, the effect of dynamic properties must be measurable.

The determination of the threshold values brings about the problem of the mechanism of the detection of a stimulus by a subject. Recently studies were carried out of the behaviour of observers, who had to detect signals in the presence of noise. For our purpose we shall have to investigate here the applicability of the psychophysical theories in the case of threshold measurements.

The aim will be to separate as much as possible the dynamic characteristics of the receptors of the peripheral nerve fibres and of the central nervous system. If two different senses are compared, as will be done hereafter, the problem of specificity of the receptors
will come up for discussion as a matter of course.

The conclusions of the experiments will only be valid for relatively small stimuli, as the experiments are always near-threshold measurements. Also, in all psychophysical experiments the same part of the skin of the inner side of the forearm was stimulated. This part of the skin is rather homogeneous and no trouble was to be expected from underlying bone structures.
CHAPTER II

PSYCHOPHYSICAL ASPECTS OF THRESHOLD MEASUREMENTS

§1. Measurement of thresholds: the problem of detection of a signal in the presence of noise

A threshold is usually defined as the magnitude of a stimulus which yields a prescribed probability of producing a sensation. The fact that a well-defined stimulus sometimes causes a sensation and sometimes fails in this respect indicates that fluctuations influence the realization of sensation.

The notion of a threshold needs further specification. Is this an essential limit for a certain sensory system, or an arbitrary value of the stimulus, influenced by certain experimental conditions? Sometimes a real threshold is found, independent of the procedure of the experiment. In other cases the performance of a subject is totally dependent on the instructions given to him.

When an observer gives a positive response after a stimulus, the question arises whether this response was a reliable one. The observer can have guessed. The reliability of a response can be easily tested by presenting a mixture of real stimuli and stimuli of zero intensity. In many test situations observers have been shown to give positive responses in cases where a zero intensity was presented. To make sure that a so-called false alarm is not a pure guess but a real mistake another experiment can be carried out. Three intervals in time are presented to the observer and in one of the intervals a near-threshold stimulus is given. The observer is asked in which of the intervals he experienced the stimulus most clearly and also to give his second choice. Now let us consider the possibilities of the second choice in case of wrong first choice decisions. After the first wrong choice one of the two remaining intervals will contain the stimulus. If out of the two remaining intervals the observer choses more frequently the interval containing the stimulus, he will experience in his sense system more activity in this interval than in the other. If, however, the observer merely guesses, both remaining intervals will be chosen equally frequently, and the presence of a missed stimulus does not increase the activity, determining a sensation.
Such and other experiments 14,15) done with sound and visual stimuli indicate that observers do not guess. So if they give a false alarm it is a mistake. That is a certain activity in the sense system is mistaken for a stimulus, indicating that spontaneous activity or fluctuations of existing activities must be present in the nervous system. Spontaneous activities or fluctuations have indeed been found almost everywhere in the nervous system, peripherally 5,8) as well as centrally 81).

In general a threshold measurement can thus be considered as the recording of the decisions of an observer who tries to detect signals in the presence of noise. His policy of detection may be influenced by the value that is attached to a false alarm or to a missed signal.

§2. Mathematical treatment of the detection model

An exact and full account of the theory of detection is given by Peterson Birdsall and Fox 12). Other studies on the subject have been published by Van Meter and Middleton 10) by Tanner, Birdsall and Swets 14,15) and by Fitzhugh 3). Most experiments by Tanner, Swets and others have been done with noise added externally to the sense system. Munson and Karlin 4) applied the theory to threshold measurements in hearing. Their way of description will be mainly followed.

In this chapter the fluctuating neural activity when a stimulus is present will be called signal + noise. The fluctuating activity at zero intensity will be indicated as noise.

![Diagram](image)

**Fig. 3.**

a. The fluctuation of the neural activity without and with a signal presented (noise and signal + noise respectively).

b. All fluctuations can be thought of to occur only in the discriminant level which simplifies the picture.
A subject observes during a well-defined interval of time the activity somewhere in his nervous system. From this observation he has to decide whether or not a stimulus has been presented. In fig. 3a the probability of the activity during an observation being at a certain level is plotted in the case of noise alone and in the presence of signal + noise. The observer decides on a signal when the activity observed exceeds a certain value. This value is shown in fig. 3a as the discriminant level. It is clear that when the activity exceeds the discriminant level in case of noise alone a false alarm occurs. Thus the probability of a false alarm in the situation of fig. 3a is given by the shaded area. It is not probable that an observer is able to keep this discriminant level exactly constant, so also this level may be expected to fluctuate. To simplify the picture it is assumed that for small signals the variances of noise and of signal + noise are the same. The relevant quantity determining the occurrence of a false alarm is the difference between the noise level and the discriminant level when noise alone is present. All fluctuations are now thought of to occur only in the discriminant level, the probability density function of which is called detection curve (fig. 3b). The same is done in case of signal + noise and because of the assumption made the same detection curve is obtained. It is assumed furthermore that a monotonous function will describe the relation between the intensity of the stimulus and the average nervous activity in the observation interval. The final model is shown in fig. 3b, which is equivalent to the model of fig. 3a. The noise and signal + noise levels are constants in a series of experiments with a certain intensity of the stimulus. The discriminant level is fluctuating, as shown by the detection curve. The variability in this level is referred back to effective stimulus levels. So the detection curve can be described as a function \( f(x) \) of stimulus magnitudes \( x \).

From fig. 3b it is readily seen that

\[
P_N (N) = 1 - P_{SN} (N) = \int_{0}^{\infty} f(x)dx
\]

\[
P_{SN} (SN) = 1 - P_N (SN) = \int_{-\infty}^{S} f(x)dx
\]

where

\[
\int_{-\infty}^{\infty} f(x)dx = 1
\]
\[ s = \text{signal strength} \]

\[ P_N(N) = \text{probability of the decision "no signal" when zero intensity is presented} \]

\[ P_{SN}(N) = \text{probability of a false alarm} \]

\[ P_N(SN) = \text{probability of a missed signal} \]

\[ P_{SN}(SN) = \text{probability of correct detection of a signal} \]

As signals travel in the nervous system in the form of action potentials \( f(x) \) may not be a continuous function. This is especially the case if only few action potentials should suffice to evoke a sensation. Then the distribution \( f(x) \) will be a discrete distribution and the integrals in (1) have to be replaced by sums. However, if many action potentials are needed or graded synaps potentials are important, it should be expected that \( f(x) \) can be considered as a continuous function.

The hypothesis will be tested that \( f(x) \) can be described by a normal distribution expressed in stimulus magnitudes. Then (1) can be written in more detail

\[
P_N(N) = 1 - P_{SN}(N) = \frac{1}{\sigma \sqrt{2\pi}} \int_{0}^{\infty} e^{-\frac{(x-d)^2}{2\sigma^2}} \, dx
\]

\[
P_{SN}(SN) = 1 - P_N(SN) = \frac{1}{\sigma \sqrt{2\pi}} \int_{-\infty}^{s} e^{-\frac{(x-d)^2}{2\sigma^2}} \, dx
\]

where

\[ d = \text{mean of normal distribution} \]

\[ \sigma = \text{standard deviation} \]

This can be written in the form

\[
P_N(N) = \frac{1}{2} + \frac{1}{\sqrt{\pi}} \int_{0}^{\frac{d}{\sigma \sqrt{2}}} e^{-y^2} \, dy
\]

\[
P_{SN}(N) = \frac{1}{2} + \frac{1}{\sqrt{\pi}} \int_{0}^{\frac{s-d}{\sigma \sqrt{2}}} e^{-y^2} \, dy \tag{2}
\]

One particular set of experiments with a known intensity of the
stimulus yields the values of \( P_N(N) \) and \( P_{SN}(SN) \). Entering these figures into the tables of the normal distribution produces values of

\[
\frac{d}{\sigma\sqrt{2}} \quad \text{and} \quad \frac{s-d}{\sigma\sqrt{2}}
\]

When \( s \) is known, \( d \) and \( \sigma \) can be calculated in the measure of the stimulus.

Another feature of the concepts developed above is the possibility of measuring the observer's efficiency. According to this model the observer can reach an optimum performance by shifting his detection curve. For instance, let us consider a series of \( m \) trials with stimuli of zero intensity and \( n \) trials containing a stimulus of constant strength. The score reached by the observer can be defined as

\[
Q = n \, P_{SN}(SN) - m \, P_N(N)
\]

With the expressions (2) it can be shown that \( Q \) is maximum for

\[
\frac{d^2}{2\sigma^2} = \frac{(s-d)^2}{2\sigma^2}
\]

If \( m = n \), optimum performance is reached when \( d = 1/2 \, s \).

An essential condition for the success of these experiments is, of course, the use of well-trained observers.

In the experiments described in the following chapters three different procedures, referred to as \( a \), \( b \) and \( c \), are used in threshold measurements.

\( a \) The observer knows the strength of the stimulus \( s \) and the interval in which the stimulus is given but he does not know the sequence of "zero" stimuli and "real" stimuli, which have an equal probability of occurrence.

The observer will alter his value of \( d \) when a different value of \( s \) is presented. At every stimulus strength a value of \( d \) and \( \sigma \) is found. Consistency with the model requires a constant value of \( \sigma \), independent of \( s \). The discriminant level \( d \) may or may not be optimum. This method is not sufficiently sensitive for checking the applicability of the normal distribution.

\( b \) The observer knows the interval in which the stimulus is given; he does not know the sequence of stimuli, having four or five equally probable fixed intensities, one of which is zero.

The observer has to keep his discriminant level constant now.
The probability of detection can be plotted as a function of stimulus strength on normal probability paper. In case of a normal distribution the curve should be a straight line. This method is much more sensitive for testing this point, because the variable d is constant here.

The observer is given the opportunity to vary the intensity of the stimulus himself. His instruction is to find a just noticeable stimulus intensity. He can have as many trials as he wants. The actual strength of the stimuli remains unknown to him.

This method is, of course, only preferable when a quick and rough determination of the threshold is wanted. The discriminant level is an unknown factor, dependent on the attitude of the observer.

§3. Results of detection experiments with touch and warmth stimuli

The instrumental equipment used in measuring the thresholds will be discussed in later chapters.

In fig. 4 the probability of a positive response in an experiment of type b is shown for warmth stimuli. The stimulus was a linearly increasing temperature. With this particular example the stimulus duration was 0.38 sec. Stimuli of five different intensities, one of which was of zero intensity, were mixed at random. The total number of trials was 360 with 72 trials at each intensity. The integrated normal curve represents the probabilities very well, because a straight line fits the measured points. So the detection curve can be described by a normal distribution.

In fig. 5 similar measurements of probabilities are collected for a linearly increasing deformation during 0.16 sec. Fig. 6 shows the same for sinusoidal deformations in four intensities with 40 trials each. For all three subjects it can be concluded that the measured probabilities of one series fit to an integrated normal distribution within the experimental error. However, when considering all series with deformation stimuli a slight deviation is found because most of the series show a false alarm rate that is slightly too high. This points to a skewed distribution or to some non-linearity in the system. As the deviation would give rise to corrections smaller than the accuracy of measurement in one series, all the single series will be approximated by a normal distribution.

The detection curve having been approximated by a normal distribution, it is now possible to consider the results of experiments of type a in more detail. In table I the results of several series are shown. Each series consists of sets of 60 or 70 trials, one half
Figure 4.
Percentage of probability of a positive response at different intensities of warmth stimuli. At zero intensity the percentage of false alarms can be seen. The symbols $\chi$ and $\sigma$ denote the mean and the standard of the detection curve.

Figure 5.
Percentage of probability of a positive response at different intensities of touch stimuli. The symbols $\chi$ and $\sigma$ denote the mean and the standard deviation of the detection curve.

Figure 6.
Percentage of probability of a positive response at different intensities of sinusoidal touch stimuli. The symbols $\chi$ and $\sigma$ denote the mean and the standard deviation of the detection curve.
of which were of zero intensity and the other half of a certain fixed intensity. Each set produces a value of \( \sigma \) and \( s/d \). Sets of different fixed intensities, and of variable other experimental conditions (e.g. exposure time), are averaged in one series. No significant correlation was found between intensity of the stimulus \( s \) and the value for \( \sigma \), neither between \( \sigma \) and the other variables introduced in one series. As half the number of trials consists of zero intensity, \( s/d \) has to equal 2 for optimum detection. The value of \( s \) with \( \text{P}_{\text{SN}} (\text{SN}) - \text{P}_{\text{SN}} (\text{N}) = 85\% \) has been taken as a unity rather arbitrarily, the reasons for which will be given later. This value of \( s \) was found by graphical interpolation. The mean values of \( \sigma \) and \( s/d \) for the various series are given in table I.

### Table I

Mean values of \( \sigma \) and \( s/d \) in different series of experiments

<table>
<thead>
<tr>
<th>Series</th>
<th>Subj.</th>
<th>Warmth</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>number of trials</td>
<td>( \sigma )</td>
<td>( s/d )</td>
<td></td>
</tr>
<tr>
<td>I</td>
<td>E</td>
<td>2080</td>
<td>0.34</td>
<td>1.69</td>
<td></td>
</tr>
<tr>
<td>II</td>
<td>E</td>
<td>1560</td>
<td>0.32</td>
<td>1.70</td>
<td></td>
</tr>
<tr>
<td>III</td>
<td>E</td>
<td>1560</td>
<td>0.36</td>
<td>1.66</td>
<td></td>
</tr>
<tr>
<td>I</td>
<td>R</td>
<td>2080</td>
<td>0.32</td>
<td>1.99</td>
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<tr>
<td>II</td>
<td>R</td>
<td>1560</td>
<td>0.31</td>
<td>2.68</td>
<td></td>
</tr>
<tr>
<td>III</td>
<td>R</td>
<td>1560</td>
<td>0.32</td>
<td>2.17</td>
<td></td>
</tr>
</tbody>
</table>

The standard deviation of all values of \( \sigma \) and \( s/d \) in table I amounts to 15 - 25\% of the stated values. Owing to the large scattering in the numerical results definite conclusions are rather difficult to draw. It seems that with few exceptions the subjects did not reach optimum detection, especially so with lower intensities, but it is emphasized that the subjects had no training in this respect. Given the value of \( s/d \), a theoretical \( \sigma \) can be calculated. In the region of the \( s/d \) found the normal distribution requires that \( \sigma \) should have values in the range 0.33 - 0.35 which is not contradictory to the measured values.
The value of $\sigma$ in stimulus measure could serve as an adequate definition of a threshold. However, such a definition is never used in physiological literature. A threshold is more commonly defined as a stimulus intensity with a certain probability of perception.

As was mentioned before, a subject can shift his detection curve in the course of the experiments. When this happens, both the probability of a false alarm, $P_{SN}(N)$, and the probability of correct detection, $P_{SN}(SN)$, will change. From fig. 3b it can be seen that the probability of perception defined as $P_{SN}(SN) - P_{SN}(N)$ will be less dependent on the shift of the detection curve than $P_{SN}(SN)$.

The threshold will be defined as the stimulus intensity which yields a probability of perception of 85%. When procedure a is used in the experiments $P_{SN}(N)$ varies with the intensity of the stimulus applied, contrary to $P_{SN}(N)$ in one series in procedure b. However, the threshold will be defined in the same way in both cases.

§4. Some special problems of the detection model. The noise spectrum

A problem that will be encountered concerns the summation of two stimuli. It is evident that two independent stimuli, each apart having a probability of detection of $P_1$ and $P_2$, will be detected both together with a probability of $P_1 + (1 - P_1) P_2$. When the observer has only limited receiver abilities because he can concentrate on only one of the stimuli, the probability of the combined stimulus will be less. When two stimuli are applied simultaneously and the experimental probability equals the probability of detection of a stimulus of an intensity that is the algebraic sum of the intensities of the two stimuli, complete summation exists. Such summation can be measured best with psychophysical procedure b, when zero intensity, two separate stimuli, and a combination of the two are mixed.

Another question that will be met in later chapters is how detection behaves as a function of exposure time of a stimulus of constant intensity. The relation was investigated for vibrational touch stimuli using procedure b. In figs. 7a and 7b the results of one subject are shown; it appears that little or no influence was seen. A second observer also did not show an improvement of detection with longer exposure times up to 3 sec. This is a curious phenomenon as it would be expected that sampling nervous activity of longer duration or more samples taken during one exposure should improve
Detection considerably.

This problem offers an opportunity to specify the phenomenon of noise encountered in threshold measurements. Noise activities in the nervous system always have positive values. So these activities have a positive mean value. Every fluctuation can be considered as a modulation superimposed on this mean value. By taking more samples the experimentally found \( \sigma \) generally should decrease, a decrease equivalent to a lowering of the threshold. Only if the different samples are completely correlated no decrease in \( \sigma \) will be found. Complete correlation means a non-fluctuating level of activity in different samples during the observation interval. The experiments did not show a lowering of threshold with longer stimulus duration, indicating that components with periods between 0.17 and 3 sec are not present in the modulation.

However, periods longer than 3 sec are present in the noise because of the variability of detection during one series. When the noise contains components with longer periods, it is clear that such a phenomenon can have repercussions in the succession of positive and negative responses of the observer. Components with periods larger than
the time between two successive observations should make a positive response more probable after a positive than after a negative response. The same can be said reversely for a negative response. For some series of 360 trials, where stimuli succeeded with 15 - 20 sec intervals with 5 different intensities arranged in random fashion, the probability of combinations of successive positives and negatives was calculated. All bigram combinations were about equally probable, indicating that fluctuations in the noise interfere with the detection of stimuli more than 15 sec apart. By diminishing the intervals between the stimuli, more information can be obtained about the lower frequencies in the noise spectrum, but such experiments were not done.

Moreover, by measuring a threshold more than once under equal experimental conditions a variation over longer periods is found. As the threshold is considered as a certain signal to noise ratio it is not relevant in this respect whether the variability over several weeks or months is called drift or variation in sensitivity or noise.

Many experiments with warmth stimuli were done with temperatures increasing linearly with time. In some of these experiments the time was measured from the beginning of the stimulus till the response of the observer. The scattering in these so-called delay times gives an indication as to the frequencies in the noise spectrum. Fig. 8a illustrates this point. When only high frequencies e.g. > 10 Hz, are interfering with the stimulus, the time of detection should be determined within a few tenths of a second. Low frequencies, however, make
the time of detection very uncertain in different trials. Fig. 8b shows that indeed rather large differences in delay times are found. The histogram of the delay times reflects in some way the probability density function of the discriminant level.

Thus far some noise data have been gathered from psychophysical evidence. However, from electrophysiological data some conclusions may be drawn about the noise in the peripheral nerve fibres. Fig. 9 shows histograms of intervals of action potentials in cold fibres of the rat taken from pictures by Boman 29). Two stationary activities with a duration of 22 sec at two different temperatures are compared. The distribution resembles the gamma-distribution, but there are no short intervals because of the recovery time needed before a new action potential can be fired (see also 5, 8).

It can be seen in fig. 9 from the values of the mean and the standard deviations that fluctuations in the temperature measured amount to 0.5 and 3°C respectively.

![Variability of intervals of action potentials in a single cold fibre. Calculations were made from pictures in a publication of Boman 29).](image-url)
De Vries calculated the temperature fluctuations which a receptor of 1 μ diameter would show spontaneously. The number of atoms in the receptor being \( N \), the relative energy fluctuations inside the receptor are

\[
\Delta E = \frac{\sqrt{6N}}{6N} \frac{1}{2} kT
\]

Since the temperature is proportional to the energy the temperature fluctuations will be

\[
\Delta T = \frac{\sqrt{6N}}{6N}
\]

With \( N = 10^{11} \) and \( T = 300^\circ K \) de Vries arrived at temperature fluctuations of about \( 4.10^{-4} \) °C with an average lifetime of \( 10^{-5} \) sec.

Assuming that the receptor is a cylindrical membrane of 1 μ diameter a thickness of 0.1 μ and a length of 1 μ, the number of atoms is roughly estimated as \( 5.10^9 \) and \( \Delta T = 2.10^{-3} \) °C with an average lifetime of \( 10^{-5} \) sec. To trigger the nerve a fluctuation of the receptor potential must have a duration of about \( 10^{-4} \) sec. The "effective" temperature fluctuation will thus be about \( 7.10^{-4} \) °C, as the fluctuations over about 10 lifetimes are averaged. Thinner membranes have greater temperature fluctuations, but their heat capacity is smaller and the resistance of heat flow to the surroundings is not much dependent on the thickness of the membrane. For this reason thinner membranes have greater \( \Delta T \) but a shorter lifetime. Both factors influence the effective fluctuation by the square root of the volume cancelling each other. Even when it is presumed that temperature fluctuations of the atoms in a receptor are not fully independent of each other, the spontaneous temperature fluctuations will be much lower than the electrophysiologically found fluctuations in activity of one receptor.

In checking the fluctuations obtained from psychophysical experiments against the electrophysiological findings it must be remembered that sensation is determined by the output of many receptors. The area over which the output of the receptors is summated is assumed to be 25 cm². In Howell's Textbook of Physiology it is stated that in the human forearm about 14 cold spots per mm² are found. To identify this with the number of receptors may be called a rash assumption, but other more reliable quantitative data are lacking. So in 25 cm² there should be \( 4.10^4 \) receptors. With a fluctuation of 1°C per receptor the effective noise over the whole area reduces to 0.005°C, when no integrating mechanism in the time is used. With psychophysical measurements to be described later on, the detection curve was measured for a linear decrease of temperature during
2 sec. The sigma of the detection curve appeared to be equivalent to a decrease in temperature of about 0.02°C. If all figures used are reliable this should indicate that besides noise in the peripheral nerves an additional noise exists, which should have its origin in the central nervous system. Given the fact that the activity of the cold fibres decreases at a higher temperature, the absolute effective fluctuations should increase with a higher skin temperature, giving a higher threshold value. This is not found (38, 60), which is an indication that the noise is for the greater part of central origin.

More certainty exists concerning the origin of the noise in the tactile sense system. The sensitive large touch fibres show very rarely spontaneous activity. This electrophysiological fact has been found in cats, dogs and frogs. Assuming this also to be true for the human sense of touch, the noise must originate in the central nervous system. Unlike the ear, the touch receptors are not nearly limited in their sensitivity by the Brownian motion.

In conclusion it can be said that noise in the skin sense system displays activities that can be mistaken for a stimulus. Fluctuations with longer periods are probably present, which could be called drift or variation in sensitivity. When a threshold is measured in dependence of some parameters, it is required that trials are performed with different values of the parameters intermixed. Series taken apart with one parameter held constant, cannot be compared with other series taken afterwards, because of slow fluctuations in the sense system.
CHAPTER III

DYNAMIC PROPERTIES OF THE WARMTH SENSE ORGAN

§1. Experimental method

The investigation of dynamic properties demands stimuli of a quantitatively well-known time course. When thermodes or highly absorbing infrared radiation are applied as a stimulus, the temperature as a function of time is not accurately known at the receptor layer of the skin. The skin is too complex to allow a sufficiently exact calculation of the temperature distribution during stimulation and, moreover, the depth of the receptors is highly uncertain. Vendrik and Vos, therefore, used microwave radiation of suitable wavelength \((\lambda=10\, \text{cm})\). The absorption coefficient of this radiation in waterlike tissues is so small that the skin above the fay layer is practically uniformly raised in temperature. So in this region where the receptors are situated heat conduction does not play an important part during the first few seconds. The change in temperature of the surface of the skin is the same as the change in temperature of the receptors, neglecting the loss of heat from the surface.

In this study also microwave with a free space wavelength of 10 cm was used, generated in pulses by a magnetron. The radiation was transmitted by a rectangular waveguide with a cross-section of \(7.2 \times 3.6\, \text{cm}^2\). The mode of propagation was \(H_{01}\), indicating that electrical field strength varies across the longer axis of the cross-section as a sine, whereas it is constant in the direction perpendicular to this axis. During the experiments the inner side of the forearm was gently pressed against the end of the waveguide. This end was provided with a copper flange, covered by a thin layer of cork to prevent cooling of the skin.

A considerable fraction of the incident energy is reflected from the surface of the arm, which by interference with incident waves causes a standing wave, measured by means of a standing wave meter. To prevent energy losses from these reflections, three stubs could be inserted into the broader side of the waveguide at distances of a quarter wavelength of each other. Their individual depths in the waveguide were determined by trial and error till a standing wave ratio of nearly unity was obtained. In this way by introducing another reflection with suitable phase and amplitude the reflection against the arm was extinguished. It was ascertained that no sparking occurred at the stubs.
The experiments were done with power standing wave ratios of 0.65 - 0.90. In order to calculate the loss of energy resulting from the measured standing wave ratios, the voltage of the incident wave at the point of the standing wave meter is represented by $e^{i\omega t}$. At a certain distance from the standing wave meter the waveguide is terminated by an impedance having a reflection factor $\rho = |\rho| e^{i\phi}$. For the power standing wave ratio is found

$$S_p = \frac{(1 - |\rho|)^2}{(1 + |\rho|)^2}$$

The relative energy reflected from the termination as a function of $S_p$ is

$$|\rho|^2 = \left( \frac{1 - \sqrt{S_p}}{1 + \sqrt{S_p}} \right)^2$$

At worst this energy is lost. Substituting the lowest value of $S_p$, used during the experiments, in the expression for $|\rho|^2$, it appears that the loss of energy cannot be more than 2%. So the mentioned variability in standing wave ratios gives rise to variations in energies, which can be neglected.

The energy delivered by the radar equipment was measured by a calorimetric method. The calorimeter consists of a cylindrical glass tube in torpedo form. It was filled with water and placed inside the waveguide pointing to the magnetron. The microwaves are not reflected by this tube but totally absorbed. During the calibration a constant, known waterflow was maintained in the tube. A measured quantity of water was thus warmed up. Temperature differences between inflow and outflow of the calorimeter were measured by a thermocouple. The energy per pulse delivered by the magnetron was 0.0296 cal/pulse ± 3%.

The repetition frequencies of the pulses used in the experiments are in the range of 20 Hz up to 500 Hz, corresponding to a variation of the intensity of radiation.

By means of a thermocouple extended across the end of the waveguide in the direction of the longer axis, skin surface temperatures could be measured during irradiation. The thickness of the wires of the thermocouple was 0.05 mm and their junction was situated in the middle of the aperture. As the wire is perpendicular to the electric field no radiation pick-up occurred. With exposure times of about 1 sec it was found that the increase in skin temperature amounted to 0.0038 °C/pulse ± 20%. The large variation in measured values were presumably caused by irreproducible contact of the thermocouple with the skin.
Fig. 10.
Schematical drawing of the experimental situation. The upper drawing shows the standing wave meter and the three stubs by which additional reflection is obtained. The lower drawing pictures three dimensionally the increase of temperature in the tissue of the arm.

The energy distribution along the broader side of the waveguide is a \( \cos^2 \) function and the energy in directions perpendicular to the surface of the skin decays exponentially (fig. 10). Thus the temperature distribution after irradiation can be expressed by (see fig. 11)

\[
T = T_0 e^{-\beta x} \cos^2 \frac{\pi}{b} y
\]

(4)

where

\( \beta \) = absorption coefficient

\( T_0 \) = temperature increase on the line \( x = 0, y = 0 \)

\( b \) = length of broader side of the waveguide

The total amount of energy applied to the arm is given by

\[
E = \int_{-\frac{b}{2}}^{\frac{b}{2}} \int_{-\frac{b}{2}}^{\frac{b}{2}} T_0 e^{-\beta x} \cos^2 \frac{\pi}{b} y \, \rho \, c \, \rho \, dx \, dy
\]

(5)

with

\( h \) = height of the waveguide

\( \rho \) = density of the tissue of the arm

\( c \) = specific heat

\( E \) = energy delivered by the microwave
From (5) the following expression is obtained

\[ E = \frac{1}{2} T_0 \rho c \frac{h b}{\beta} \]  

For \( T_0 \) was found 0.0038 °C/pulse; \( \rho c \) is about 0.9 cal/cm³/°C \( \beta \) is about 0.9 cal/cm³

\( h \times b = 25.9 \text{ cm}^2 \) and \( E \) appeared 0.030 cal/pulse.

Inserting these values in (6) yields \( \beta = 1.5 \text{ cm}^{-1} \) which is in excellent agreement with the value found by Cook 33).

In the above calculations no heat conduction in the arm or from the surface of the skin was considered. Therefore the temperature of the skin after a short irradiation (0.2 sec) was measured. It appeared that ten percent of the increase of temperature was lost after 3.3 ± 0.5 sec. When the skin was covered by a cork layer the time of decay of the temperature was not significantly influenced. So the heat loss to the surroundings is negligible.

In order to see if the decay time can be understood from thermal properties of the tissue, the temperature distributions will be determined here as a function of time in two perpendicular cross sections parallel to the ZY and to the ZX plane (fig. 11). The time will be calculated after which the temperature in the point \( x = 0, z = 1/2 h, y = 0 \) shows a drop of 10% from the original increase. As was pointed out, the temperature distribution in the plane \( x = 0 \) is a \( \cos^2 \) function. This distribution resembles the solution of the differential equation in case of the conduction of heat in one dimension from a pointed heat source

\[ T = \frac{T_0}{\sqrt{\frac{y^2}{4\pi kt}}} \]  

\( \beta x \)
with
\[ \int_{-\infty}^{\infty} T \, dy = \frac{\theta_o}{\sqrt{4\pi}} \int_{-\infty}^{\infty} e^{-y^2/4kt} \, d\frac{y}{\sqrt{4kt}} = \theta_o \]

where
- \( T \) = increase of temperature along the Y axis
- \( k \) = diffusivity
- \( t \) = time after onset of point source
- \( \theta_o \) = constant

Expanding (7) in series:
\[ T = \frac{\theta_o}{\sqrt{4\pi kt}} \left( 1 - \frac{y^2}{4kt} + \frac{y^4}{32kt} - \ldots \right) \quad (8) \]

The real temperature in the plane \( x = 0 \) is:
\[ T = T_o \cos^2 \pi \frac{y}{b} \quad -\frac{b}{2} < y < \frac{b}{2} \]
again expressed in a series
\[ T = T_o \left( 1 - \frac{y^2}{b^2} + \frac{y^4}{3b^4} - \ldots \right) \quad (9) \]

The terms containing \( y^2 \) in (8) and (9) equal for
\[ \theta_o = T_o \sqrt{4\pi kt}, \quad \text{and} \quad t_r = \frac{b^2}{4\pi^2 k} \quad (10) \]

So at the time \( t_r = \frac{b^2}{4\pi^2 k} \) (7) approximates the temperature distribution as a function of time for \( y \ll \frac{b}{\pi} \).

Given the \( \cos^2 \) temperature distribution, it can be proved that for large \( t \) the temperature at \( y = 0 \) will be
\[ T = \frac{T_o}{\sqrt{4\pi kt}} \int_{-\frac{b}{2}}^{\frac{b}{2}} \cos^2 \pi \frac{y}{b} \, dy = \frac{T_o b}{2 \sqrt{4\pi kt}} = 0.89 \frac{\theta_o}{\sqrt{4\pi kt}} \]

For large \( t \) the proposed distribution (7) gives for the temperature at \( y = 0 \):
\[ T = \frac{\theta_o}{\sqrt{4\pi kt}} \]

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The difference between both values of T amounts to 11 %.
From the time t₁, the temperature at y = 0 can be shown to be represented by (7) with an accuracy better than this 11 %.

At what time is \( T = 0.9 \ T₀ \) for \( y = 0 \)?
From (7) it appears that

\[
T = \frac{θ₀}{\sqrt{4π\,kt}} = 0.9 \ T₀
\]

and with (10)

\[
T = 0.9 \ \frac{θ₀\sqrt{π}}{b} = \frac{θ₀}{\sqrt{4π\,kt}}
\]

which yields

\[
t = \frac{1}{0.81} - \frac{b²}{4\,κ\,κ²} \]

The temperature distribution was adapted after the time \( t₁ = \frac{b²}{4\,κ\,κ²} \)
thus the time needed for a 10 % decrease is

\[
\frac{b²}{4\,κ\,κ²} \left( \frac{1}{0.81} - 1 \right)
\]

With \( b = 7.2 \ \text{cm} \) and \( κ = 1.4 \times 10^{-3} \ \text{cm}²/\text{sec} \) the time wanted is about 220 sec, which is much too high compared with the experimental value. Consequently the \( \cos² \) temperature distribution is not responsible for the measured time of decrease.

Next, with the distribution of the temperature in the plane \( y = 0 \) an exponential distribution of the type \( T = θ₀ \ e^{-βx} \) is to be expected.
The time for which \( T = 0.9 \ T₀ \) at \( x = 0 \) can be found from

\[
T = \frac{1}{\sqrt{4π\,kt}} \int_{-∞}^{∞} f(x') \ e^{-\left(\frac{1}{4\,κ\,κ²}\left(x-x\prime\right)^2\right)} \, dx'
\]

This solution of Laplace, see \( 32 \) page 34, is, of course, essentially the same as the solution used above. As in this case the situation is approximated by a semi-infinite solid, the solid is supposed to be continued on the negative side of the plane \( x = 0 \) with a distribution

\[
T = T₀ \ e^{βx}
\]

Heatflow through the plane \( x = 0 \) is thus zero. Moreover, the exponential functions are approximated by \( 1 - β \ x \) and \( iβ \ x \) respectively, this being certainly permissible for \(-0.1 < x < 0.1 \ \text{cm} \) with \( β = 1.5 \ \text{cm}^{-1} \).
With these assumptions (11) can be written

\[ T = \frac{T_o}{\sqrt{4\pi kt}} \left\{ \int_0^\infty (1+\beta x') e^{-\frac{(x-x')^2}{4k\pi t}} dx' + \int_{1-\beta x'}^\infty e^{-\frac{(x-x')^2}{4k\pi t}} dx' \right\} \]  
(12)

Further calculation gives

\[ T = T_o \left( 1 - \frac{\sqrt{\pi \beta}}{\pi} \right) \]  
for \( x = 0 \)

Therefore \( T = 0.9 \ T_o \) occurs at the time

\[ t = 0.01 \ \frac{\pi}{4k\beta^2} \]

With \( k = 1.4 \times 10^{-3} \text{ cm}^2/\text{sec} \) and \( \beta = 1.5 \text{ cm}^{-1} \) the time for a 10% decrease is found to be 2.5 sec (fig. 11a).

The measured time was 3.3 sec. The arm is thus cooling off mostly by inward flow of heat, because loss of heat from the surface to the surroundings could be neglected. The longer times found in the experiments may be caused by impression of the thin wires of the thermocouple into the skin.

Deriving from (12) the temperature at depths less than 0.1 cm which is certainly within the range of the depth of the receptors, the expression is obtained

\[ T = T_o \left\{ 1 - \beta \sqrt{\frac{4kt}{\pi}} \frac{x^2}{4kt} - \beta x \frac{2}{\sqrt{\pi}} \int_{-\frac{x}{\sqrt{4kt}}}^0 e^{-y^2} dy \right\} \]

The temperature after a short irradiation at a depth of 0.04 cm, which is a reasonable value, is shown in fig. 11a together
with the surface temperature \((T_o = 10^\circ C, k = 1.4 \times 10^{-3} \text{cm}^2/\text{sec}, \beta = 1.5 \text{ cm}^{-1})\).

Jaeger \(^{58}\) considered the case in which the blood supply in the skin removes the warmth from the irradiated area. Compared with experimental data his calculations show very little influence of the bloodstream for values of time smaller than 50 sec. As is indicated in fig.11a the temperature distribution responsible for the disturbing heat flow causes a 10% deviation at the receptor-layer after about 5 seconds.

When the arm is exposed to microwave the constant energy per unit of time causes a linear increase of temperature with time as long as no appreciable heat conduction has taken place. Demanding the deviation from linearity to be not more than 10%, irradiation times of about 10 seconds are still allowed. For if a sudden jump in temperature at the receptor layer shows a decrease of 10% after 5 seconds, the presumed linear increase due to constant irradiation will come out 10% too low after 10 seconds.

The subject determines the time of occurrence of a stimulus. He works through a program which is not known to him.

The schematically drawn experimental set-up in fig.12 shows how a subject can perform a series of 10 trials on his own. At every position of a programming switch set by the subject, he pushes a button, obtaining a stimulus of a preset exposure time. The programming switch determines whether a "zero" or a "real" stimulus is given.
The subject writes down the program he experiences.

The variable exposure times were obtained by a stabilised monovibrator driving a relais. Exposure times were determined with 1% accuracy.

Besides the normal aperture of the waveguide of 3.6 x 7.2 cm² also apertures of 2.5 x 7.2 cm² and 6.0 x 7.2 cm² were used. Greater variations in cross-sectional areas are limited by too much reflection, so that a mismatch cannot easily be prevented.

§2. Results of measurements

Threshold energies were determined with exposure times in the range of 0.1 - 10 sec. The psychophysical procedure a (II § 2) was used. At each exposure time probabilities with 4 different energies were measured. At a certain energy known to the subject 6 or 7 series of 10 trials were done. So the measurement of a threshold at one exposure time includes 240 to 280 trials, half of which were of zero intensity. Series with different intensities and different exposure times were intermingled.

The probability of perception is defined as the probability of report of sensation minus the probability of a false alarm (II § 3). The curve representing the probability of perception versus the intensity of the stimulus is S-shaped. An example of a measured "probability" curve is shown in fig. 13.

The threshold is defined as the energy that yields a score of 85%, this being the percentage that could be determined most accurately. As all experimental probability curves showed the same shape, a standard curve was fitted to the measured probabilities of perception.
This could be done with an uncertainty of 15%; thresholds could thus be determined with an accuracy of ± 15%.

In figs. 14 and 15 the thresholds of two well-trained subjects are plotted as a function of the exposure time. A third untrained subject gave a similar result, but with considerably larger experimental errors.

Similar threshold measurements with reduced and increased area of irradiation (2.5 x 7.2 cm\(^2\) and 6.0 x 7.2 cm\(^2\)) yielded the same dependence on exposure time as is shown in figs. 14 and 15.

![Figures 14 and 15](image)

Threshold energy as a function of exposure time.

Circles: experimentally determined values of threshold energy.

Full line: theoretical curve of peripheral adaptation.

Broken line: theoretical curve of central adaptation.

The characteristic features of the measured curves are:

1) Threshold energy increases initially with exposure times up to about 1 - 2 sec, which means that a steeper rise of temperature is more "economical" in reaching sensation.

2) Then the curves tend to flatten off, indicating that in this region threshold temperature rise is not dependent on the rate of change of temperature.

3) Finally, threshold energy increases proportionally with exposure time, the threshold rate of temperature change being constant. This suggests that a linear increase of temperature if not felt in a few sec, will not be felt any more, of course, within reasonable limits.
The variations of cross-sections were intended to investigate the influence of the irradiated area on the threshold curves. The experiments with different areas were done with intervals of several months. It appeared later that a drift in sensitivity makes a comparison of absolute thresholds impossible. The shape of the curves is not significantly dependent on the area of irradiation.

Skin temperatures before irradiation were sometimes measured. No influences of variations in these temperatures were found, in agreement with Ebaugh and Thauer 38), and Lele 60).

§3. Interpretation grounded on electrophysiological data

In the first place one can think of the dynamic behaviour of the peripheral receptors as a possible explanation of the experimental results. Dodt, Zotterman and Hensel 35) 43-49) have investigated electrophysiologically the dynamic behaviour of the cold and warmth receptors of the cat and the dog. At constant temperatures a stationary activity is seen as a rule. After a sudden change of temperature the temperature fibres at first respond with a considerable change of activity (overshoot), this dropping to a new stationary value (fig.16).

\[ f_T = AT_0 + BT_0e^{-t/T}, \]  

(13)

The quantities A and B in fig.16 mostly found by Hensel and Zotterman have negative values. This means that activity diminishes at higher temperatures. In the discussion below it is not relevant whether A and B are negative or positive.

Mathematically the change in activity of a group of receptors after a steplike change of temperature can be described approximately by:

The dynamic response of temperature fibres in the cat as found by Hensel and Zotterman.
where

\[ f_r = \text{change of neural activity} \]
\[ (\text{number of action potentials per sec}) \]
\[ T_o = \text{steplike change in temperature (}^{\circ}\text{C}) \]
\[ A \text{ and } B = \text{constants of the receptorsystem (number of action potentials per sec per }^{\circ}\text{C}) \]
\[ \tau_e = \text{time constant of the receptor system (sec)} \]
\[ t = \text{time after onset of step (sec)} \]

Hensel\(^{49}\) gives another expression with two time constants. However, the influence of the second time constant (0.01 sec) is quantitatively negligible and, moreover, we do not think experimental evidence has thus far justified the assumption of this second time constant.

The above formula describes neural activity changing with regard to an already existing activity, which is not taken into account. In other words, activity is measured counting from a physiological "zero". For if it is true, that temperature receptors display a stationary activity, a non-peripheral adaptation mechanism must be active to prevent such activity from being felt because of the common experience that stationary conditions are experienced as the absence of sensation.

Naturally, the assumption is made, that the receptor system is working linearly for the small temperature rises needed to measure threshold. Electrophysiological observations give support to this assumption.

If the temperature does not change steplike but linearly with time (fig.17) as it does in our case, then neural activity can be obtained

Fig. 17.

Response of temperature fibres to a linearly changing temperature. The curve is a consequence of the response shown in fig. 16.
by integration of (13):

\[ f_r = aAt + abT_r \left( 1 - e^{-t/\tau} \right) \]  

(14)

with

\[ T = at \]
\[ T = \text{temperature (°C)} \]
\[ a = \text{rate of change of temperature (°C per sec)} \]
\[ t = \text{time after onset of the stimulus} \]

Assuming that perception is obtained when the activity \( f_r \) equals or surpasses a value \( f_s \) during the exposure time \( t_e \), the following expression is obtained for the threshold change of neural activity as a function of irradiation time \( t_e \)

\[ f_s = aAt_e + abT_e \left( 1 - e^{-t_e/\tau} \right) \]

The threshold temperature rise will be

\[ \text{at}_e = \frac{f_s}{A + B} \frac{\tau}{t_e} \left( 1 - e^{-t_e/\tau} \right) \]  

(15)

When \( t_e = 0 \)

\[ \text{at}_e = \frac{f_s}{A + B} \]

and for \( t_e \gg \tau \),

\[ \text{at}_e = \frac{f_s}{A + B} \frac{\tau}{t_e} = \frac{f_s}{A} \]

In figs. 14 and 15 the solid curve is drawn according to (15). The best fit to the experimental results for exposure times smaller than 3 sec is obtained by taking \( B/A = 2.0 \) and \( \tau_0 = 0.25 \) sec. The same quantities of all experiments (3 subjects and 3 different areas) fall within the range of \( B/A = 2 - 4 \) and \( \tau_0 = 0.2 - 0.4 \) sec.

In electrophysiological experiments the cold receptors in the tongue of the cat appeared to have a time constant in the range 0.3 - 2.2 sec. Records of the activity of warmth fibres show a dynamic response that might be described with a time constant somewhat smaller than found for cold receptors. So the values of \( \tau_0 \) in our experiments are in the range of comparable electrophysiological
data. The same can be said about the values of $B/A$. The mathematical description of dynamic properties given above appears to be applicable to electrophysiological data and to psychophysical experiments with exposure times smaller than 3 sec.

With exposure times exceeding 3 sec the experimentally found threshold energy tends to increase linearly with $t_e$. This could be explained by the assumption that no stationary activity is present i.e. $A = 0$. The time constant should then be about 1 sec. However, this assumption is contrary to electrophysiological observations. Moreover, the shape of the measured curve, having a more or less flat region, does not agree with the assumed model.

For these reasons it is necessary to think of a mechanism that inhibits the stationary activity. Such mechanism must be situated in the central nervous system.

§4. Adaptation in the central nervous system

Landgren has investigated the cortical reception of cold impulses from the tongue of the cat. His registrations show a marked adaptation. However, the corresponding activity in peripheral nerves was not measured by him. So a definite conclusion from these observations cannot be drawn.

The results of section 3 also led to the conclusion that a central inhibition is existing, a dynamic process which will be called central adaptation. In spite of the fact that adaptational mechanisms are known in the central nervous system, only very few quantitative data are available about the complex system involved. This makes a detailed analysis of this phenomenon very difficult. One can devise numerous models explaining the dynamic behaviour found: chemical exhaustion, feedback mechanisms etc. with various quantitative descriptions.

To describe the experimental results the following mathematical model was tried. Suppose a central adaptation mechanism gradually neutralizing every new level of peripheral activity. It is plausible to assume that the output of such a system is an exponentially decreasing function of the input, i.e. the peripheral activity. The time constant of this central adaptation will be called $\tau_2$. The dynamic properties are described by

$$\frac{df_r}{dt} = \frac{f_o}{\tau_2} + \frac{df_o}{dt} \quad (16)$$

\[f_r = \text{neural input obtained from (14)}\]

\[f_o = \text{neural output}\]
With \( f_0 = 0 \) at \( t = 0 \) and substituting (14) in (16) the solution of the differential equation is

\[
f_0 = \frac{aB}{\frac{1}{\tau_2} - \frac{1}{\tau_1}} \left( e^{-t/\tau_1} - e^{-t/\tau_2} \right) + \frac{aA}{\frac{1}{\tau_2}} \left( 1 - e^{-t/\tau_2} \right)
\]

Thresholds are found from the condition \( f_0 > f_s \) at \( t = t_e \). So the expression is obtained

\[
f_s = \alpha t_e \left( \frac{B}{e^{-t_e/\tau_1} - e^{-t_e/\tau_2}} \left( e^{-t_e/\tau_1} - e^{-t_e/\tau_2} \right) + \frac{A}{t_e/\tau_2} \left( 1 - e^{-t_e/\tau_2} \right) \right)
\]

At \( t_e = \infty \) it follows from (17)

\[
\alpha = \frac{f_s}{A/\tau_2} = \text{constant}
\]

This model however, does not give a very good fit to the measured curves, as the minimum slope of the curves of figs. 14 and 15 is not reached by the solution (17). The best values of the parameters are in the range \( \tau_1 = 0,2 - 1 \text{ sec}; \tau_2 = 2 - 4 \text{ sec}; \frac{B}{A} = 0,4 - 3. \)

Instead of a system influencing peripheral inflow gradually, one can think of a system which cancels a new level of peripheral activity after a retardation time \( \tau_3 \). Such a model gives a good fit to our observations, the retardation time being in the range 2 - 4 sec. (figs. 14 and 15).

The combination of the two foregoing models consisting of a system in which the peripheral activity is neutralized gradually after a retardation time, seems to be most likely. However, the quantitative data thus far obtained are not accurate enough to evaluate this model. The measurements discussed above would seem to indicate that there occurs a retardation time somehow in the central adaptation system.

Because of the properties of this central adaptation mechanism, the slow components in the noise spectrum (see II §4) must originate in the central nervous system. These slow components should not be of importance when generated at levels more peripheral than the centres where the central adaptation mechanism is located.
CHAPTER IV
THE COLD AND WARMTH SENSE; CENTRAL ADAPTATION

§1. Resemblances and differences of the cold and warmth sense

It would be worth while to carry out similar experiments on cold sensation as have been done on warmth sensation. For it might be possible that the results would give evidence concerning the problem whether separate cold and warmth receptors exist. However, an experimental device comparable to the radar equipment giving a cold stimulus of a well-known time course at the receptor layer does not exist. Cold stimuli, whether by radiation or by conduction do not give the required result because the complexity of the skin and the unknown depth of the receptors prevent an exact calculation of the time course of the temperature. However, an attempt will be made to approximate the time course of the stimulus to see whether we can arrive at some conclusions.

First some data from the literature will be compared.

1. Ebaugh and Thauer 38) found that thresholds for warmth and cold were constant with skin temperatures from 28 to 33°C and with air temperatures from 15 to 26°C. The warmth threshold was at these temperatures higher by a factor 1.3 than the threshold for cold under the same experimental conditions where radiation was used. Lele 60) found with skin temperatures in the range of 25 to 35°C approximately the same threshold for an increase as for a decrease in temperature. His experiments were done with thermodes conducting warmth to or from the skin.

2. The number of cold spots in the forearm amounts to about 14 per mm², the number of warmth spots about 1.5 per mm² 7). Some experiments are described which suggest that the cold receptors could be situated somewhat more superficially in the skin. In electrophysiological experiments cold fibres are found much more frequently than warmth fibres.

3. Summation takes place over a wider area in the case of warmth stimuli than for cold 53,54). In a linear dimension the difference reaches even a factor 3.
4. Barbizet c.s. 23) studied the loss of sensitivity in the skin for warmth or cold when lesions were present in the central nervous system. Their clinical observations revealed that lesions on all levels in the central nervous system could cause loss of sensitivity to warmth or cold alone or to both. They pointed out that insensitivity to cold is always accompanied by a raise in threshold for warmth, but not reversed.

From a physical point of view one kind of receptors should suffice for measuring temperature. In human sensation, however, the feeling of warmth is totally different from the feeling of cold and is not experienced as an equivalent negative of the cold sensation. This does not necessarily mean that there exist separate sense organs for cold and warmth in the skin. A sensation of warmth may originate from centres in the nervous system which are fed by the output of the receptors for cold or reversed. In fact all data compiled above can be explained by the existence of one kind of receptors. The nervous centres for warmth should then get their input from larger areas on the skin than the centres for cold. Recently Boman 29) has expressed doubt about the existence of warmth receptors on account of electrophysiological observations. The few so-called warmth receptors found, could be in fact subserving pain.

How difficult it is to arrive at a definite conclusion in this respect was shown by a preliminary experiment. Two adjacent areas on the forehead were cooled respectively warmed by radiation simultaneously. An infrared source was applied for warmth; the radiation to a block of dry ice (CO₂) to cool the skin. The total area irradiated had a diameter of about 4 cm. Simultaneous application of cold and warmth on different parts of the skin revealed two typical aspects. When with a certain magnitude of the cold stimulus the simultaneous warmth stimulus was adjusted in strength in order to minimize sensation, a mixed feeling of faint cold and pain became apparent at temperature changes of a few tenths of a degree centigrade. Moreover, a sensation of warmth was easily extinguished by a cold stimulus in contrast with the reversed situation.

Again, these facts can be explained in two ways. A schematical picture is given in fig. 18, where the case of separate receptors for warmth and cold is compared with that of a single receptor system. Both hypothetical schemes show a summation over larger areas for warmth. This explains the fact that warmth is more easily extinguished by opposite temperature changes on adjacent areas than cold, as the output of more receptors are summated.

The determination of cold and warmth spots or the exclusive sensitivity to cold of some parts of the body cannot give final
evidence for a separate receptor system. Moreover, the determination of sensitive spots is difficult because the sensation after point stimulation is not very well defined, certainly not with respect to the difference between heat, pain and warmth.

From all arguments cited above there is none that gives conclusive evidence for a one receptor system, whereas some phenomena can only be explained with some difficulty. So it is likely that there exist two kinds of receptor systems of about equal sensitivity. The smaller density of warmth receptors is compensated for by a larger summation area. In stationary conditions both systems send forth an activity that is neutralised by a central adaptation mechanism. Nevertheless within a limited range threshold temperature changes are not dependent on skin temperature, a fact which is in favour of a linear description of dynamic properties.

The question which will be considered now is whether time constants of cold and warmth receptors will be different or not. There are two alternatives for giving a cold stimulus viz. radiation to a cold object or contact with and conduction to an object with pre-set temperature (thermode). Which of the two methods is to be preferred when a rapid change of temperature is required, can readily be calculated. First consider a semi-infinite solid with zero initial temperature and the surface at a temperature \( T_0 = \alpha t \). Carslaw and Jaeger (\(^{[22]}\) page 45) give the expression for the temperature at a depth \( x \) and at the time \( t \):

\[
T = 4 \alpha t \text{erfc} \frac{x}{\sqrt{4kt}}
\]
with \( k \) = diffusivity
\[
\alpha = \text{rate of change of temperature} \ \text{(°C/sec)}
\]

\[
i^2 \text{erfc} \ x = 1/4 \left[ \text{erfc} \ x - 2 \ x \left( \frac{1}{\sqrt{\pi}} e^{-x^2} - \ x \ \text{erfc} \ x \right) \right]
\]

\[
\text{erfc} \ x = \frac{2}{\sqrt{\pi}} \int_{x}^{\infty} e^{-y^2} dy
\]

Inserting \( k = 1.4 \times 10^{-3} \ \text{cm}^2/\text{sec} \) and \( \alpha = 1 \ \text{°C/sec} \), which can be easily obtained, the temperature was calculated at two different depths \( x = 0.01 \) and \( 0.05 \ \text{cm} \). The result is given in fig. 19a. The receptors are almost certainly situated in the region considered.

![Fig. 19.](image)

**Temperature versus time:** a. with the surface forced at a temperature \( T = \alpha t \), b. in case of irradiation of the skin.

When radiation is used, it is difficult to obtain in experimental practice surfaces of a very low constant temperature, because the deposition of ice on the surface cannot easily be avoided, certainly not in the presence of the arm because of the water secretion. For these reasons the flux that can be obtained is limited. An estimation shows that a flux of \( 5 \times 10^{-3} \ \text{cal per sec and per cm}^2 \) is obtainable without much difficulty. Again consider a semi-infinite solid with zero initial temperature. The flux of heat at the surface \( (x=0) \) is constant \( (P_o) \). The solution given in page 56 is:

\[
T = \frac{2P_o \sqrt{kt}}{\lambda} \ i \ \text{erfc} \ \frac{x}{\sqrt{4kt}} \quad (19)
\]
with $\lambda = \text{conductivity}$

$$i \operatorname{erfc} x = \frac{1}{\sqrt{\pi}} e^{-x^2} - x \frac{2}{\sqrt{\pi}} \int_x^\infty e^{-y^2} dy$$

Using the values $k = 1.4 \times 10^{-3}$ cm$^2$/sec, $\lambda = 1.3 \times 10^{-3}$ cm$^0$C sec
and $P_0 = 5 \times 10^{-3}$ cal per sec and per cm$^2$ the temperature has been calculated at the depths of 0.01 and 0.05 cm. The temperature in dependence of time is shown in fig. 19b for different depths. It is apparent from fig. 19 that a fast changing temperature can be obtained more readily by means of thermodes than by non-penetrating radiation. Therefore a thermode with linearly increasing or decreasing temperatures was constructed. The experimental set-up is shown in fig. 20.

![Experimental set-up to obtain linear temperature variations in the inner compartment of the double thermode. In a bias flow water of another temperature is injected at $I_1$. The retardation in bottle $L$ filled with aluminium shavings has a linearizing effect. The variation of temperature in the outer compartment is obtained by injection of water at $I_2$. All shaded areas indicate isolation for heat loss.](image)

A bias flow of water of 30°C was maintained (100 cm$^3$/sec). This could be changed by valve $B$, but all experiments described below were done with the same flow.

Another flow is maintained between the magnetic valve $M$, the small pump $P$, and the thermostat $T_1$ in order to keep these parts at the same temperature. By means of the electrically operated valve $M$
cold or warm water from $T_1$ is mixed with the bias flow. The water-pressure has to be lowered at $I_1$ to make injection possible. The mixed flow now passes a retardation chamber $L$ with different outlets $C_1$, determining the retardation time. The bottle $L$ is filled up with aluminium shavings. The partial retardation and the mixing have a linearizing effect upon the temperature increase. The water now reaches the thermode on which the arm is resting. The upper side of the thermode is covered by copper foil.

The inner compartment of the thermode showed a linear increase of temperature some time after opening $M$ during about 12 seconds when the upper valve $C_1$ was open. The inner thermode had an area of $4 \times 7$ cm$^2$ and a volume of 15 cm$^3$. The outer compartment was 1 cm wide with an area of $26 \times 14$ cm$^3$. The volume of $L$ was 1000 cm$^3$.

Water at a constantly higher or lower temperature could be injected from $T_2$ at $I_2$ by a hand-operated valve $C_2$. The change of temperature in the outer compartment was more sudden.

The dead space at $I_1$ and $M$ was less than 3 cm$^3$. The leads from $I_1$ to the thermode were taken as short as possible. So also rapid changes of temperature could be made by using the lowest valve $C_1$. The valve used thus determines the rate of change of temperature in the thermode but also the length of time that the increase is linear. The valve $M$ is opened during a time determined by a monovibrator. In this way different durations of the stimulus are obtained.

The first experiments concerned the comparison of warmth and cold thresholds under similar conditions. The psychophysical procedure of type $b$ was used (see II §2). The results of the 85 % thresholds and the related values of $\sigma$ of the normal distribution are given in table II.

<table>
<thead>
<tr>
<th>subject</th>
<th>cold threshold °C</th>
<th>$\sigma$°C</th>
<th>warmth threshold °C</th>
<th>$\sigma$°C</th>
</tr>
</thead>
<tbody>
<tr>
<td>E</td>
<td>0.14 ± 0.01</td>
<td>0.05</td>
<td>0.17 ± 0.02</td>
<td>0.06</td>
</tr>
<tr>
<td>dH</td>
<td>0.12 ± 0.01</td>
<td>0.04</td>
<td>0.22 ± 0.03</td>
<td>0.07</td>
</tr>
<tr>
<td>R</td>
<td>0.14 ± 0.02</td>
<td>0.05</td>
<td>0.19 ± 0.02</td>
<td>0.06</td>
</tr>
</tbody>
</table>

All temperature changes were linear within 10 % the rise times being in the range of 1 - 3 sec. The series, consisting of 160 trials with 4 intensities, were taken for cold and warmth successively, so direct comparison is not possible. However, all subjects show a somewhat
lower threshold for cold, the mean ratio between warmth and cold threshold being 1.45. The range of exposure times is not appropriate to give information concerning the dynamic properties. However, shorter stimulus durations are unfavourable from practical and theoretical points of view. With the values of table II which relate to the surface of the skin, the corresponding quantities have been calculated at the depth of the receptors (0.03 - 0.04 cm) using fig. 19. The result is that the $\sigma$ for the warmth receptors equals about 0.03 °C and the $\sigma$ for the cold receptors 0.02 °C (see II §4).

Another series of experiments consisted of the measurement of delay times. In sessions of about half an hour the subject was presented with a series of cold or of warmth stimuli consisting of linear changes of temperature on the inner thermode. The time of occurrence and the rate of change of temperature were unknown to the subject, who was asked to flash a light as soon as he experienced a stimulus. The temperature of the thermode was measured by a thermocouple and a galvanometer. The deflection of the galvanometer together with the reaction flash of the subject was recorded. The Moll galvanometer used had a response time of about 0.2 sec. For short stimulus durations the recorded temperature had to be corrected for the lag of the galvanometer.

The measured delay times are shown as a function of the rate of change of temperature in figs. 21, 22 and 23 for three subjects respectively. It appears that the cold sense behaves very similar as the warmth sense.

When some uncertain presumptions are taken for granted the equivalent curves of figs. 14 and 15 can be calculated. Estimating the depth of the receptors at 0.035 cm, the temperatures at the receptors can be calculated with (18). The delay time must be corrected for a reaction time of the subject, caused by a finite time needed for transmission of nerve messages and for operation of the light flash. The shortest delay after a large stimulus appeared to be about 0.4 sec. The corrected reaction times are thus 0.4 sec shorter than was measured.

The temperature at the receptor layer is now calculated for the corrected reaction times. This was done for the mean curves shown in figs. 21, 22 and 23, the results being given in figs. 24, 25 and 26. The similarity with figs. 14 and 15 is apparent, the time constants being in the same range for cold and for warmth, with one exception. Subject E yields a larger retardation time for cold (7 sec) than previously found in III §4 for the warmth sense (3 sec). The curve of this subject representing the warmth stimuli with thermodes is not well known for small rates of change of temperature. However, in view of the measurements a shorter retardation time than 7 sec is not
Delay times as a function of rate of change of temperature measured at the surface of the arm.

**Figs. 21 and 22.**
Fig. 23.
Dependence of delay times on the rate of change of temperature measured at the surface of the arm.

Figs. 24, 25 and 26.
Delay times corrected for the reaction time of the subject, versus the temperature of the presumable receptor layer at the moment of detection. The mean curves of figs. 21 - 23 have been used for calculation.
unlikely (fig. 23). Subject R yields results that are in good agreement with data obtained from the microwave experiments. From the measurements of all three subjects it is concluded that dynamic behaviour of the cold sense is very similar to the sense of warmth. The time constants of the cold sense might be somewhat larger than found for the warmth sense, but with one exception they are well within the range of previously calculated time constants of the warmth sense. An exact calculation of the time constants involved is not justifiable in view of the corrections and the assumptions made. The retardation time found is not much dependent on the depth of the receptors contrary to the time constant of peripheral adaptation determined by the initial slope of the curves in figs. 24, 25 and 26.

§2. Summation and the direct demonstration of central adaptation

The phenomenon of spatial summation offers in principle an opportunity to investigate central adaptation apart from the adaptation of the receptors. Suppose, that two adjacent skin areas send their afferent nerve fibres to the same summation centre. Stimulation of one area will cause adaptation in this summation centre, which can be demonstrated and measured by determining the threshold stimulus of the other area. Thus possible peripheral adaptation is excluded. Unfortunately, a warmth stimulus is very unsuitable for these kind of experiments. The main reason is that the temperature increase caused by a warmth stimulus does not disappear immediately after the stimulus. On the contrary, the temperature remains increased for a considerable time, as was shown before, because tissue is a relatively poor heat conductor. The consequence is that even if the summation centre should be completely adapted to the higher peripheral nervous input from the first area, the threshold stimulus of the second area would be little or not increased. A rapidly forced decrease of temperature by applying cold does not give the required result because cold itself acts as a stimulus. It might be hoped that the marked overshoot of the receptor activity would be useful in this respect. The fact that the activity is higher than the corresponding temperature rise will cause "over-adaptation". After the rise in temperature is over, this over-adaptation might cause a measurable increase of the threshold of the second area (see fig. 27).
Given the "overshoot" effect in peripheral nerve fibres, a hypothetical central adaptation occurs which is too high compared with the stationary activity at the end of the rise in temperature.

First it is necessary to gain quantitative information concerning the area of summation. Often the capability of localisation of a stimulus is used for the determination of a summation area. The underlying hypothesis of this method is that the convergence of sensory nerves, determining the extensiveness of a summation area, also limits the capability of localisation. It is not at all certain that this hypothesis is true.

A combined experiment was done. Both summation and localisation were measured, the former by determining probabilities of perception of combined and single stimuli as explained in II, § 4.

Two areas of 2 x 2 cm² could be exposed to infrared radiation for 3 sec. It was not known to the observer whether one or both nor which area was exposed. The distance between the two areas remained constant during one series, consisting of 160 trials. Each series yields four probabilities viz. probability of false alarm, the probabilities of correct detection of each of the two possible single irradiations $P_1$ and $P_2$ and the probability of correct detection of a combined irradiation $P_C$. The results for one subject with the distance of the two areas as parameter are given in table III. The maximum probability of detection of the combination in case of no summation $P_{\text{max}}$ and the probability in case of full summation $P_{\text{summ}}$ are calculated according to II § 4.
Table III

The probabilities of detection of two single stimuli and a combined stimulus compared with calculated probabilities with and without summation

<table>
<thead>
<tr>
<th>Distance cm</th>
<th>false alarm %</th>
<th>P₁ %</th>
<th>P₂ %</th>
<th>P₃ %</th>
<th>P&lt;sub&gt;sum&lt;/sub&gt; %</th>
<th>P&lt;sub&gt;max&lt;/sub&gt; %</th>
</tr>
</thead>
<tbody>
<tr>
<td>4.5</td>
<td>2.5</td>
<td>65</td>
<td>25</td>
<td>92.5</td>
<td>95.5</td>
<td>74</td>
</tr>
<tr>
<td>8.5</td>
<td>2.5</td>
<td>45</td>
<td>20</td>
<td>85</td>
<td>85</td>
<td>56</td>
</tr>
<tr>
<td>15.5</td>
<td>2.5</td>
<td>15</td>
<td>32.5</td>
<td>65</td>
<td>68</td>
<td>43</td>
</tr>
</tbody>
</table>

Subj. k

It is clear that nearly full summation is still present at distances of 15.5 cm on the inner side of the forearm. At the same time it appeared that stimuli somewhat above threshold strength could be localised with limited reliability at a distance of 15.5 cm. The very interesting relation between summation and localisation falls, however, outside the scope of this study.

The measurement of "over-adaptation" was done with microwave. The output of the radar equipment could be transmitted through one of two apertures of equal area 3.0 x 7.2 cm<sup>2</sup>, mounted above each other. By mechanical means the microwave was switched from one aperture to the other. So first a fatiguing stimulus could be given, followed by a test stimulus on the adjacent area. From the summation experiments it will be clear that the total area used (6.0 x 7.2 cm<sup>2</sup>) gives a summated output.

Experiments carried out with the idea as explained in fig. 27 in mind, yielded, however, negative results, as no increase in threshold could be found. It must be stressed that this result does not rule out the existence of central adaptation because any effects that might be expected were of necessity small.

§3. Cold and warmth stimuli simultaneously applied to adjacent areas.

Still another possibility for demonstrating central adaptation might be found by measuring the warmth threshold after cooling the skin. The decrease in temperature will cause a change in peripheral nervous activity which must be followed by the central adaptation
Figs. 28 and 29.

Thresholds of linear temperature stimuli after an application of a conditioning stimulus to an adjacent area. The slope of the linear test stimulus is indicated by parallel lines; the onset of the test stimulus can thus be seen readily.

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Thresholds of linear temperature stimuli after an application of a conditioning stimulus to an adjacent area. The slope of the linear test stimulus is indicated by parallel lines; the onset of the test stimulus can thus be seen readily.

---

55
Figs. 30 and 31.
Thresholds of linear temperature stimuli after an application of a conditioning stimulus to an adjacent area. The slope of the linear test stimulus is indicated by parallel lines; the onset of the test stimulus can thus be seen readily.
level. But as the central adaptation is a relatively slow process the return of the adaptation level can be followed by applying test stimuli at different times after the onset of the cooling. Immediately after cooling we should expect the threshold for warmth to be raised, to return to normal some time after the cooling. In order to make sure that the measured effect is of central origin, cooling and warming can be applied to adjacent areas, where summation occurs.

To meet these requirements the experimental equipment of fig. 20 was used. The linear change of temperature at the inner thermode was applied as a test stimulus. The conditioning stimulus was forced upon the outer compartment of the thermode. Both temperatures were recorded by means of thermocouples and galvanometers (Moll) together with the light flash given by the subject when he experienced the test stimulus.

In sessions of half an hour the subjects were presented with the fatiguing stimulus which was well above threshold, followed by a linear test stimulus after an unknown interval. The task of the subjects was to press a button as soon as they felt the definite warmth or cold of the second test stimulus.

In figs. 28 - 31 the results of the measurements are presented. They reveal a striking difference between the cold and warmth sense. The warmth sense indeed shows the expected increase of threshold after application of a cold stimulus with a return to normality after some time. The sense of cold, however, does not show much of an increase in threshold. The behaviour of the threshold of the warmth sense can be explained by either of the two schematical drawings in fig. 19, which means that a single receptor system is sufficient to account for these experiments.

The different behaviour of the sense of cold needs an explanation. As the decrease of activity of the cold receptors of the adjacent area apparently does not summate with the increase of the output of the test area, the central adaptation is likely to occur at a lower level in the nervous system than summation. Then a decrease in activity is simply not transmitted to higher centres, contrary to the warmth sense system where evidently summation of increasing and decreasing activities takes place.

Another solution of the problem may be found in the assumption that activity in the sensory system for cold prevails over the activity elicited by warmth. In that case the activity caused by warmth is inhibited by the activity of the cold fibres. The central adaptation of the sense of cold causes the return of the threshold value for warmth. In the nervous pathway of activity elicited by cold the centres for central adaptation, summation and inhibition should occur.
The explanation of these facts through a single receptor system would demand somewhat strange presumptions about the central adaptation centres.

It will be noted that the return of the warmth threshold shows an abrupt course in spite of the spreading of the measured points. Here again a retardation time of about 11 sec is found, now in the recovery phase of the threshold. This time is longer than the retardation time found in fatiguing the central adaptation centres for warmth (2-4 sec).

After surveying all facts considered in this chapter it will be apparent that no evidence was found for the absence of warmth receptors. In mammals these receptors are probably outnumbered by the cold receptors, but their action is demonstrated in electrophysiological experiments. Also in lower animals, besides cold sensitive organs, very specialised warmth sense organs have been found.

However, the remarkable fact stands that both cold and warmth sense are equally sensitive and similar in dynamic behaviour.
CHAPTER V

DYNAMIC PROPERTIES OF THE SENSE OF TOUCH

§ 1. Experimental method

As the comparison of dynamic properties of the temperature sense organ and the sense of touch is of interest, a linear time course of the stimulus has been used here in the investigation of the sense of touch analogous to the experiments on the temperature sense organ. As will be seen below, information about the dynamic response of a system can sometimes be obtained more readily by sinusoidal stimulation. Sinusoidal displacements are generated much easier than usable sinusoidal changes in temperature. Therefore, also sinusoidal displacements have been applied.

The deformation in the skin is obtained by pushing inward or pulling outward a small circular area of skin. The exact deformation of the receptors is very difficult to describe, of course, but it will be presumed that the deformation is a linear function of the displacement of the stimulated skin area. It is clear that the largest deformation occurs at the circumference of the circular area.

The displacements of the skin linear in time were brought about by means of a pneumatic system. This consisted of two pneumatic variable resistances (Foxboro) connected to a bellows. The bellows moved a circular piston which was in contact with the skin. The equivalent circuit is given in fig. 32. The switch F represents a nozzle which connects the system with free air and can be closed by a flapper operated electromagnetically. The system is driven by air under a pressure of 8 kg/cm². Normally when the nozzle is not closed

\[
\text{displacement} = \frac{\tau_1(R_1 + R_2)C}{\tau_2(R_3 + R_2)C}
\]

Fig. 32.

Schematic representation of a pneumatic system serving to obtain linear displacements. During the stimulus the bellows C is filled with air through variable resistances R₁ and R₂. R₃ represents the small resistance of a nozzle F.
the pressure in the bellows C is constant at a near atmospheric value. To present the stimulus the nozzle is closed and the bellows is extended. Initially this extension is linear. After opening the nozzle air is escaping from C at a much slower rate because of the relatively small difference in pressure between C and free air (fig. 32). The displacement was measured by a displacement meter of the inductive type. The variable resistances $R_1$ and $R_2$ allowed the velocity of the displacement to be varied.

Sinusoidal displacements were obtained with an electrodynamic driving unit connected to a piston. The displacements were measured by the variation in capacity of condensorplates attached to the vibrator. (Fielden proximity meter). The restoring force of the driving coil of the electrodynamic system was enlarged by means of an extra spring. The spring constant was $300 \text{gr/mm}$ and the natural frequency of the system was 80 Hz.

To avoid the spreading of transversal surface waves over the skin, the inner side of the forearm was gently pressed against a perspex plate provided with a hole (diameter 2.5 cm) through which the skin was stimulated by the piston. Great care was taken that the initial deformation of the skin by the piston was as small as possible.

When applying sinusoidal deformations some extra precautions were necessary. Already at frequencies of 15 Hz the skin does not follow the vibrating piston exactly, which can be seen with stroboscopic illumination. To make sure that outward movements, too, were followed the skin was stuck to the piston. The vibrator was mounted quite free from the table where the arm was resting to prevent a disturbing conduction of vibrations through the table. In order to avoid disturbing transient phenomena the sinusoidal stimuli were raised and reduced in strength with time constants of about half a second.

The total duration of the vibrational stimuli was 3.5 sec. The duration of the linear deformation was determined by a stabilised monovibrator, the time constant of which could be varied. The electrodynamic systems were driven by a power amplifier with cathode follower output because of the necessity to use low frequencies.

Under 1000 Hz compressionwaves are much less important than shearwaves. Shearwaves in the upper skin layers are damped out very soon under the perspex plate. In this way the deformation of the superficial receptors is restricted to the immediate surroundings of the piston. The width of the uncovered skin between piston and perspex plate is 0.6 cm. As the velocity of the shearwaves in the upper skin layers of the arm have a velocity of about $2^m/\text{sec}$ the deformation pattern will be only slightly dependent on the frequency up to frequencies of about 170 Hz.
§ 2. Results of measurements with linearly increasing stimuli

Interpretation

The threshold total displacement was determined at stimulus durations of between 0.1 and 4 sec, applying psychophysical procedure a (II § 2). At each duration the probabilities of perception of four different velocities were measured. Six series of 10 trials were done at each velocity. So one threshold was determined from 240 trials, half of which consisted of zero stimuli. Series with different durations and different velocities were mixed. The experimental conditions were the same as shown in fig. 12.

Here again the threshold is defined at 85% probability of perception, the probability of perception being the probability of correct detection minus the probability of a false alarm.

![Experimentally determined probability of perception versus the deformation applied to the skin. Stimulus duration 0.45 sec.](image)

In fig. 33 an example of a probability curve is given. Thresholds could be determined with about 15% accuracy by adapting a standard curve to the measured points as has been mentioned previously (III § 2). In figs. 34 and 35 the thresholds of two well-trained subjects are shown for stimuli of different durations. Two different pistons were applied having a diameter of 0.9 and 2.1 cm respectively.

The most characteristic feature of the measurements is the approximately constant velocity of the threshold stimuli represented by a straight line through the origin. A constant threshold velocity is an indication for complete adaptation of the system with a time
constant which is small in comparison with the stimulus durations involved. The occurrence of a constant threshold velocity in these experiments is supported by the evidence obtained from measurements with sinusoidal stimulation and from electrophysiological experiments.

In figs. 34 and 35 threshold displacements at short stimulus durations deviate from the straight line. Stimuli of longer durations applied over larger areas also show a deviation from the constant velocity. In the graphs a displacement is indicated where a sensation of pressure appears which shows much less adaptation.
Thus far inward displacements have been used to stimulate touch receptors. However, the question arises whether the touch receptors in the skin are equally sensitive to inward or outward displacements of the skin. If equal sensitivity exists for displacements in both directions the touch receptor system will behave in accordance with fig. 36a and no discrimination can be made by a subject between inward and outward movements.

Experiments were carried out in which a subject had to state whether his skin was pushed or pulled under experimental conditions as described in the previous section. At the starting-point of the piston there was an impression of 0.6 mm in the skin. This impression was deepened or diminished with about equal velocity. Both kinds of stimuli had equal probability of occurrence. The duration of the stimulus was 0.2 sec, the diameter of the piston was 2.1 cm. The results of correct and wrong statements have been gathered in table IV.

Table IV

<table>
<thead>
<tr>
<th>Displacement</th>
<th>Subject E</th>
<th></th>
<th>Subject R</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>correct</td>
<td>wrong</td>
<td>correct</td>
</tr>
<tr>
<td>0.4 mm</td>
<td>8</td>
<td>12</td>
<td>10</td>
</tr>
<tr>
<td>(\approx 0.7) mm</td>
<td>56</td>
<td>24</td>
<td>61</td>
</tr>
</tbody>
</table>
Small displacements of 0.4 mm being about 2 x threshold are not correctly judged in so far as the direction of deformation is concerned. This is in agreement with fig. 36 a. With greater displacements, however, the direction of the displacement can be felt, but presumably here impressions reach a value where a sensation of pressure is going to play a part. This makes the two kinds of stimuli unequal, because with larger displacements other receptors become active.

§3. Mathematical description of the results

The touch sensory system shows complete adaptation. A simple physical model which has the same dynamical properties as the touch sensory system is pictured in fig. 36 b. We use a mechanical model here because a complete analogy is found of the dynamic properties of the sense of touch to mechanical properties of a so-called Pacinian corpuscle which is a touch receptor apparently. The mentioned analogy will be treated in more detail in VI §4.

The differential equation representing the dynamic behaviour of the mechanical model of fig. 36 b can be written as

\[
\frac{dI}{dt} = \frac{dO}{dt} + \frac{O}{\tau}
\]

where

- \(I\) = input displacement (mm)
- \(O\) = output displacement (mm)
- \(\tau\) = time constant of the system (sec)
- \(t\) = time (sec)

The applied stimulus linear in time is described by \(I = Dt\) with \(D\) = velocity of displacement (mm/sec)

The solution of the differential equation (20) in this case is

\[
O = D \tau (1 - e^{-t/\tau})
\]

Now it does not matter whether the receptor is deformed one way or the other. Every deformation yields a positive activity irrespective of the direction of the deformation. So the receptor output \(O_r\) will be proportional to \(|O|\):

\[
O_r = \alpha |O|
\]
\( \alpha = \text{constant (number of action potentials per mm and per sec)} \)

Hence

\[ O_r = \alpha |D| \tau (1 - e^{-t/\tau}) \]  \hspace{1cm} (21)

To produce a threshold sensation \( O_r \) has to equal or to surpass a certain value \( S \) during the time of application of the stimulus \( t_e \). Threshold is thus given by

\[ S = \alpha |D| \tau (1 - e^{-t_e/\tau}) \]

The threshold displacement as a function of duration of the stimulus equals

\[ |D| t_e = \frac{S t_e}{\alpha \tau (1 - e^{-t_e/\tau})} \]  \hspace{1cm} (22)

When \( t_e = 0 \)

\[ |D| t_e = \frac{S}{\alpha} \]

and for \( t_e \gg \tau \)

\[ |D| t_e = \frac{S}{\alpha \tau} t_e \quad \text{or} \quad |D| = \text{constant} \]

The last expression describes the experimental findings in figs. 34 and 35 with values of \( D \) of about \( 1 \, \text{mm/sec} \). It appears that a value for \( \tau \) cannot be determined from these measurements with sufficient accuracy. This will be done in experiments with sinusoidal stimuli.

Assuming that pressure receptors determine the threshold at longer durations of the stimulus, the curves of figs. 34 and 35 can be divided in two parts: the straight line giving the threshold for the touch receptors and the curved line determined by the pressure receptors. It is known that these pressure receptors do not show complete adaptation contrary to the touch receptors. The threshold in that case should be described in complete analogy of the temperature receptors III §3 (15).

\[ |D| t_e = \frac{S}{A + B \frac{\tau}{t_e} (1 - e^{-t_e/\tau})} \]  \hspace{1cm} (23)

Both expressions (22) and (23) yield threshold curves that are compared in fig. 37. Consequently the measured curve must be a combination of the two. Estimated from the curved line in figs. 34 and 35 the time constant of the pressure receptors should be about 0.5 sec.
It may be objected against the interpretation given above that as the activity described by (21) is constant for $t >> T$, the duration of the stimulus will influence the detection possibilities of the subject. In II §4, however, it was shown that increase of stimulus durations from 0.1 up to 3 sec did not improve significantly the detection of touch stimuli.

§4. Results of threshold measurements with sinusoidal stimuli

Determination of the time constant

Many investigations have been made concerning vibrational sensitivity of the human skin. A complete survey of the literature is given by Keidel. However, it was necessary for our purpose to have the measurements done with the precautions mentioned in §1.

The threshold was determined in exactly the same way as was done for linear stimuli. The diameter of the piston was 1.3 cm. An example of an experimental probability curve is shown in fig. 38. Again, every threshold is the result of 240 trials, performed with the experimental set-up of fig. 12.

The thresholds at different frequencies are plotted in figs. 39 and 40. At a frequency of about 25 Hz a sudden change in slope of the threshold curve is seen which is in agreement with other investigations. Generally, the threshold curve shows a minimum in the range of 200 - 400 Hz. At higher frequencies the threshold increases considerably.
To calculate the response of the proposed system after sinusoidal stimulation, the differential equation
\[ \frac{dI}{dt} = \frac{dO}{dt} + \frac{O}{\tau} \]
is used again. Here
\[ I = C e^{i\omega t} \]
and for \( O \) is written
\[ O = C e^{i(\omega t - \phi)} \]
where
- \( C \) = Input amplitude (mm)
- \( \omega = 2\pi f \)
- \( f \) = frequency in Hz
- \( \gamma \) = relative amplitude of the response
- \( \phi \) = phaseshift of the response relative to the input

From the expressions given above it follows that
\[ \gamma = \frac{\omega \tau}{\sqrt{1 + \omega^2 \tau^2}} \tag{24} \]

The output of the receptors \( O_r = a|O| \) will be a rectified sine function, \( a \) being again the number of action potentials per sec and per mm.

The half-cycles of the receptor activity have an amplitude \( a \gamma C \)
Now \( a \gamma C \) has to equal a value \( S \) in order to obtain a probability of perception of 85%. So for the threshold amplitude is found
\[ C = \frac{S}{a} \sqrt{1 + \frac{1}{\omega^2 \tau^2}} \tag{25} \]
which at very low frequencies becomes \( C = \frac{8}{\alpha} \frac{1}{\omega\tau} \)

Furthermore, the phaseshift \( \phi \) is found from 

\[
\tan \phi = \frac{1}{j\omega\tau}
\]  

(26)

In figs. 39 and 40 the solid line is drawn according to (25), with \( \tau = 0.03 \) sec and \( S/\alpha\tau = 370 \) and 430 \( \mu \)/sec respectively.

Threshold of vibrational stimuli as a function of frequency. Full line represents the theoretical curve according to formula (25). Broken line shows deviation from the theoretical curve.

The latter values are too low compared with the results in the previous section which yielded \( S/\alpha\tau = 0.8 \) mm/sec. The difference is significant because the accuracy of both values is about 10\%. However, both series of experiments have been done some time after each other.
For a more direct comparison of the two stimuli the subjects were tested by intermingled linear and sinusoidal stimuli. Using psychophysical procedure b (II § 2), zero stimuli, two different amplitudes at a frequency of 2 Hz, and a linear stimulus were presented in a random fashion. The stimulus duration was 0.98 sec. The transients at the start and at the end of the 2 Hz stimuli were damped by RC filters. The diameter of the piston was 1.3 cm.

The result is very convincing. Stimuli of 2 Hz with an amplitude of 32μ were perceived with about equal probability as linear stimuli with a total deformation of 410μ. The values of S/ατ given in table V have been calculated by making use of the fact that probabilities of perception are normally distributed.

Table V

<table>
<thead>
<tr>
<th>Stimulus</th>
<th>S/ατ (mm/sec)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>subject E</td>
</tr>
<tr>
<td>vibration</td>
<td>0.37</td>
</tr>
<tr>
<td>linear</td>
<td>0.35</td>
</tr>
</tbody>
</table>

The accuracy being about 15 %, the difference between vibrational and linear stimuli are not significant. The conclusion must be that differences in sensitivity over longer periods are rather large and the question arises whether the time constant is to be considered as a constant. Judging from the data given by other authors 94) the shape of the threshold curve does not change very much. So in spite of the fact that no direct measurements are available about the constancy of the dynamic properties over longer periods, the time constant is unlikely to be subject to great fluctuations.

Thresholds at frequencies exceeding 30 Hz are not in agreement with the proposed model, as the threshold amplitude has to remain constant. It may be that this discrepancy can be explained by the properties of the nerve. Assuming the receptor potential to have an amplitude that does not depend on the frequency, the triggering of the nerve should present a threshold curve as shown in fig. 41, in consequence of the excitability curve of the nerve. This excitability curve as a response to a constant current 7) is also pictured in fig. 41.

Direct experiments stimulating a nerve fibre with a.c. currents indeed reveal a similar type of threshold curve as drawn in fig. 41 106).
The excitability of a nerve in response to a constant current.

Threshold of a nerve excited by sinusoidal currents in consequence of the excitability curve.

Probably the shape of this curve being the result of experiments done with nerves of the squid and the frog applies equally well to the nerve fibres of mammals.

The vibration thresholds show a minimum at about 250 Hz, which means that the top of the excitability curve of the touch fibres is at about 2 msec after application of a constant stimulus. This value of the so-called utilization time is of the right order of magnitude.

It may be objected that the excitability curve is only valid for subthreshold stimulation. After the occurrence of a spike the nerve needs time to recover. At high frequencies it is often seen that after a spike some periods of the stimulus do not give a response. However, after the nerve has recovered, approximately the same excitability course might be valid.

Finally we may point out that the auditory nervous system has about the same shape of threshold curve. The maximum sensitivity is reached here at a frequency of 800 Hz as was calculated by Zwislocki (109).
CHAPTER VI
ELECTROPHYSIOLOGICAL EXPERIMENTS

§1. Purpose Experimental method

Quantitative electrophysiological data concerning the time-course of adaptation of the touch sense system are not available. Keidel measured the response of touch fibres in the frog's skin with sinusoidal stimulation. The range of frequencies he used was not suited to calculate a time constant. Therefore electrophysiological experiments were undertaken to see if any properties corresponding to psychophysical evidence could be found.

Recordings of the activity of touch fibres of the cat were made. Ten different animals have been used in the experiments. The cats were anaesthetized by nembutal administered intraperitoneally. In one case a chloralose-urethane solution was used. The sural nerve was dissected and freed from surrounding tissues. This cutaneous nerve passes down the leg, runs superficially into the heel and supplies the skin of the toes and the dorsum of the foot. In most cases the nerve was cut centrally but sometimes the connection was maintained. After pulling off the sheath of the nerve it was tried with needles to split up the nerve into fine strands. This was the most troublesome part of the preparation because it was very difficult to avoid injuries to the nerve fibres.

A separated nerve strand was put over a platinum electrode, the earth electrode was laid in a pool of Ringer solution containing the rest of the nerve bundle.

The action potentials were amplified by a balanced preamplifier and made visible on a Nagard oscilloscope. The deflection of the spot on the screen could be recorded continuously. At the same time the action potentials could be made audible through a loudspeaker.

In the experiments described below only the hairless skin of the toes was stimulated. A nerve strand showing the highest activity after stimulation of one of the toes, was selected and used for the recordings.

The same precautions as mentioned in V §1 were taken in deforming the skin. Both linear and sinusoidal displacements were obtained by means of the electrodynamical system described before. The toe was fastened to a fixed point. The displacements were transmitted to the skin by a small hollow steel rod stuck to a part of the toe.

The displacements could be measured by an inductive type of displacement meter (Philips) or by a capacitive type (Fielden). The first type possessed a calibrated scale; the other meter was calibrated
by observing the displacements through a microscope. The output of the displacement meter served to deflect the second beam of the oscilloscope. Thus the action potentials could be recorded simultaneously with the displacement.

A responding preparation will stay intact for more than an hour, but sometimes a slow decrease in sensitivity was observed. All measurements used for a particular calculation were done within 10 minutes, in order to prevent changes in sensitivity from interfering with the relations found in one series of experiments.

§2. Dynamic properties of single responding fibres

Some preparations appeared to have one fibre responding to small touch stimuli. This was concluded from the fact that all spike potentials were equally large and no "doubling" of spikes occurred.

Very seldom spontaneous activity was found in the sensitive touch fibres, although sometimes action potentials were seen in the rhythm of the heartbeat. Those preparations could not be used for the intended measurements.

On two occasions fibres were found that did not adapt completely to a constant displacement. They were not very sensitive and showed a partial adaptation with a time constant of somewhat less than half a second. These fibres seemed to be pressure fibres, because they displayed properties that are commonly attributed to pressure receptors. In chapter V §3 a similar influence was found with the presumed pressure sense system.

The remaining touch fibres both in massive and in single fibre discharges displayed complete adaptation to a constant displacement, in agreement with the model as developed in V §3. It was calculated that the receptor activity $O_r$ after a linear deformation should be:

$$O_r = a|D|\tau (1-e^{-t/\tau})$$

For $t >> \tau$:

$$O_r = a|D|\tau = \text{constant.}$$

This was found indeed. An example is shown in fig. 42, where a nearly constant frequency is obtained during the deformation of the skin.

The above formula predicts that the same response will be obtained by pushing or pulling the skin. Sometimes this is the case with a single fibre but mostly it is not. Some fibres are more sensitive to inward displacements, others show increased sensitivity to outward movements. Many fibres together display a nearly equal sensitivity to deformations in both directions. This indicates that the proposed
The response of a single touch fibre to linear and sinusoidal stimuli. Upward deflection of the lower trace means inward displacement of the skin. Duration of linear stimulus 1.14 sec. Frequencies 1, 3 and 10 Hz. Switching the linear stimulus on and off is clearly seen as an artefact.

The occurrence of spikes apparently shifts in the direction of the top of the sine at higher frequencies. In fig. 43 the phase shift is plotted as a function of the frequency. In measuring the phase-angle of the action potentials a correction was made for the conduction time from the receptor to the electrode where the action potentials were picked up. The conduction velocity of the large touch fibres is known to be about 15 m/sec. The length of the nerve fibre over which the action potential has to travel to reach the electrode is about 5 cm. When the nerve is triggered in less than 1 msec the total
retardation time will be about 4 msec. This value has to be subtracted from the measured retardation. The correction is important only at frequencies exceeding 3 Hz.

![Phase-shift of action potentials of a single fibre responding to a sinusoidal deformation.](image)

The line in fig. 43 is adapted to the measured and corrected points with the aid of formula (26). In this way the time constant is found to be 0.053 sec.

A better way to verify the applicability of the model is to raise the amplitude slowly while the activity is recorded. Afterwards the amplitude which caused the first spike to appear is determined for different frequencies. For another preparation both the threshold amplitude and the phase of the single spikes are plotted versus the frequency in fig. 44.

![Phase-shift and threshold amplitude versus frequency. The same fibre was used for both graphs.](image)
The findings are fairly consistent with the theory. The curves are
drawn after formulas (25) and (26) with a time constant of 0.035 sec
and a S/a value of 23μ. The latter value is rather large compared
with other preparations but the real deformation at the receptor is,
of course, very uncertain. The exact place of the receptor in the toe
is not known and if the receptor is just under the vibrating piston,
the deformation of the receptor will be very small because the per­
pendicular displacement is not efficient in deforming underlying
tissues.

At higher frequencies the action potentials do not appear at every
cycle, but once in 3 or 4 cycles. This makes it difficult to obtain
comparable threshold values for these frequencies.

§3. Response of many fibres

Sensation is mostly obtained by the activity of numerous fibres.
This can be concluded from the fact that threshold is dependent on
the surface area of the skin that is stimulated. To relate electro­
physiological data with psychophysical evidence more stress has to be
put on the massive response of many fibres than on single fibre
experiments.

Response of many touch fibres to linear and sinusoidal sti­
muli. Upward deflection of the lower trace indicates inward
displacement of the skin. The action potentials are slightly
retouched to obtain a better contrast. Scale linear defor­
mation is 140 μ. Duration 1.14 sec. Frequency of the sine
10 Hz, 80 superimposed traces.

Therefore preparations containing many responding fibres have
been used to record the activity under similar conditions as described
before. In such preparations the threshold for a single spike is not
easily obtained. The phase-angle can be measured by the technique of superimposed traces. An example of this is shown in fig. 45, where the response is photographed during 80 passages of the beam over the screen. The phase-angle can be measured with a rather large experimental error as is indicated in the graph of fig. 46. Again, the angle is corrected for conduction time of the spikes. To get a rough estimate of the time constants involved two curves are calculated with $\tau = 0.034$ sec and $\tau = 0.064$ sec. The mean value of $\tau$ calculated from the measured points is 0.042 sec.

![Diagram](image)

**Fig. 46.** Phase-shift of a massive discharge in a bundle of numerous touch fibres. The phase-shift is found from recordings as shown in fig. 45.

A preparation containing not too many responding fibres offers still an opportunity to count the separate impulses. The response of such a preparation is shown in fig. 45. From this picture it is seen that inward and outward displacements give about the same response. In fig. 47 the number of action potentials counted is plotted for different velocities of the linear displacement. The total duration was 1.14 sec but only impulses after 0.14 sec are counted because the activity becomes constant after $t \gg \tau$. As $\tau$ is about 0.04 sec, the frequency of action potentials will be constant within a few percent after 0.14 sec. Now the average number of action potentials should be proportional to the velocity of displacement. This is found to hold with good approximation for displacements in both directions.

In conclusion it can be stated, that the proposed model gives a good fit to the observed activity of a number of touch fibres in the cat. The average of all time constants measured is 0.04 sec which agrees surprisingly well with the time constant of the touch receptors in the human skin found with psychophysical procedures (0.03 sec). The observed similarity gives rise to the belief that the electro-
physiologically measured activity was indeed produced by touch receptors.

§ 4. Some concluding remarks

Recent investigations of Pacinian corpuscles in the cat have revealed properties very similar to those attributed to the sense of touch. It would seem worth while to look in this direction for an explanation of the dynamic behaviour as found in previous sections.

Gray, Sato, Malcolm and Loewenstein (82, 87-89, 99-103) studied the electrical phenomena of the Pacinian corpuscle. This receptor consists of a nerve ending surrounded by a capsule which is composed of concentrically arranged lamellae and a thin, more compact inner core. The dynamic behaviour of the receptor potential is shown in fig. 36a. It appears that the receptor possesses differentiating properties and that it is sensitive to both onset and removal of a deformation. From the investigations mentioned above it was also concluded that the receptor potential is generated in the inner core or the nerve ending.

Hubbard (92) used flash photography to study the mechanical deformation inside the receptor. He showed quite clearly that after a deformation is applied to the corpuscle the inner core reaches its original shape after some time. The recovery of corpuscles taken from
the mesentery of the cat takes place with a time constant of about 5 msec. Approximately the same value is obtained for the time constant of the receptor potential. The rise time of the receptor potential is less than 1 msec.

So one is inclined to describe the dynamic mechanical behaviour by an elastic inner core surrounded by a more viscous medium. Rapid mechanical deformation is transmitted to the inner core, which can, however, regain its former shape owing to its elasticity. The receptor responds independent of the direction of deformation.

A simple mechanical model of the receptor is pictured in fig. 36b, with separated viscous and elastic components. In fig. 36c the output of such a system after a deformation linear with time is given. This might explain the constant velocity found at the threshold of linear deformations of different durations (figs. 34 and 35).

The touch receptors in the skin of the cat or in the human skin need not necessarily be Pacinian corpuscles, but it is not unlikely that any deformation receptor should show a mechanical effect as described above.

In the skin of the cat Pacinian corpuscles are found but also other end organs are present investigated by Winkelmann, who presumed that these end organs were touch receptors. The capsule of this end organ may have the same function as was demonstrated in the Pacinian corpuscle.

The method used to record action potentials permits the recording of the activity of the larger fibres only. Douglas and Ritchie found in a more or less indirect way that a large number of smaller C fibres also responded to touch stimuli in the cat. They discussed the specificity of nerve fibres in general, because it turned out that the same fibres reacted to both touch and temperature stimuli. Up to the present it was believed that some C fibres were subserving the senses of pain and itch and that others signalled temperature. Nowadays in agreement with Weddell et al. the specificity of the nerves in mediating a certain modality is seriously doubted. Furthermore, Landahl and Williams developed a model accounting for three different sensations obtained with two kinds of receptors.

Contrary to Douglas and Ritchie the single fibre preparations of Iggo displayed a marked specificity also in case of responding C fibres. A lively discussion on the subject can be found in Hensel and Zotterman showed that in mechanoreceptive fibres only a cooling of 10°C or more could elicit a response. Moreover, cold fibres were not sensitive to mechanical stimulation. Their conclusion was that a specific sensitivity is present in different receptors or nerve endings. Cohen, Landgren, Ström and Zotterman recorded the activity of cortical cells in the cat after thermal and mechanical
stimulation of the tongue. It appeared that from the responding cells about 74% were specific and about 3% showed activity after all kinds of stimulation.

From a psychophysical point of view the properties found with electrophysiological methods and ascribed to a certain modality should have a marked similarity to psychophysical data concerning reaction times, sensitivity and dynamic behaviour. This means also that if properties are found which are in striking contradiction to psychophysical evidence, valuable information about the interpretation is obtained. For instance if in touch perception a reaction time is found of less than 0.3 sec the nervous activity cannot be transmitted to the central nervous system by the slow conducting C fibres, which have a conduction velocity of about 1 m/sec. Furthermore, if modality of sensation is not determined by specific fibres but by the temporal pattern of the discharges in various fibres, a combination of a number of punctiform vibrations of different frequencies and different amplitudes should be sufficient for evoking all possible sensations, which is not very likely.

When psychophysical data are thus compared with electrophysiological evidence there are reasons to believe that only activity in specific fibres determines the sensations of temperature and touch.
CHAPTER VII

CENTRAL ADAPTATION OF THE SENSE OF TOUCH

§1. Summation and central transmission

To see whether central adaptation is existent in the touch sense system a similar method of investigation can be applied as was developed in chapter IV §2. There it was proposed to test the central adaptation by measuring the threshold after a fatiguing stimulus has been given to an adjacent area. Contrary to the warmth stimulus a fatiguing touch stimulus can be presented well-defined in duration. For this reason the method may be applied here with more chance of success than in case of the warmth sense.

Recently Békésy \textsuperscript{76, 79} has studied the interaction of two stimuli on the skin in a more or less qualitative way. He distinguished three kinds of neural interaction viz. summation, inhibition, and a combination of the two, which he called funneling. One of the most interesting observations of Békésy deals with the analogue of the rotating tone in hearing. When two vibrating pistons stimulate the skin in different places with slightly different frequencies the sensation shifts from one stimulated area to another in a rhythm dependent on the difference of the two frequencies. We found a similar effect in some experiments undertaken to demonstrate summation. Two different stimuli were applied to adjacent areas of the skin by the use of two electrodynamic systems similar to the driving unit described in V §1. In this way a ring and a concentric piston could be driven independently of each other. To prevent waves from travelling over the skin from the piston to the ring, the two parts were separated by a ring pressed against the skin and fixed to the table where the arm was resting. With the displacement meter it was ascertained that no mechanical interference occurred between the piston and the vibrating ring. The ring with a width of 2 mm had a diameter of 4.9 cm; the piston was 1.3 cm in diameter.

When the ring and the piston are vibrating each with its own frequency the intensity of the sensation changes with a rhythm dependent on the difference in frequencies. The phenomenon is observed best with near-threshold amplitudes using frequencies of about 70 Hz. The observation is possible in the range of 40 Hz to several hundred Hz.
The beat frequency ranges from 0 to about 30 Hz. As both stimuli occur within a region of the skin where partial summation occurs, as will be shown below, this phenomenon may be understood by the mechanisms of summation. In fig. 48 a possible explanation is given. It is presumed that the action potentials occur at the top of the sines. It is clear that periodically the spikes will accumulate within a short interval, increasing the probability of transmission in the higher centres in the central nervous system where summation takes place.

When two adjacent areas are stimulated by vibrations with slightly different frequencies a beating sensation is produced. This may be explained by the time of occurrence of action potentials in the nerve.

To test the summation of the stimuli applied by the ring and the piston a series of experiments were done in the same way as was described for warmth stimuli in IV § 2. The skin was stimulated by short pulses applied by the ring or the piston or both. Using psycho-physical procedure b (see II, § 2) the experiment yields a probability of a false alarm, the probabilities of detection of two stimuli each by itself and both together. In table VI these probabilities are compared with the probability in case of complete summation \( P_{\text{sum}} \) and the maximum probability in case of no summation \( P_{\text{max}} \), according to II § 4. The second series consisted of 80 trials the other series of 180 trials.
Table VI

The probabilities of detection of two single stimuli and a combined stimulus compared with calculated probabilities with and without summation.

<table>
<thead>
<tr>
<th>Series</th>
<th>False alarm</th>
<th>$P_{\text{ring}}$</th>
<th>$P_{\text{piston}}$</th>
<th>$P_C$</th>
<th>$P_{\text{summ}}$</th>
<th>$P_{\text{max}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>7.3%</td>
<td>33%</td>
<td>46.5%</td>
<td>74%</td>
<td>88%</td>
<td>64%</td>
</tr>
<tr>
<td>2</td>
<td>1.25%</td>
<td>35%</td>
<td>60%</td>
<td>82%</td>
<td>95%</td>
<td>74%</td>
</tr>
<tr>
<td>3</td>
<td>2.2%</td>
<td>44%</td>
<td>63%</td>
<td>89%</td>
<td>97%</td>
<td>79%</td>
</tr>
<tr>
<td>4</td>
<td>4.4%</td>
<td>89%</td>
<td>68%</td>
<td>97%</td>
<td>99.9%</td>
<td>96%</td>
</tr>
</tbody>
</table>

subject E

All series show incomplete summation of the stimuli applied by the ring and the piston. The percentage of summation will be calculated later. For the moment it suffices to know that there is partial summation which is essential for the proposed demonstration of central adaptation.

§2. Experimental results

The fatiguing stimulus being a vibration with a frequency of 80 Hz, was administered by the ring. The test stimulus applied by the piston consisted of a pulse with a rise time of about 10 msec, a time of decay of 50 msec, and a total duration of 70 msec. In one series both fatiguing and test stimulus were applied by the piston to show the influence of the different location of the two stimuli.

When the subject pressed a button a fatiguing stimulus of pre-set duration occurred, followed by a test stimulus after a pre-set time. The subject could vary the strength of the test stimulus till he was of the opinion that threshold had been reached. He could perform as many trials as he wished to arrive at the threshold value. Psychophysical procedure c (II, § 2) was thus used, yielding threshold values in relatively few experiments. The disadvantage is, of course, that the fluctuations of the detection criterium of the subject are not known.

The experiments can be divided into three parts. First, a constant fatiguing stimulus is followed by a test stimulus after different intervals. Secondly, this interval is held constant but the amplitude of the fatiguing stimulus is varied. Thirdly, a fatiguing stimulus of
constant amplitude but varying in duration is followed by a test stimulus after a fixed interval.

A fatiguing touch stimulus with strength \( F \) and duration \( t \) is followed after a time \( \tau \) by a test stimulus being an impulse of strength \( Y \). The variation of \( Y \) represents the course of central adaptation. The experimental conditions are shown schematically above the graphs. The strength of the stimuli are given relative to the threshold in normal conditions.

In figs. 49 and 50 three curves are shown, each with a different parameter. This is clarified in the figures by schematic drawings representing the fatiguing stimulus \( F \) with a duration \( t \), followed after an interval \( \tau \) by a test stimulus \( Y \). All amplitudes are plotted in relative measures. The thresholds for vibration of the ring or for the impulse of the piston are taken as the unity of their respective stimulus strength.

Also in one of the three series of experiments both the fatiguing and the test stimulus were applied by the same piston. Compared with
the curve representing the results of separated stimuli, adaptation is present to a greater extent in case of stimulation of the same area. This could be explained in two ways. Either the receptors show a second adaptation with a larger time constant or summation was not complete. The latter case will be more likely because the partial summation found experimentally can explain quantitatively this difference in adaptation, which will be shown in the next section.

It will be noted in figs. 49 and 50 that small stimuli cause little or no central adaptation. On the other hand, the curves with the amplitude of the fatiguing stimulus $F$ as the variable show that a test stimulus with a strength of $3 \times$ threshold will always be experienced independently of $F$. This may be explained by a maximal adaptation in the higher centres or by a limited capacity of transmission to these centres.

The large fatiguing stimuli have probably activated the pressure receptors as well, but it is clear that only the central adaptation of the touch system was measured.

§3. Discussion

Lindblom investigated the touch units in the frog's skin. He found that a number of receptors can trigger the same nerve, thus forming a touch unit. Moreover, there was a drop in excitability for all remaining receptors when one receptor of the unit was stimulated. This was explained by the antidromic impulses coming from the site of branching of the afferent fibre. The antidromic impulses were set up by the activated receptor; so there exists a system of mutual inhibition. The existence of such a mechanism can be thought of as an objection against the measurements of central adaptation as described in §2. The adaptation measured could have been a peripheral effect caused by antidromic impulses from adjacent areas. This problem will be considered more closely.

Here below three different situations will be compared as regards their measure of summation and peripheral inhibition. The summation experiments mentioned in §1 of this chapter and the experiments on central adaptation with variable $t$ will be used for quantitative interpretation.

1. No summation nor inhibition.

The probability of detection of a combined stimulus $P_c$ can be found from the probabilities of the separate stimuli $P_1$ and $P_2$

$$P_c = P_1 + (1 - P_1)P_2$$

This is contradictory to the summation experiments (Table VI).
2. Complete summation; partial peripheral inhibition.

The activities induced by the ring and by the piston will be denoted by \( A_1 \) and \( A_2 \) respectively. The activity from the combined stimulus will be \( \alpha A_1 + \beta A_2 \) with \( \alpha < 1 \) and \( \beta < 1 \). Because of the geometry of the ring and the piston it is likely that \( \beta < \alpha \).

As the detection curve is approximated by a normal distribution (chapter II), the probabilities measured in the summation experiments must fit to a straight line on probability paper. The straight line can be determined e.g. by the false alarm rate and the probability of one of the single stimuli. This means that the remaining probabilities yield a value for the other single stimulus and the combined stimulus relative to the first single stimulus. In this way \( A_2 \) and \( \alpha A_1 + \beta A_2 \) are expressed relative to \( A_1 \). This has been done for the summation experiments in §1 of the present chapter, for which \( \beta \) is in the range of 0.50 - 0.80. This result can be applied to the experiments concerning central adaptation, which are now supposed to show peripheral adaptation because of antidromic impulses. From the fact that \( \beta \) is larger than 0.50 it can be deduced that mutual inhibition occurs in no more than 50 % of the total number of receptors. Thus the maximal adaptation obtainable by stimulating the adjacent area can be 50 %, compared with stimulation of the same area. It appears from figs. 49 and 50 that adaptation is about 70 % when separated stimuli are applied, compared with adaptation reached by two stimuli at the same area. As both values are significantly different the proposed absence of central adaptation together with a partial peripheral inhibition is not consistent with our measurements.

The assumption of a partial summation yields still larger values of \( \beta \). So this possibility also is contradictory to our measurements.

3. Partial summation, no peripheral inhibition.

In this case the combined stimulus causes an activity that can be divided into three different parts; a summated activity \( \alpha A_1 + \beta A_2 \) and two parts of the activity which are not summated: \( (1-\alpha)A_1 \) and \( (1-\beta)A_2 \). The ring encircles the piston in which situation it is likely that \( \beta > \alpha \).

It is assumed that the noise in the three parts mentioned is not correlated. In that case the combined probability \( P_c \) will be

\[
P_c = P_1 + P_2 + P_3 - P_1P_2 - P_1P_3 - P_2P_3 + P_1P_2P_3
\]

The probabilities for the three different parts to be distinguished in the activity are denoted by \( P_1 \), \( P_2 \) and \( P_3 \) respectively. Again, from the straight line on probability paper \( P_c \) can be calculated for different \( \alpha 's \) and \( \beta 's \) with known relative values of \( A_1 \) and \( A_2 \). For every \( \alpha \) the corresponding value of \( \beta \) is found by trial and error. According to the experimental results shown in figs. 49 and 50 it is
required that the receptors stimulated by the piston share their corresponding centres in the central nervous system with fibres coming from the receptor stimulated by the ring at least for 70%. This means that $\beta$ must be at least 0.7 when $A_2$ denotes the activity elicited by the piston. In this way values for $\beta$ are found in the range of 0.70 - 1.0, giving a perfect fit to the measured summation experiments. These values are also in agreement with the experiments concerning the central adaptation. The conclusion is that central adaptation rather than peripheral mechanisms accounts for the measured curves in figs. 49 and 50.

A further explanation of the adaptation curves is difficult for exactly the same reasons as mentioned in the discussion of the central adaptation of the warmth sense organ. There is no doubt that mathematical models can be developed describing the experimental curves with time constants of a few seconds. To correlate such models with properties of the central nervous system will not be possible at the moment.

The difference between the sense of touch and the warmth sense is the absence of a retardation time because here adaptation starts without measurable delay. Moreover, this adaptation is not complete.

ACKNOWLEDGEMENTS

The author is greatly obliged to the Director of Philips Telecommunication Industries in Hilversum for his readiness to place a complete radar set at his disposal. It is also a pleasure to express appreciation for the valuable technical assistance of Mr. W. Röttgers in all experiments and for the help of Mr. B. de Haan in constructing the apparatus of fig. 20. The author is indebted to the Department of Medical Illustration for making the drawings, and to the Technical Service of the University.
SUMMARY

In this study an investigation was described concerning adaptation of the senses of temperature and touch in the skin. Adaptation was defined here as a dynamic property by which sensation does not have a constant magnitude but diminishes with a continuous and constant stimulation.

It was attempted to correlate electrophysiological data with results obtained from psychophysical experiments. The latter always were threshold measurements.

On a basis of already existing theories, threshold experiments were considered as measuring the rate of detection of stimuli in the presence of neural noise. The noise activities in the nervous system have a positive mean value. Fluctuations may be described as a modulation of this mean activity. Presumably, the most important sources of noise are located in the central nervous system.

By irradiation of the skin with microwaves (λ = 10 cm) a linear increase of temperature was obtained in order to investigate the dynamic response of the warmth sense organ. Microwave radiation shows a relatively small absorption in moist tissues, yielding an almost uniform rise in temperature in the skin layers containing the receptors.

There exists an extensive literature concerning the activity in nerve fibres elicited by cold or warmth stimuli. It turns out that in these specific fibres a stationary activity shows a transient change, dropping in an exponential way to a new stationary value. The time constant of this partial adaptation is about 1 sec for cold fibres. No quantitative data about the warmth fibres are available.

Our psychophysical experiments indicate the presence of two different adaptation mechanisms. One time constant of about 0.3 sec was found, almost certainly belonging to the adaptation of the receptors, while a slower process pointed to another adaptation, having its origin in the central nervous system. This adaptation is complete, thus preventing stationary activities from being perceived. There are indications that the central adaptation starts to influence the transmission of activities after a retardation time of a few sec.

A similar investigation of the sense of cold is difficult to realize because the temperature of the receptors after the application of a cold stimulus is not known with sufficient accuracy. Comparable measurements on the cold and warmth sense were undertaken with equivalent experimental conditions. Both the sensitivity and the dynamic properties of the sense of cold show a surprising similarity to the
warmth sense. Nevertheless neither these nor other data do produce conclusive evidence against the existence of separate cold and warmth receptors.

Results of measurements with simultaneous application of cold and warmth stimuli show a marked difference between the two senses, which fact might be explained by a different way of processing for cold and warmth activities through the central nervous system.

Also, the sense of touch was investigated by means of stimuli increasing linearly in time. In agreement with electrophysiological evidence the results indicate the existence of complete adaptation. By the use of sinusoidal stimuli a time constant of this complete adaptation could be measured. This time constant appeared to be 30 msec.

Electrophysiological experiments were done with touch nerve fibres of the cat. Complete analogy was found with properties observed in psychophysical experiments. The time constant found here was 40 msec.

The observed similarity between psychophysical and electrophysiological data indicate that touch and temperature sensations are mediated by specific nerve fibres.

In the touch sensory system, too, a central adaptation was demonstrated, this being not complete. No retardation time was found here, in contrast with the sense of temperature. The time constants involved are of the magnitude of a few sec. The experimental method gave rise to reflections on the properties of summation of the receptor activities in different skin areas.
Samenvatting

Een onderzoek werd verricht naar adaptatieverschijnselen bij de warmtezin en de deformatiezin in de huid. Adaptatie wordt daarbij gedefinieerd als een dynamisch gedrag waarbij de sensatie tijdens continue constante stimulering niet constant blijft, maar afneemt. Getracht werd om electrophysiologische gegevens te correleren met resultaten van psychophysische proeven. De laatstgenoemde experimenten bestonden steeds uit drempelwaarde metingen.

Aan de hand van reeds bestaande theorieën, werden deze drempelwaarde experimenten opgevat als de meting van de detectie van stimuli temidden van neurale ruis. De ruisactiviteiten in het zenuwstelsel hebben een positieve gemiddelde waarde. Fluctuaties kunnen worden beschreven als een modulatie van deze gemiddelde ruisactiviteit. Vermoedelijk zijn de belangrijkste bronnen van ruis gelegen in het centrale zenuwstelsel.

Om dynamische karakteristieke grootheden te meten van het warmtezintuig diende een in de tijd lineair oplopende temperatuur als stimulus. Aangezien de ligging der receptoren een onzeker factor is, werden microgolven ($\lambda = 10$ cm) gebruikt om de huid te verwarmen. Deze straling heeft een relatief geringe absorptie in waterrijke media, zodat een vrijwel homogene verwarming wordt verkregen in de huidlagen waar de receptoren moeten zijn gelegen.

Uit de literatuur van electrophysiologische proeven omtrent de koude en warmte receptoren blijkt, dat in de corresponderende zenuwvezels een stationaire activiteit wordt aangetroffen, die na verandering van temperatuur aanvankelijk een grote verandering te zien geeft om na enige tijd op een nieuw stationair niveau te komen. De gemeten tijdconstanten van deze gedeeltelijke adaptatie zijn van de orde van 1 sec voor de koude receptoren. Van de warmte receptoren zijn geen quantitatieve gegevens bekend. De resultaten van onze psychophysische experimenten wijzen erop, dat er twee verschillende adaptatie processen optreden. De ene, die een tijdconstante van ongeveer 0,3 sec blijkt te hebben, betreft zeer waarschijnlijk de adaptatie van de receptoren, terwijl de andere zijn oorsprong heeft in het centrale zenuwstelsel. Deze centrale adaptatie zorgt ervoor, dat de stationaire activiteit der temperatuur receptoren niet wordt gepercipieerd. Vermoedelijk treedt deze centrale adaptatie op na een vertragingstijd van enkele seconden.

Een gelijksoortige meting voor het koude zintuig stuit op moeilijkheden, omdat het temperatuurverloop ter plaatse van de receptoren

Metingen met gelijktijdige toepassing van koude en warmte stimuli gaven voor beide zintuigen een markant verschil te zien, dat doet vermoeden, dat de wijze van verwerking van de activiteiten van de koude en de warmte receptoren in het centrale zenuwstelsel verschillend is.

Ook de tastzin werd onderzocht met lineair in de tijd toenemende deformaties. In overeenstemming met electrophysiologische ervaringen werden hierbij verschijnselen gevonden, die duiden op een volledige adaptatie. Met behulp van sinusvormige deformaties kon de tijdconstante van de volledige adaptatie worden gemeten. Deze bleek ongeveer 30 msec te zijn. Electrophysiologische experimenten werden aan tast zenuwvezels van de kat gedaan. Hierbij werden volkomen dezelfde eigenschappen gevonden; de tijdconstante bedroeg hier 40 msec.

De gevonden correlatie tussen psychophysische en electrophysiologische gegevens maken het waarschijnlijk, dat temperatuur- of tast-perceptie tot stand komt door activiteit van specifiek gevoelige receptoren.

Bij de tastzin werd ook een centrale adaptatie gevonden, die, in tegenstelling met de temperatuurzin, onvolledig blijkt te zijn. De tijdconstanten, die hier een rol spelen zijn van de orde van enkele seconden. Hier treedt geen retardatie op, zoals bij de temperatuurzin het geval is. De meetmethode geeft aanleiding tot een beschouwing omtrent summatie eigenschappen van de activiteit van receptoren in verschillende huidgebieden.
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ERRATA

Adaptation of the senses of temperature and touch.

Page 17, last formula: $P_{SN}(N)$ should read $P_{SN}(SN)$.

Page 25, last sentence: should be

Page 25, last sentence: figure 9: amount to 0.5 and 30°C resp

Page 25, last sentence: are in the region 0.5 – 30°C.

Page 25, last sentence: the stated temperatures

Page 25, last sentence: 32°C and 29°C in upper and lower

Page 25, last sentence: drawings should be reversed

Page 27, line 7 from top: higher skin temperature

Page 27, line 7 from top: should read

Page 34, second formula from top: $TT$ should be square root of $TT$

Page 81, fig. 48: actionpotentials should read actionpotentials.
STELLINGEN

I
De psychophysische meting van dynamische eigenschappen is een belangrijk hulpmiddel bij de bepaling van de betekenis van electrophysiologisch gemeten activiteiten.

II
Het door Williams en Landahl ontworpen model voor de schakeling van neurale elementen verbonden met koude en warmte receptoren is inadequaat om bekende eigenschappen van het temperatuurzintuig te kunnen beschrijven.

C.M. Williams and H.D. Landahl
20, 309-315, 1958

III
De veronderstelling van Sarnoff en Yamada, dat Pacini lichaampjes in de pancreas dienst doen bij de regeling van de arteriële druk, is vermoedelijk niet juist, omdat deze receptoren eigenschappen vertonen, die voor dit doel niet geëigend zijn.

S.J. Sarnoff and S.J. Yamada
Circulation Res. 7, 325 - 335, 1959
Dit proefschrift VI § 4

IV
Om het verschijnsel van summatie van plaats aan te tonen, worden de experimentele resultaten vaak onjuist geïnterpreteerd.

L.C. Greene and J.D. Hardy

V
Het door Rosenblatt ontworpen perceptron, een model van een "lerende" waarnemer, verdient aandacht.
Aan neurologische waarnemingen zijn argumenten te ontlenen om te onderstellen, dat het proces van het geheugen en het leerproces inderdaad verloopt, zoals door dit model wordt aangegeven.
Het "oneconomisch" gebruik van neuronen in dit model wordt gecompen-
seerd door het economisch gebruik van erfelijkheids informatie en de flexibele eigenschappen van het systeem.

F. Rosenblatt. Psychol. Rev. 65, 386 - 408, 1958

VI
Wanneer een figuur bestaande uit van een centraal punt uitgaande zwarte en witte sectoren wordt gefixeerd, worden rondgaande bewegingen waargenomen. Taylor verklaart dit effect door een oscillatorisch optreden van wederzijdse inhibitie van naburige elementen in de retina vergezeld van adaptatie.

Verloopt de adaptatie exponentieel, zoals experimenteel is aange­toond, dan kan geen oscillatiet effect optreden. Meer waarschijnlijk is het, dat ofwel spontane fluctuaties in de activiteit van de elementen in de retina ofwel de onwillenkeurige oogbewegingen oorzaak zijn van het verschijnsel. De laatste mogelijkheid wordt plausibel gemaakt door het feit, dat het genoemde verschijnsel zeer sterk optreedt, indien de figuur heen en weer wordt bewogen.


VII
De verwaarlozing van de thermodynamische potentiaal der suspensie in de door Kahlweit gegeven uitdrukking voor de Donnan - E.M.K. gemeten tussen twee zoutbruggen is onvoldoende verantwoord.


VIII
De met statistische methoden qualitatief bewezen verschijnselen van buitenzintuigelijke waarneming en psychokinese maken een quantitatief onderzoek naar de toepasbaarheid van statistische wetten in principe onmogelijk.


IX
Met moderne gelijkrichters kan een omzetting van wisselspanning in gelijkspanning voor grotere vermogens worden gerealiseerd zonder buitensporig hoge kosten. Het verdient overweging in laboratoria, waar gevoelige elektrische metingen worden gedaan, waarvoor de wisselspanningsfrequentie storend is (bijv. physiologische laboratoria) slechts een gelijkspanningsnet toe te laten.
In verband met het feit, dat frequente verandering van onderwerp van concentratie een extra vermoeiing teweeg brengt, is het wenselijk na te gaan of in het onderwijs het aantal verschillende vakken, dat per dag of per week wordt gedoceerd, moet worden beperkt.

De wettelijke verplichting om een proefschrift te doen vergezellen van een zestal stellingen buiten het eigen specialisme vergroot de mogelijkheid van verwarrende berichtgeving door niet-specialisten omtrent een bepaald vakgebied.

Academisch statuut: hoofdstuk III art. 25

E.G.J. Eijkman
4 December 1959