QUANTITATIVE ASPECTS OF CUTANEOUS SENSORY ADAPTATION. I*

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A method has been described for recording action potentials in single nerve fibres from single tactile receptors in the skin of the frog (Adrian, Cattell, and Hoagland, 1931). Leads were placed on one of the dorsal cutaneous nerves cut near the skin to record the antidromic impulses which are produced in a suitably selected single fibre by stimulation of some cutaneous area (cf. Hoagland, 1932). The action potentials were amplified and then recorded with a loud speaker and with a Matthews oscillograph used with a rotating mirror and camera. Stimulation of any desired frequency, duration, or intensity was secured by applying to the skin surface a jet of compressed air interrupted by a toothed disc fitted to a dental drill and revolved by a motor.

The receptors of the frog's skin were found to adapt very quickly to a continuous air jet, the rate of adaptation being comparable to that of an ordinary nerve fibre and thus differing from the slow adaptation of stretch receptors in muscle (Matthews, 1931).

With repeated air blasts of short duration, i.e. about 5σ, only a single impulse is set up for each puff of air. If the frequency of stimulation is sufficiently great the end organ soon fails to follow every stimulus, more and more impulses being dropped out until the response ceases entirely. In a previous paper Cattell and Hoagland (1931) examined this failure, which they regarded as an example of sensory adaptation; the rate of failure depends primarily upon the frequency of stimulation, the duration of the stimulus, and the inter-

* The experiments described in this paper were carried out in the Physiological Laboratory at Cambridge University, thanks to the kindness of Dr. E. D. Adrian who made available to me the necessary facilities.
val between the stimuli. The time for complete adaptation, up to the complete failure of responses, was found to vary from a few seconds at high frequencies of excitation to more than an hour at low frequencies.

II

For the purposes of these experiments "adaptation" may be defined by measuring its rate as the speed of decline of frequency of the electrical responses in a single afferent fibre when an intermittent air pulse of constant frequency from a constant-pressure source is applied to the skin, at a fixed distance from it. Preliminary experiments with different discs showed that after the beginning of failure of response to continuing intermittent stimulus, the curve describing the failure of response in any given experiment follows either one or another of two simple empirical formulas. To ascertain the possible significance of these formulas, adaptation was measured as functions of various time relations of the stimulus as determined by properties of a series of discs. In this way, for example, the rate of decline in frequency might be measured as a function of the size of the notches in the disc, and as a function of the duration of the rest period between stimuli, as determined by the amount of solid area left between the notches.

A series of six celluloid discs of 26 mm. diameter was constructed, with from one to six notches in each disc. The notches were carefully cut so that they were all of equal size, corresponding to a constant duration of stimulus of 5.6\(\sigma\) when the disc was rotated at 17.5 revolutions per second, the speed used throughout the experiments. Certain significant properties of the series of discs are given in Table I.

### Table I

<table>
<thead>
<tr>
<th>No. of notches in disc</th>
<th>Stimuli time (Second)</th>
<th>Stimulus time (s)</th>
<th>Area removed Area retained</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>17.5</td>
<td>S/R = 0.111</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>35.0</td>
<td>S/R = 0.251</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>52.5</td>
<td>S/R = 0.428</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>70.0</td>
<td>S/R = 0.670</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>87.5</td>
<td>S/R = 0.994</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>105.0</td>
<td>S/R = 1.500</td>
<td></td>
</tr>
</tbody>
</table>
To facilitate changing the discs during an experiment, a method devised by Dr. McKeen Cattell and used by us in our previous experiments was employed. One of the notches of each disc was continued through to the centre, so that the disc could be slipped on and off between small metal plates fitted to the end of the dental drill shaft and forced together by a spring. In this way, not only was changing the discs facilitated but the position of the air nozzle clamped to the drill immediately above the revolving notches was kept fixed—a matter of considerable importance in maintaining constancy of stimulation throughout an experiment.

Fig. 1 is a reproduction of the series of discs. In all of the preparations used brain and cord were pithed so that no movements of the frogs occurred after setting the nozzle in position above the receptor.

Fig. 2 gives typical photographic records for two preparations showing the decline in frequency of impulses after failure begins. The disc used was No. 5 (Table I), which causes rapid adaptation.

![Fig. 1. Outlines of series of discs × 0.5.](image)

The method of averaging employed may possibly have a bearing on the form of the equations here used to relate frequency of response to time. The procedure consisted in counting the number of impulses in a convenient period as measured by the time marked on the record after adaptation had begun to manifest itself by the first dropping out of an impulse in the series of responses to the stimulus. Since the frequency of stimulation varied from disc to disc, and since the number of impulses per unit time on the records decreases rapidly with adaptation, it was convenient to use a kind of moving average in which the times corresponding to a convenient number of impulses were measured. Trial computations showed no discrepancies in the forms of the curves of adaptation with wide variations in the number of impulses in the units used for averaging.

Fig. 3 is an example of the typical decline in frequency (expressed as percentage of the maximal frequency), plotted against the time from the first appearance of failure to respond, for Discs 1, 3, and 6. The points represent two sets of random observations for each of
Fig. 2. Typical records showing, in two preparations, the decline in frequency of impulses after beginning of failures of response.
these discs taken over a period of about half an hour. The good fit of
the curves to both these sets of observations shows that no irreversible
changes influencing adaptation had taken place in the course of the
experiment.

![Graph](image1)

**Fig. 3.** Plot of per cent frequency of response against time, after the first failure
of response to intermittent stimulation for Discs 1, 3, and 6. The experiment
shows two sets of observations for each disc.

![Graph](image2)

**Fig. 4.** Rectified form of the curves of Fig. 3.
Fig. 4 gives the rectified form of these curves; it is seen that they are fairly described by the equation

$$t = -k \log f + C,$$

where $t$ is the elapsed time, $f$ is the corresponding per cent frequency of response, and $-k$ is the measure of adaptation, the velocity constant of the process of adaptation.

This empirical equation is essentially of the form of that of a first order process, if it should be assumed that the frequency depends upon the concentration of a substance which is used up during stimulation. Adaptation is also seen to be more rapid to discs with larger numbers of notches and with relatively higher ratios of $S/R$. This obvious increase in rate of adaptation ($-k$) with increase of $S/R$ is suggestive when one considers the apparently reversible nature of the adaptation process. We may picture adaptation as occurring during the time that each stimulus is on and recovery taking place reversibly at the same time but with the recovery greatly accelerated during the intervening rest periods, the value of $-k$ being essentially proportional to the equilibrium constant for the reversible system.

To test the effect of stimulus duration and of the rest period duration of the revolving discs on $-k$, a series of twenty-eight preparations was examined. The skin was stimulated by the interrupted air jet and the responses were photographed. For discs with few notches and with relatively long rest periods, such as Disc 1, the impulses were found to follow the stimulus for several minutes with a subsequent progressive decline in frequency which might last an equally long period. To conserve photographic paper, sample records were taken at measured intervals of from 5 to 20 seconds. With the discs above Disc 2 in the series it was usually possible to photograph the complete adaptation on one record as is shown in Fig. 2 with Disc 5. The first disc tested was generally No. 6, which produced the maximal adaptation of the series, and this first disc was then used as a control. After obtaining records in haphazard order from all the discs of the series, the first disc, generally Disc 6, was again used. If the rate of adaptation to this control disc as recorded by the loud speaker, and subsequently verified quantitatively from the photographs, was the same at the end as at the beginning of the experiment, lasting about 20 minutes, the preparation was assumed to have suffered no irreversible changes. This test of the integrity of the preparation is important since many preparations show progressive failure despite care in shielding the nerve.
from the air and in bathing the tissues with fresh Ringer's solution. Out of twenty-eight preparations, seventeen only showed constancy of adaptation to the control disc. The remaining eleven experiments were accordingly discarded as irrelevant to the present discussion.

Room temperatures were recorded by a thermometer placed near the preparation and fluctuations of more than 0.2°C were seldom recorded during an experiment. There was little day-to-day fluctuation of the room temperature, which remained at approximately 17 ±1°C. The stimulating air used was essentially at the temperature of the room, since it had ample time to cool after compression in a large storage tank and was piped for a considerable distance through the building. The jet blown on a thermometer bulb did not change its temperature by as much as 0.1°C. Cooling of the skin by evaporation was prevented by painting it with oil. The nerve was shielded from the stimulus by drawing it into a glass tube containing the leads to the electrical recording system and packing cotton soaked in Ringer solution around both ends of the tube. Moist packing was also placed around the incision, including the millimeter or so of nerve between the junction with the animal and the entrance of the nerve into the glass tube.

To compare the effects of the ratio S/R for different discs the per cent decline in frequency was calculated; 100 per cent was the maximal frequency of response, corresponding to a one-to-one relation with the stimulus frequency of the disc. In this way absolute differences in adaptation rates due to the fact that the disc stimulates at different frequencies were eliminated and the relative adaptation rates became comparable.

III

Two different forms of adaptation curves were obtained with the seventeen preparations successfully examined. The first type of result has already been mentioned and is given in Figs. 3 and 4. Here adaptation is typically described by the equation.

\[ t = -k \log f + C. \]

The second result is represented by characteristic adaptation curves which, while superficially resembling the curves of Fig. 3, differ fundamentally in the type of empirical relation describing them. Fig. 5 is the typical plot of such an experiment for three of the discs, and Fig. 6 shows these curves rectified. The logarithm of the time is nearly

\[ 1 \text{ In the present experiment it has not been possible to vary } S/R \text{ from disc to disc without also varying the frequency of stimulation (cf. Table 1). } \]
Fig. 5. Plot of per cent frequency of response as a function of time for three discs showing rapid early failure of response as contrasted to the curves of Fig. 3.

Fig. 6. Rectified form of the curves of Fig. 5.
enough an inverse linear function of the logarithm of the per cent frequency. The curve is hyperbolic, described by the equation

\[ s = af^{-b} \]

where \( f \) and \( t \) are respectively frequency and time, and \( a \) and \( -b \) are constants. The constant \( -b \) is defined as the adaptation rate in the sense in which \( -k \) was defined above. This comparison of \( -k \) and \( -b \) is obvious when logarithms are taken on both sides of the hyperbolic equation,

\[ \log t = \log a - b \log f \]
\[ \log t = K - b \log f \]

\( -b \) is seen to be the slope of the line relating \( \log t \) and \( \log f \).

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**Fig. 7.** Figure showing constancy of response to control Disc 6 over an interval of about 20 minutes. The plot shows three sets of data taken at intervals of from 5 to 10 minutes during an experiment.

Fig. 7 is a plot of per cent frequency vs. time from three records with Disc 6 made at intervals of from 5 to 10 minutes during an experiment. The plot shows great constancy of response to Disc 6.
The difference in the forms of the two equations for adaptation rate suggests possible uncontrollable experimental differences, and these were accordingly looked for but were not found. The preparations showing logarithmic adaptation were scattered quite at random among those showing hyperbolic adaptation. In several cases a particular nerve would show either the logarithmic or the hyperbolic adaptation while an adjacent nerve in the same frog tested imme-

<table>
<thead>
<tr>
<th>Disc No.</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
</tr>
</thead>
<tbody>
<tr>
<td>6</td>
<td>0.0504</td>
<td>0.38</td>
<td>0.305</td>
<td>1.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>8 A</td>
<td>0.0305</td>
<td>0.146</td>
<td>0.57</td>
<td>1.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>0.0380</td>
<td>0.258</td>
<td>0.221</td>
<td>1.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>11 A</td>
<td>0.00296</td>
<td>0.323</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>11 B</td>
<td>0.0944</td>
<td>0.348</td>
<td>0.665</td>
<td>1.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>13 A</td>
<td>0.0200</td>
<td>0.145</td>
<td>0.109</td>
<td>0.713</td>
<td></td>
<td></td>
</tr>
<tr>
<td>15 A</td>
<td>0.0094</td>
<td>0.161</td>
<td>0.456</td>
<td>1.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Means</strong></td>
<td><strong>0.0387</strong></td>
<td><strong>0.064</strong></td>
<td><strong>0.227</strong></td>
<td><strong>0.337</strong></td>
<td><strong>0.584</strong></td>
<td><strong>1.00</strong></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Disc No.</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
<td>0.0907</td>
<td>0.857</td>
<td>0.682</td>
<td>0.675</td>
<td>0.820</td>
<td>1.00</td>
</tr>
<tr>
<td>7</td>
<td>0.686</td>
<td>0.813</td>
<td>0.675</td>
<td>0.820</td>
<td>1.00</td>
<td></td>
</tr>
<tr>
<td>8 C</td>
<td>0.730</td>
<td>0.787</td>
<td>0.787</td>
<td>1.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>16 B</td>
<td>0.563</td>
<td>0.658</td>
<td>0.620</td>
<td>0.835</td>
<td>1.00</td>
<td></td>
</tr>
<tr>
<td>17 B</td>
<td>0.239</td>
<td>0.675</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Means</strong></td>
<td><strong>0.302</strong></td>
<td><strong>0.553</strong></td>
<td><strong>0.717</strong></td>
<td><strong>0.748</strong></td>
<td><strong>0.860</strong></td>
<td><strong>1.00</strong></td>
</tr>
</tbody>
</table>
Immediately afterwards would show the other of the two characteristic forms. In two cases a shift from the logarithmic to the hyperbolic form of curve occurred during the course of the experiment, despite the fact that adaptation to Disc 6 was maintained constant to the end. Of the seventeen preparations, nine were of the logarithmic type and six were of the hyperbolic type, while two showed a change from one type to the other in the course of the experiments. It so happens that in the figures presented logarithmic adaptation is shown as occurring with Discs 1, 3, and 6, and hyperbolic with Discs 2, 4, and 5, but there is in fact no tendency for a particular disc to give a particular type of adaptation curve, as may be seen from Tables II and III. In numbering the experiments the numbers refer to individual frogs and the letters A, B, C, and D refer to different dorsal cutaneous nerve preparations in the same frog.

Fig. 8 is a plot of the mean values of the adaptation rate \( -k \), as a function of the ratio \( \frac{\text{Stimulating time}}{\text{Resting time}} \) for each disc of the series.

Fig. 8. Plot showing linear relation between the ratio \( S/R \) and the mean velocities of the logarithmic type of failure.
Fig. 9 is a plot of the values of $-b$ as a function of the logarithm of the ratio $\frac{\text{Stimulus time}}{\text{Resting time}}$.

While statistically the data are meager, especially more so for some discs than for others, a plot of the means is justifiable since plots for individual preparations, while showing considerable variation, follow, in general, the functions shown by the means.

![Graph showing the linear relation between $-b$, the velocity of hyperbolic failure, and the logarithm of S/R.](image)

**Fig. 9.** Figure showing the linear relation between $-b$, the velocity of hyperbolic failure, and the logarithm of S/R.

The foregoing experiments were undertaken with a view to elucidating the kinetics of cutaneous sensory adaptation but the findings do not at present warrant much in the way of theoretical generalizations. It is clear that responsiveness of a receptor declines rapidly during the time that the stimulus presses on the skin and that this responsiveness returns partially in the brief interval between stimuli. Several paradigms have been proposed which could account for the quantitative aspects of this effect, but more experiments are necessary before it will be possible to decide in favor of any one mechanism.
The fact that some preparations give logarithmic adaptation while others give hyperbolic adaptation is difficult to account for. It is possible that these two forms may be limiting cases of a single general underlying equation. It is interesting in this connection to note that in two preparations clear shifts occurred from logarithmic to hyperbolic adaptation during the course of the experiments.

There are certain limitations to the method. One of these was the impossibility of keeping the frequency of stimulation and the duration of the stimulus constant when varying the ratio $S/R$ from disc to disc. The ratio $S/R$ may be shown to be equivalent to $\frac{Fd}{1-Fd}$ where $F$ is the frequency and $d$ is the constant duration of the stimulus. It is clear, therefore, that frequency is a variable along with $S/R$ and may modify the adaptation in some way independently of $S/R$. One can compare adaptations by using the per cent decline of the frequency of impulses as a measure of the response, but, experimentally, frequency of stimulation was a variable along with $S/R$.

SUMMARY

1. Adaptation of tactile receptors in the skin of the frog to excitation by an intermittent jet of air is measured and correlated with certain properties of a series of notched discs used to interrupt the air stream.

2. Adaptation in fifteen cases is found to be described by either one of two empirical formulas,

$$t = -k \log f + C, \text{ for nine preparations}$$

$$t = a f^{-b}, \text{ for six preparations}$$

where $f$ is the per cent frequency at time $t$ and $-k$ and $-b$ are constants defining the rate of adaptation.

CITATIONS


Matthews, B., 1931, *J. Physiol.*, 71, 64.