FITTING ADAPTATION MODELS TO VELOCITY STEP RESPONSES:
SIMULATION OF NORMAL AND ABNORMAL RESPONSES

P. L. M. Huygen and M. G. M. Nicolasen

Department of Otolaryngology, University Hospital Nijmegen, The Netherlands

Reprint address: P. L. M. Huygen, Ph.D., Department of Otolaryngology, University Hospital Nijmegen, P.O. Box 9101, 6500HB Nijmegen, The Netherlands

Abstract — A method is described to obtain suitable parameter values for an adaptation model that can be used to simulate velocity step (VS) responses. The input parameters are the dominant time constant fitted to the first part of the VS response and the time of reversal in nystagmus direction. This method allows a particular solution for the model previously defined by others with a vestibulo-ocular reflex (VOR) time constant, a time constant of adaptation, and a fixed (unitary) gain of the adaptation element. However, because it might be arbitrary to assume a unitary gain, we also studied a more general model with a variable gain element. It appeared that patients showing short responses had a short VOR time constant and less adaptation than normal. Patients exhibiting prolonged responses appeared to have an excessively long VOR time constant and more adaptation than normal, presumably to compensate for the long time constant.

Keywords — VOR; gain; time constant; phase reversal.

INTRODUCTION

A model for the vestibulo-ocular reflex (VOR) has been established (1,2) which accounts for the excessive phase lead of the VOR at ultralow frequencies (3), the reversal in direction of postrotatory nystagmus in the velocity step (VS) response (4), and the decay of the slow phase velocity (SPV) of the nystagmic response to constant acceleration (5). Several authors (1-4,6) have emphasized the problem that the pseudo first-order time constant that can be fitted to VOR responses, in fact represents the dominant VOR time constant, which is apparently shortened by the effect of adaptation.

Various numerical methods for fitting adaptation models to VS responses have been described (7,8), all of which pertain to the classical model with unity gain. So far, these have only produced scarce evidence about adaptation behaviour in pathological conditions.

In the present study, abnormal VS response types were first identified on the basis of model-independent response parameters, one of which later appeared to be linked to adaptation behaviour. For the abnormal response types, a “general” adaptation model was then simulated (see Appendix), in search of characteristic differences, if any, from the normal response type in terms of model parameters. The general model was the above-mentioned classical model (1,2) with a variable gain element (it might be arbitrary to assume a fixed — unity — gain, beforehand). The method that was followed produced a variety of particular solutions, all of which yielded suitable simulations, as is illustrated below.

As is explained under Methods, it proved possible — on the basis of various theoretical arguments — to outline the complete set of all possible solutions to the simulation problem by identifying 3 boundary conditions. Within these conditions, the variability of each relevant model parameter was analyzed in order to find those parameters, if any, which displayed “overall”, that is, unconditional, sig-

Received 31 October 1990; Revision received 18 July 1991; Accepted 22 July 1991.
significant differences between the different response types.

The results indicate that adaptation plays a special part in mechanisms that compensate for pathological changes in the VOR. Adaptation may also be invoked to explain earlier observations on the "adaptability" of the VOR to long-standing nonphysiological conditions.

THEORY

Description of a Classical Model

The adaptation network depicted in Figure 1a has a transfer equation that is equivalent to that proposed by Malcolm and Melivill Jones (2) if \( m = r \).

The input coming from the left, that is, the semicircular canal system, is divided over a direct path and a leaky integrator with a time constant (\( T_a \)), a negative feedback loop (gain \( r \)) and an attenuator (\( m \)). The output of the loop is proportional (by a factor \( m \)) to the integral of the input signal as previously conceived (1); it also represents the "shifting reference level" previously hypothesized (1,2). This reference level is subtracted from the direct signal at the next summation point. The adaptation network of Figure 1a is incorporated into the left part of the schema in Figure 1b. The input is now shown (head velocity, \( h \)), and the integrating canal system is taken to be a first-order system with the time constant \( T_c \) of cupular restoration and the gain, or primary sensitivity coefficient, \( k \). This part of the network is associated with the peripheral vestibular system (6). The afferent signal leads to a central summation point within the positive feedback loop conceived by Robinson (9), with the leaky brain stem integrator with time constant \( T_b \) and gain \( B \), which is an alternative for Raphan and colleagues' "velocity storage mechanism" (10). The output of this network is a compensatory eye velocity signal (\( \dot{e} \)), which is further processed by the oculomotor integrator to control eye position. The dynamics of the latter have been neglected here.

![Diagram](https://example.com/diagram.png)

**Figure 1.** A network for the adaptation model with time constant \( T_A = T_a/r \) of adaptation and variable gain \( M = mlr \). (a) Adaptation network. (b) Complete network (except oculomotor plant), including the positive feedback loop with the leaky brain stem integrator. Modified from Robinson (9) and Buettner and colleagues (23). \( k \), primary sensitivity coefficient; \( T_c \), time constant of cupular restoration; \( B \) and \( T_b \), gain and time constant, respectively, of the brain stem integrator; \( s \), Laplace complex frequency. If \( m = r \), then \( M = 1 \), which applies to the classical model. See text for further explanation.
Adaptation Models and Velocity Step Responses

Transfer Equation

The transfer equation for the network in Figure 1b (in Laplace notation) is

\[ \frac{\dot{e}(s)}{h(s)} = \frac{sK}{(sT_j + 1)} \times \left[ 1 - \frac{(m/r)}{(sT_c/r + 1)} \right], \quad [1] \]

where \( T_j \) is the dominant VOR time constant, which is

\[ T_j = T_c/(1 - B), \quad [2] \]

and

\[ K = k/(1 - B) \quad [3] \]

(omitting the minus sign indicating compensatory eye movement), which is achieved by following Robinson's proposal (9) that \( T_b \) is close to \( T_c \). Thus the first term on the right of equation [1] is the canal system which is lumped with the brain stem integrator in order to represent the VOR system without the influence of the adaptation mechanism, the latter of which is represented by the second term.

Velocity Step Response

The time-domain response of the system with transfer equation [1] to a VS of 90°/s, with the substitution variables \( M \) and \( T_A \) replacing the fixed combinations in equation [1], that is,

\[ M = m/r; \quad T_A = T_a/r \quad [4] \]

is:

\[ v(t) = V[(T_A + (M - 1)T_j)] \cdot \exp\left(-t/T_j\right) \]

\[ - \frac{M}{T} \cdot \exp\left(-t/T_c\right)/(1 - B). \quad [5] \]

Here, \( v(t) \) is SPV at time \( t \) after the step, which has initial velocity \( V \), where

\[ V = (K/T_j)90°/s, \quad [6] \]

\( K/T_j \) being the gain of compensatory eye velocity. When in equation [4] \( m = r \), then \( M = 1 \), that is, we have the classical model (1,2).

With

\[ \beta = T_A/T_j \quad [7] \]

and

\[ C = \beta/M + 1 - 1/M, \quad [8] \]

equation [5] reduces to

\[ v(t) = \left[ C \cdot \exp\left(-t/T_j\right) - \exp\left(-t/T_A\right)\right] \]

\[ \times M V/\left(\beta - 1\right). \quad [5a] \]

The time of reversal of nystagmus direction \( t_0 \) at which \( v(t) = 0 \) can be derived from equation [5a] as

\[ t_0 = T_j \cdot \ln(C)/(1 - \beta). \quad [9] \]

A Response Parameter to Assess Adaptation Behaviour

To characterize adaptation, we tentatively used the parameter \( Q \), which can be directly assessed from the VS response. \( Q \) is defined as a quotient:

\[ Q = T/T_0, \quad [10] \]

\( T \) being the dominant time constant fitted to the primary phase response (that is, its SPV) in a first-order approximation. It is demonstrated below that \( Q \) relates to the amount of adaptation, which is defined below.

For clarity, in the text below \( Q \) has been replaced by \( Q_{obs} \), \( T \) by \( T_{obs} \) and \( t_0 \) by \( t_{obs} \), respectively, to distinguish values actually observed from those derived from model calculations.

Assessing the Change in Dominant Time Constant

As explained below, it appeared to be convenient to define a substitution variable \( \alpha \), which assesses the relative difference in the initial slope or in the dominant time constant:

\[ \alpha = 1 - T/T_1. \quad [11] \]
Curvature, Attenuation, and Cancellation

Some additional parameters were defined to evaluate the downward curvature (that is, in the semilog plot!), the degree of attenuation and overall cancellation of the primary phase of the VS response:

\[
\%\text{curvature} = \left(1 - \frac{G_3}{G_1}\right)100\%, \quad [12]
\]
\[
\%\text{attenuation} = \left(1 - \frac{G_3}{G_2}\right)100\%, \quad [13]
\]
\[
\%\text{cancellation} = \frac{M}{N}100\%; \text{ see below.} \quad [14]
\]

The parameter \(G\) is the "Gesamtamplitude" or cumulative eye displacement (CED) at \(t = t_{\text{obs}}\), which can be derived from time integral expressions in \(v(t)\):

\[
G_1 = V T_{\text{obs}}[1 - \exp(-t_{\text{obs}}/T_{\text{obs}})]
= V T_{\text{obs}}[1 - \exp(-1/Q_{\text{obs}})], \quad [15]
\]
\[
G_2 = V T_1[1 - \exp(-t_{\text{obs}}/T_1)], \quad [16]
\]
\[
G_3 = \left[C T_1[1 - \exp(-t_{\text{obs}}/T_1)]
- T_\Delta[1 - \exp(-t_{\text{obs}}/T_\Delta)]\right]
\times MV/(\beta - 1). \quad [17]
\]

The above parameters have the following meaning: \%curvature measures what percentage of CED (up to time \(t_{\text{obs}}\)) has "disappeared" relative to the extrapolated first-order response (with time constant \(T_{\text{obs}}\)); \%attenuation takes a similar measurement, but now relative to the (hypothetical) nonadapted first-order response (with time constant \(T_1\)); \%cancellation is calculated just as \%attenuation in equation [13], but with infinite time instead of \(t_{\text{obs}}\). It should be noted that \%curvature can also be interpreted as a measure of the error made by using the first-order approximation.

The "Amount" of Adaptation

By saying that two different VS responses show different "amounts" of adaptation, we mean that, after the elimination of any differences in the initial slope (or dominant time constant \(T_{\text{obs}}\)), they show different degrees of downward curvature—equation [12]—in the semilog plot. An increase in the \%curvature goes with an increase in the \%attenuation, and such behaviour relates to an increased gain attenuation and phase lead of low frequencies in the frequency domain (Bode plot).

Material and Methods

Normal Subjects and Patients

The normal subjects were 12 healthy volunteers (7 men, 5 women, aged 22 to 50 years), in whom \(t_{\text{obs}}\) and \(Q_{\text{obs}}\) could be assessed in 19 responses (there was no clear nystagmus reversal in 5 responses). The patients were 500 consecutive patients examined in the period from August 1988 to July 1989. Subjects who showed spontaneous nystagmus were excluded. Only the VS responses that showed clear nystagmus reversals were used.

Vestibular Methods

All of the rotatory tests were performed in complete darkness with the eyes open. The VS
test was carried out with the subject seated on a rotatory chair (Tönnies, Freiberg, Germany). After $0.8\,^s^2$ acceleration and a period of $90\,^s$ constant velocity long enough to let the perrotatory nystagmus subside, the chair was stopped with $200\,^s^2$ deceleration. Nystagmus was measured with dc electronystagmography. Eye movements were calibrated before each test. The horizontal nystagmic responses were recorded on paper and analog tape; off-line computer measurement and analyses of SPV ($^s$) were performed as described previously (11–13).

**Analysis of Response Data**

The dominant time constant ($T_{obs}$ in s) was obtained from the VS response by fitting a weighted regression line to the plot of log(SPV) for each nystagmus beat versus the time after the sudden stop. The weighting procedure acknowledged the logarithmical transformation of SPV with a weight of $[v(t)]^2$; the time window was approximately 0 to $0.5t_{obs}$, that is, it pertained to the primary phase of the response only. The reversal time $t_{obs}$ was measured by interpolating the moment at equal distances in time between the last beat of the first phase and the first beat of the secondary phase of postrotatory nystagmus. As reported elsewhere (14), the normal values of $t_{obs}$ for the present group of subjects were: mean 45 s and 5th and 95th percentiles 37 and 55 s, respectively (after logarithmical transformation). The previously established 5th and 95th percentiles in the distribution of $T_{obs}$ were 11 and 26 s, respectively (15). Normal values for $Q_{obs}$ were established by probit plot analysis (without parameter transformation). The method used to identify abnormal responses employed the above objective response parameter data (see Results).

**Simulation and Further Data Analysis**

We were facing the problem that simulation of the more general model required 3 input parameters, where only 2 were available. To allow at least some comparison with previously reported results, we attempted the choice of the preset values of $M = 1$ and $T_A = 100$ s, in alternation. Both these choices seem to be arbitrary, but in fact only the latter is, as the former appears to be relevant because it pertains to one of the 3 boundary conditions that could be identified and which, taken together, outline the set of all the possible solutions. These 3 boundary conditions are (i) the condition $M = 1$ (for $M > 1$ the model shows peculiar phase behaviour as discussed below); (ii) the condition of equal time constants ($\beta = 1$ in equation [7], see part II of the Appendix) and (iii) the condition that for each set of input parameters, it appears that simulation is only possible for values of $M$ higher than a minimum value. For each of the 3 boundary conditions, the values for the relevant parameters were calculated for all of the individual responses. The data in the normal group were used to derive 90% normal ranges (after logarithmical transformation) from probit plots. For the abnormal response types, the 5th and the 95th percentiles are presented for the relevant parameters in these 3 boundary conditions. Relevant differences were tested for their significance using Wilcoxon's test ($P = 0.05$). Only “overall”, that is, unconditional, significant differences, if any, were considered further.

**RESULTS**

**Normal Values of $Q_{obs}$**

The 90% normal range for the response parameter $Q_{obs}$ was 0.28 to 0.39 (mean 0.33).

**Identifying Abnormal Response Types**

In the patients, we looked for response types with “typical patterns”, that is, specific combinations of abnormal/normal values of
the observed response parameters. As previously reported (16), two VS response types, the one with a significantly short time constant $T_{\text{obs}}$ ($T^-$) and the other with a significantly long time constant ($T^+$), were predominant. In the present study, while we were also looking at the parameters $t_{\text{obs}}$ and $Q_{\text{obs}}$, it appeared that in the patient sample there were 2 response types with typical patterns, each in a significantly higher frequency than expected ($x^2$ test, $P < 0.05$) because of the separate relative frequencies of $T^-$, $T^+$, $Q^-$, and $Q^+$, respectively. The expressions $T^-$, $T^+$, and $Q^-$, $Q^+$ indicate significantly low or high values of $t_{\text{obs}}$ and $Q_{\text{obs}}$, respectively. The response type with the pattern $T^+T^+Q^+$ (21 cases) was designated “short response type.” The type with the pattern $T^-T^-Q^-$ (24 cases) was designated “prolonged response type.” The etiology of the patients showing either one of these response types is presented in Table 1.

### Table 1. Etiology in Two Groups of Patients with Short and Prolonged VS Responses

<table>
<thead>
<tr>
<th>Etiology</th>
<th>Short response</th>
<th>Prolonged response</th>
</tr>
</thead>
<tbody>
<tr>
<td>Labyrinthine defect</td>
<td>17</td>
<td>3</td>
</tr>
<tr>
<td>unilateral</td>
<td>14</td>
<td></td>
</tr>
<tr>
<td>bilateral</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Multiple sclerosis</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Progressive supranuclear palsy</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Cerebral hemisphere tumour</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>21</strong></td>
<td></td>
</tr>
<tr>
<td>Hyperventilation syndrome</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>proven</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>suspected</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>Motion sickness</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Unknown</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>24</strong></td>
<td></td>
</tr>
</tbody>
</table>

*With tympanic membrane perforation or radical cavity.

### Table 2. Values as Observed for Response Parameters and the Values Derived for Model Parameters Pertaining to Simulations of the “Average” Short, Normal, and Prolonged Response Type. Goal Values Are Shown in Bold Print. $T_e$ is Assumed To Be 6s for the Calculation of the Model Parameters $k$ and $B$

<table>
<thead>
<tr>
<th>Response type</th>
<th>Short</th>
<th>Normal</th>
<th>M = 1</th>
<th>$\beta = 1$</th>
</tr>
</thead>
<tbody>
<tr>
<td>V (°/s)</td>
<td>57</td>
<td>45</td>
<td>48</td>
<td></td>
</tr>
<tr>
<td>$T_{\text{obs}}$ (s)</td>
<td>5.9</td>
<td>16</td>
<td>31</td>
<td></td>
</tr>
<tr>
<td>$t_{\text{obs}}$ (s)</td>
<td>28</td>
<td>46</td>
<td>64</td>
<td></td>
</tr>
<tr>
<td>$Q_{\text{obs}}$</td>
<td>.21</td>
<td>.35</td>
<td>.48</td>
<td></td>
</tr>
<tr>
<td>$T_1$ (s)</td>
<td>6.0</td>
<td>17.8</td>
<td>48</td>
<td>60</td>
</tr>
<tr>
<td>$T_2$ (s)</td>
<td>100</td>
<td>100</td>
<td>39</td>
<td>60</td>
</tr>
<tr>
<td>$M$</td>
<td>.19</td>
<td>.63</td>
<td>1</td>
<td>.94</td>
</tr>
<tr>
<td>$\beta$</td>
<td>17</td>
<td>5.6</td>
<td>1.9</td>
<td>1</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>.001</td>
<td>.10</td>
<td>.35</td>
<td>.48</td>
</tr>
<tr>
<td>%curvature</td>
<td>2.2</td>
<td>9.4</td>
<td>14</td>
<td>15</td>
</tr>
<tr>
<td>%attenuation</td>
<td>3.8</td>
<td>17</td>
<td>34</td>
<td>41</td>
</tr>
<tr>
<td>%cancellation</td>
<td>19</td>
<td>63</td>
<td>100</td>
<td>94</td>
</tr>
<tr>
<td>gain = $V/90$</td>
<td>.63</td>
<td>.50</td>
<td>.51</td>
<td></td>
</tr>
<tr>
<td>$K = \text{gain} \cdot T_1$</td>
<td>3.8</td>
<td>8.9</td>
<td>24</td>
<td>31</td>
</tr>
<tr>
<td>$k = \text{gain} \cdot T_2$</td>
<td>3.8</td>
<td>3.0</td>
<td>3.1</td>
<td></td>
</tr>
<tr>
<td>$B = 1 - T_e / T_1$</td>
<td>0</td>
<td>.86</td>
<td>.86</td>
<td>.90</td>
</tr>
</tbody>
</table>

*Curve number refers to Figure 2.
**The Results of the Simulations**

For the different response types, mean values for the response parameters and some of the relevant "fitting" simulations are presented in Table 2. These and other relevant simulations of VS responses are shown in Figure 2.

For the normal responses, a goal (preset) value of $T_D = 100$ s, which has been indicated by some relevant studies (1-5, 7, 8), resulted in a mean value of $M = 0.6$ (curve 8).

With the assumption of $T_e = 6$s, $k$ and $B$ were calculated for the sake of the Discussion, using equations [2] and [3], from which it follows that

$$K/T_1 = k/T_r.$$

\[18\]

For all of the 21 separate short responses ($T_{obs} = 2$ to 9 s), a goal value of $T_D = 100$ s resulted in lower values of $T_1$ (2 to 9 s) and for all the parameters relating to adaptation ($M$, $\alpha$, $\%$ curvature, $\%$ attenuation, and $\%$ cancellation), except $\beta$ which showed a high value (curve 4, Table 2). Figure 2 shows that the ad-

![Figure 2. Semilog plot of simulated VS responses for the "average" normal, short, and prolonged response, scaled to $V = 100^o/s$. The $v(t)$ ranges from $1^o$ to $100^o/s$ in the two juxtaposed panels; the top one for L-beating and the bottom one for R-beating nystagmus. Note that $0 < v(t) < 1^o/s$ in either direction cannot be shown in this presentation; it has been calculated by solving that $t_0 = t_{obs}$. The continuous curves (1 through 10) pertain to the values of the second-order model "fitted" to the average responses as specified in Tables 2 and 3. All the curves were derived from equation [5], except curves 8, 7, and 10, which were derived from equation [A13]. The straight lines (a through d) indicate extrapolated first-order behaviour as derived from the equation $v(t) = 100 \exp(-T_{obs}/t_{obs})$; the $T_{obs}$ values were those included in Table 2. The shaded area indicates the normal range for $t_{obs}$; it emphasizes that curves 1 through 4 represent a short response and curves 9 and 10 a prolonged response. The values for the relevant parameters can be found in Tables 5 and 6. The broken curves (c, e) were obtained by imposing the "normal" $C_{obs} = 0.35$ value (for the condition $M = 1$, curve 5, Table 8) on the abnormal response types. For example, $t_0$ for the short response type is calculated at (5 s) 0.35 = 17 s. This procedure involved the following parameter values: curve c, $T_1 = 6.4$ s; $T_A = 70$ s, $M = 1$, $t_0 = 17$ s; curve e, $T_1 = 35.8$ s; $T_A = 371$ s, $M = 1$, $t_0 = 88$ s, which implies that the parameters $\alpha$, $\beta$, $\%$ curvature, and $\%$ attenuation are equal to those for the normal response (curve 5, Table 3). This makes it clear that the abnormal responses are not just time-scaled versions of the normal response and that the normal amount of adaptation would mean too much adaptation (decay) for the short response type (compare curve d to curves 1 through 4) and too little adaptation (decay) for the prolonged response type (compare curve e to curves 9 and 10). For clarity, it is not shown that similar procedures for the conditions minimum value of $M$ and $\beta = 1$ yield curves that are close to either curve e or d.
adaptation characteristics of the average normal response, if imposed on the average short response, would mean too much adaptation (decay): compare curve d to curves 1 through 4. In all of the 24 separate prolonged responses ($T_{obs}$ 27 to 38 s), satisfactory model simulations could be obtained, though with some complications in most cases. A goal value of $M = 0.00$ was used in 15 cases, it appeared that only the solution with $M = 1$, $T_1 = T_A = t_{obs}$ (with $T = 0.5t_{obs}$ and $a = 0.5$, see Appendix, part II) yielded reasonable simulations (Figure 2, curve 10). It is clear that the prolonged response type showed very high values of the parameters $T_1$ and the adaptation parameters ($M$, $a$, %curvature, and %attenuation) except $\beta$, which showed very low values. In Figure 2, it is demonstrated that the adaptation characteristics of the average normal response, if imposed on the average prolonged response, would imply too little adaptation (decay); compare curve c to curve 9.

Table 3 shows the values of the parameters that are linked to the boundary conditions for the average normal and the short responses. Tables 2 and 3 refer to a number of curves shown in Figure 2, which demonstrate that each of the sets of parameter values presented in these tables yielded a suitable simulation (note that differences in $v(t)$ are exaggerated at low velocity values in the semilog plot).

**Assessing the Variability in Model Parameter Values**

The variability in the values of the relevant model parameters, as derived from the individual responses in the 3 boundary conditions, is presented in Table 4. The value of $\alpha$ for the condition $\beta = 1$ equals that of $Q_{obs}$. At each boundary condition, each parameter showed significant differences between the response types (except $T_A$ at the condition minimum value of $M$). Given the fact that the responses were selected on significantly abnormal values of the descriptive parameters, the present significant differences are trivial: all of the values of the adaptation parameters are directly linked to the value of $Q_{obs}$ (Table A1) and, therefore, reflect the differences in the value of this parameter between the response types. The only thing that really matters, is which parameters show significant differences between the response types, independent of the boundary conditions, that is, throughout the whole range of their variation.
Table 4. The Variability in Individual Parameter Values at the 3 Boundary Conditions for Each Response Type*

<table>
<thead>
<tr>
<th>Boundary condition</th>
<th>Response type</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Short†</td>
</tr>
<tr>
<td>M = 1</td>
<td></td>
</tr>
<tr>
<td>$T_1$ (s)</td>
<td>1-9</td>
</tr>
<tr>
<td>$T_A$ (s)</td>
<td>148-</td>
</tr>
<tr>
<td>$\beta$</td>
<td>38-22000</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>-.025</td>
</tr>
<tr>
<td>%curvature</td>
<td>.04-4.9</td>
</tr>
<tr>
<td>%attenuation</td>
<td>.04-7.2</td>
</tr>
<tr>
<td>%cancellation</td>
<td>100</td>
</tr>
<tr>
<td>Minimum value of M</td>
<td></td>
</tr>
<tr>
<td>$T_1$ (s)</td>
<td>1-9</td>
</tr>
<tr>
<td>$T_A$ (s)</td>
<td>12-110</td>
</tr>
<tr>
<td>$M$</td>
<td>.002-.20</td>
</tr>
<tr>
<td>$\beta$</td>
<td>3.2-34</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>-.058</td>
</tr>
<tr>
<td>%curvature</td>
<td>.005-6.1</td>
</tr>
<tr>
<td>%attenuation</td>
<td>.005-11</td>
</tr>
<tr>
<td>%cancellation</td>
<td>.2-20</td>
</tr>
<tr>
<td>$\beta = 1$</td>
<td></td>
</tr>
<tr>
<td>$T_1$ (s)</td>
<td>1-12</td>
</tr>
<tr>
<td>$T_A$ (s)</td>
<td>1-12</td>
</tr>
<tr>
<td>$M$</td>
<td>.11-.35</td>
</tr>
<tr>
<td>$\alpha = Q_{obs}$</td>
<td>.10-.26</td>
</tr>
<tr>
<td>%curvature</td>
<td>1.3-7.6</td>
</tr>
<tr>
<td>%attenuation</td>
<td>11-29</td>
</tr>
<tr>
<td>%cancellation</td>
<td>11-35</td>
</tr>
</tbody>
</table>

*Indications of range refer to the 5th and/or the 95th percentile of the distribution.
†Mean values are presented in parentheses only for the lognormal distributions of the normal response type.
‡Bold print indicates overall significant differences between the response types.

within the complete solution set. Two such parameters could be identified (see values in bold print in Table 4): $T_1$ and %curvature (see Discussion). Of course, also the value of the parameter $B$, being linked to that of $T_1$, showed overall significant differences, with overall ranges of $-0.5$, 0.5 to 0.82, and 0.81 to 0.94 for the short, the normal, and the prolonged response types, respectively.

Discussion

Evaluating the Observed Parameter Values

The finding of the typical response pattern $T-t-Q-$ merits special attention. The combination of a (significantly) short time constant ($T_{obs}$) and a (significantly) short reversal time ($t_{obs}$) does not imply that their quotient $Q_{obs}$ should also have a significantly low value. Yet, we found a significant predominance of significantly low values for $Q_{obs}$, that is, $Q-$. This implies that $t_{obs}$ was higher relative to $T_{obs}$ than it was in the normal response; so, apparently a change in response behaviour has occurred which has caused less decay in response than is usual in the normal condition. Similarly, we can safely conclude that in the case of the typical pattern $T+t+Q+$, which was attached to the prolonged response type, the response behaviour has changed in such a way that there was more decay of the response than usual, which caused an increase of the quotient $Q_{obs}$ towards a significantly high value.
Etiology in the Two Abnormal Response Types

The two abnormal response types identified (Table 2) have much in common with the previously outlined response types of "hypo-reflexia" and "vestibular hyperreactivity" (16). Among the cases with short responses, as could be expected, we found patients with a labyrinthine defect (16-18) as well as patients with central disturbances (19,20). Among the cases with prolonged responses, one might have expected patients with multiple sclerosis (13,16,20), the hyperventilation syndrome (15,16), otosclerosis and otitis media with tympanic membrane perforation or a radical cavity (16). For these latter types of etiology — and for Meniere's disease — it can be suggested that the "central" abnormality, that is, the increased value of $T_1$, is secondary to a peripheral abnormality. We have no idea what the peripheral dysfunction might be in connection with otitis media. Perhaps, the efferent vestibular system is relevant to adaptation, as has been suggested previously (2,6).

Evaluating the Pertinent Differences between the Response Types in Terms of Model Parameters

It appeared that only the adaptation parameter $\%$ curvature pertained to "absolute" significant differences between the response types, as can be appreciated from Table 4. The $\%$ curvature showed increasing values at increasing $Q_{obs}$ values, which were only slightly influenced by the selected boundary condition. This parameter can, therefore, be called characteristic for adaptation behaviour. The close correlation that exists between this derived model parameter and the descriptive parameter $Q_{obs}$ demonstrates that the latter also indicates the extent of the downward curvature in the VS response, which relates to the gain attenuation and increase in phase lead of low frequencies; in other words, it indicates adaptation.

The Effects of Bias

By applying the regression analysis to simulated VS responses, it appeared that $T_{obs}$ is an underestimation of the "real" $T$ owing to the effect of downward curvature. Using our ("optimum") regression analysis (see Methods), the relative difference was 10% at most, that is, in the prolonged response type. This implies that the "actual" values of $M$ and $T_1$ should be somewhat higher than presented, presumably at most some 30% and 15%, respectively. Because of the effect on $T_1$, $B$ can be assumed to be somewhat higher than indicated in Table 2 (thus $B > 0$ for the short response type with $T_1 = 6\ s$) and we may also assume that the excessively high values for $T_1$ in the prolonged response type are not exaggerated. When fitting for a fixed value of $M$, the bias presumably causes an overestimation of $T_4$ by about 30% to 40%.

Comparison with Other Data on Normal Subjects

The $T_1$ values obtained in the normal subjects (Tables 2 and 3) are more or less in accordance with those reported by others (1-5, 7,8,17,21,22), although in some instances $T_1$ values determined by other authors tended to be smaller (1,4,7) than those obtained in the present study. The present $T_1$ values agree with the values reported for the time constants of central vestibular neurons and nystagmus in alert monkeys (21,23). The value obtained by Boumans and colleagues (5) for the adaptation gain fitted for normal responses to constant acceleration ($T_A = 100\ s$) is close to the present value of $M$, which resulted from the same preset value for $T_A$ (Table 2).

The values obtained for the parameter $T_A$ for the condition $M = 1$ are generally higher than those reported previously (1-5,7,8). Apart from the "extra" bias in $T_A$ (see above), this phenomenon can be linked to the fact that our estimates for $T_1$ tended to be higher than in previous reports (1,4,7). It
should be emphasized that not $T_A$ in its own right but the combined parameter $\beta$ - see the Appendix, after equation [A9] - is relevant to adaptation. The present values for this parameter (Table 4) are not systematically different from the values that can be derived from previous reports, that is, on average 3 (21) or 14 (6) for the squirrel monkey, in the range of 4 to 9 as derived from “typical” or mean values for the time constants reported for human responses (1-5,8,22) and in the range of 1 to 30 for individual responses (7), which is close to the 90% normal range presented in Table 4 ($M = 1$).

Comparison with Other Model Studies in Patients

Although some authors have suggested the possible clinical importance of an analysis of VOR responses in terms of an adaptation model (2,7,8,17), there have been only a few attempts to analyse abnormal rotatory responses in patients in terms of vestibular adaptation. We have found 3 studies on the short response type only. Mira and colleagues (8) give an example of an abnormal response in a case of Meniere’s disease with apparently decreased $T_I$ and increased $T_A$ ($M = 1$), that is, similar to the present short response type with an increased $\beta$ value and reduced adaptation (see Figure 2, curve 1). Sills and Honrubia (7) did not find any abnormal values of either $T_I$ or $T_A$ in a group of patients with a cerebellopontine angle tumour or with a unilateral peripheral vestibular lesion, although more recently it became firmly established that $T_{obs}$ in such types of pathology tends to be significantly decreased (16,18,24). Earlier analog simulations in these types of pathology did indicate low values for $T_1$ (17).

Interpretation of Simulation Results

The Short Response. This type of response showed significantly low $T_I$ values and significantly low %curvature (Table 4). The latter observation indicates that there was only a slight departure from first-order behaviour and, therefore, poor adaptation (see Figure 2).

The lack of adaptation as found in the short response type may be adequate in the case of reduced afferent VOR activity (that is, low $K$, see Table 2), as the little activity that is left should be processed as much as possible without further loss to produce sufficient VOR output. In terms of the model depicted in Figure 1, the low $B$ value (close to zero; with an overall range of up to 0.5) in Table 2, calculated by assuming $T_c = 6$ s in equation [2], also indicates the loss of the integrative capacity of the brain stem integrator, as has already been reported by others (24).

Which Is the Crucial Adaptation Parameter?

We can be pretty confident about the observation that in most of the prolonged re-
sponses, \( M \) and \( \beta \) are close to unity, because in those cases only the direct solution with equal time constants applied. In the case of the short response type, however, it is impossible to say at present which of the two model parameters, \( M \) or \( \beta \), is responsible for the poor adaptation. This problem might be solved by invoking complete solutions (see Appendix IV).

**Theoretical Implications of a Variable Adaptation Gain**

**Frequency Behaviour.** We have analysed the overall frequency behaviour, which can be derived from the transfer equation [1].

The amplitude ratio \( AR \) is

\[
AR = \omega T_1 \left\{ \frac{1}{[(1 - M)^2 + \omega^2 T_1^2]} \right\} \\
\left\{ \frac{((\omega^2 T_1^2 + 1) \cdot (\omega^2 T_A^2 + 1))]^{1/2}}
\]

[19]

and the phase (\( \Phi \)) with reference to head velocity is

\[
\Phi = \frac{1}{2} \pi - \tan^{-1}(\omega T_1) \\
+ \tan^{-1}\left[\frac{\omega T_A/(1 - M)}{-\tan^{-1}(\omega T_A)}\right].
\]

[20]

Figure 3 shows a Bode plot for some relevant cases. For \( M = 1 \) the system is second-order lead (maximum 180° phase lead, reference head velocity, see Figure 3, curve 1) and thus anticomparatory in the ultra-low frequency (ulf) range (that is, below 0.01 radians/s or 0.0016 Hz on the basis of \( T_A = 100 \) s, see Figure 3). For \( M \neq 1 \), the gain behaviour is pseudo first-order lead with an ulf gain factor of \(|1 - M|\). For \( M < 1 \) the phase lead is between 90° and 0°, in the middle-frequency (mf) range (0.016 to 0.16 Hz), with a low-frequency (lf) lead of more than 90° (first- to second-order lead, see Figure 3, curve 2). For \( M > 1 \) phase behaviour is, peculiarly enough,
third-order (lead-lag), and the phase (see Figure 3, curve 3) shifts from (maximally) 90° lead (uf) by the addition of (maximally) 270° lag to a net 180° lag (mf). Realizing that we did not observe phase inversion in any of our patients in steady state responses to sinusoidal stimulation, we regarded $M = 1$ as a boundary condition and therefore did not perform a fit to the model with $M > 1$.

**Functional Considerations.** Two important notions emerge from the above analysis of frequency behaviour and of phase behaviour in particular.

The first notion is that in a network such as that depicted in Figure 1, values of $M$ close to unity can best be avoided. If the gain factor $M$ fluctuates, which is a reasonable assumption within the context of a neuronal network, then a gain (that is, $M$) that passes unity would cause phase inversion (Figure 3, curve 3), which is likely to be very disturbing. The situation seems to be comparable with the paradigm of wearing inverting prisms, which is known to be very nauseating, at least initially (25). It can be suggested that the symptoms of motion sickness and the like, which many of our patients with prolonged responses appeared to have, can be attributed to large phase shifts associated with $M$ fluctuating around unity.

The second notion is that the present model may offer an elegant possible mechanism, defined in terms of systems analysis, for the phase reversal observed in the VOR “adapted” to inverting prisms (25). As far as we know, the “peripheral adaptation mechanism” (6), that is, the one being considered here, has not been invoked before to explain the phenomenon of long-term phase reversal. The present analysis shows that this can be done in a “natural” way, but there can be little doubt that, when doing so, one should also consider the probable involvement of cerebral and other “central” pathways, as has been emphasized by others (25).

**Acknowledgments**—We wish to thank Dr. L. J. M. Boumans, Dr. H. Kingma, Dr. J. J. Konijnenberg, and Dr. W. J. M. Verhagen for commenting on the manuscript.

**REFERENCES**

17. McClure JA, Lycett P, Bicker GR. A quantitative ro-
APPENDIX

Part I presents the iterative solution method, part II the equations pertaining to the particular case \( \beta = 1 \) — in equation [7], and part III a table of particular solutions pertaining to the 3 boundary conditions (see final section of Methods). Part IV presents methods with repeated iteration to obtain complete solutions (for later use), and part V presents a programme listing.

I. Iterative Solution Method

The first-order equation fitted to the primary phase of the response pertains to a condition with

\[
\text{tangent} = -V(1/T). \quad [A1]
\]

The second-order equation [5] yields the following expression for the initial slope tangent to the \( v(t) \) against \( t \) plot (\( t \) close to zero):

\[
\text{tangent} = -V(M/T_A + 1/T_1); \quad [A2]
\]

and with equation [11]

\[
\alpha = 1/(\beta/M + 1). \quad [A5]
\]

From equations [10], [A3], and [9], it follows that

\[
Q = T/T_0 = (\beta - 1)/(\beta + M)/\ln C, \quad [A6]
\]

where \( C \) comes from equation [8], that is, \( C = \beta/M + 1 - 1/M \), which by equation [A5] turns into

\[
C = 1/\alpha - 1/M. \quad [A7]
\]

In equation [A6], \( \beta \) can be substituted by using equation [A5], which yields

\[
Q = [1 - \alpha - \alpha/M]/\ln[1/\alpha - 1/M], \quad [A8]
\]

or by equation [A7]:

\[
Q = \alpha(C - 1)/\ln C. \quad [A9]
\]

Note. The separate parameters \( T_1 \) and \( T_A \) do not appear in the equations; only their ratio \( T_A/T_1 = \beta \) — equation [7] — is relevant to adaptation.

The value of \( Q \) actually measured is \( Q_{obs} \); the function

\[
f(\alpha_1) = Q_i - Q_{obs} = 0, \quad [A10]
\]

where \( Q_i \) is the value resulting from a starting value \( \alpha_1 \) and a goal value of \( M \) in equa-
tion [A8], which can be solved by using Newton’s method with the iterative use of the equation

\[ \alpha_2 = \alpha_1 - f(\alpha_1)/f'(\alpha_1), \]  

[A11]

where \( \alpha_2 \) is an improved estimate of the root \( \alpha_1 \) and \( f'(\alpha_1) \) is the first derivative of \( f(\alpha_1) \) with respect to \( \alpha_1 \):

\[ f'(\alpha_1) = \left[ Q_1/C/(\alpha_1)^2 - 1 - 1/M \right]/\ln C. \]  

[A12]

For a goal value of \( T_A \), the iteration process can be repeated each time with the value \( M = MT_A,goal/T_A \), until \( T_A \) is close enough to \( T_A,goal \).

Note. In the above procedure, instead of \( f(\alpha) \) in equation [A10], we might also look at equation [A6] as an \( f(M) \) or an \( f(\beta) \). The present function appeared to be the most favourable in terms of the possible range of initial estimates and speed of convergence of the associated iteration process.

II. Direct Solution for Equal Time Constants

A particular solution exists in closed form for the boundary condition (see final section of Methods) \( T_i = T_A \) with the following VS response (instead of equation [5]):

\[ v(t) = (K/T_i)(1 - tM/T_i)\exp(-t/T_i) \]  

[A13]

from which—see definitions in part IV, first paragraph—it follows that:

\[ t_0 = T_i/M, \]  

[A14]

\[ t_{max} = T_i(1 + 1/M), \]  

[A15]

and

\[ V_{max} = -MV\exp(-1 - 1/M). \]  

[A16]

From equation [A13] it follows, analogous to equations [A1] and [A2], that

\[ T = T_i/(M + 1) \]  

[A17]

and thus

\[ T_i = T(M + 1). \]  

[A18]

From equations [11] and [A17], we obtain

\[ \alpha = M/(M + 1). \]  

[A19]

From equations [A11] and [A17], we find

\[ Q = T/t_0 = M/(M + 1) = \alpha \]  

[A20]

and hence

\[ M = Q/(1 - Q) \]  

[A21]

and with equation [A18],

\[ T_i = T/(1 - Q). \]  

[A22]

Equation [A20] shows that for the boundary condition (see final paragraph of Methods) \( M_{max} = 1, \alpha_{max} = Q_{max} = 0.5 \).

III. A Table Method

Although Table A1 was obtained by using the iteration method (part I) and the equations in part II, the table was specially designed to make (computer) calculations superfluous (this is not the case if preset values are preferred). This table presents the values of the relevant model parameters \( M \) and \( \beta \) in the 3 boundary conditions (see final section of Methods) for a number of discrete values of the descriptive parameter—equation [10]—\( Q_{obs} = T_{obs}/t_{obs} \). For the boundary condition of a minimum value of \( M \), we plotted curves for a given constant \( M \) value and varying \( \beta \) values—equations [A5] and [A6]—in the \( Q_\beta \) plane. By trial and error, we found the value of \( M \) for which such a curve had only a single point of intersection with the line \( Q = Q_{obs} \). At this particular point, the iteration process deteriorated, because both \( f(\alpha) \)
Table A1. Particular Solutions for the 3 Boundary Conditions in Terms of the Parameters M and β for a Number of Discrete Qobs Values
(for the calculation of T₁ and Tₐ see the example given in the text)

<table>
<thead>
<tr>
<th>Qobs</th>
<th>M = 1</th>
<th>Minimum value of M</th>
<th>β = 1</th>
</tr>
</thead>
<tbody>
<tr>
<td>.10</td>
<td>22000</td>
<td>.002 34</td>
<td>.11</td>
</tr>
<tr>
<td>.12</td>
<td>4100</td>
<td>.005 12</td>
<td>.14</td>
</tr>
<tr>
<td>.14</td>
<td>1300</td>
<td>.014 3.7</td>
<td>.16</td>
</tr>
<tr>
<td>.16</td>
<td>510</td>
<td>.023 3.3</td>
<td>.19</td>
</tr>
<tr>
<td>.18</td>
<td>250</td>
<td>.050 5.3</td>
<td>.22</td>
</tr>
<tr>
<td>.20</td>
<td>140</td>
<td>.076 4.7</td>
<td>.25</td>
</tr>
<tr>
<td>.22</td>
<td>85</td>
<td>.12 4.1</td>
<td>.28</td>
</tr>
<tr>
<td>.24</td>
<td>56</td>
<td>.16 3.7</td>
<td>.32</td>
</tr>
<tr>
<td>.26</td>
<td>38</td>
<td>.20 3.2</td>
<td>.36</td>
</tr>
<tr>
<td>.28</td>
<td>28</td>
<td>.25 2.9</td>
<td>.39</td>
</tr>
<tr>
<td>.29</td>
<td>24</td>
<td>.28 2.7</td>
<td>.41</td>
</tr>
<tr>
<td>.30</td>
<td>21</td>
<td>.30 2.6</td>
<td>.43</td>
</tr>
<tr>
<td>.31</td>
<td>18</td>
<td>.33 2.6</td>
<td>.45</td>
</tr>
<tr>
<td>.32</td>
<td>16</td>
<td>.36 2.5</td>
<td>.47</td>
</tr>
<tr>
<td>.33</td>
<td>14</td>
<td>.39 2.4</td>
<td>.49</td>
</tr>
<tr>
<td>.34</td>
<td>12</td>
<td>.42 2.3</td>
<td>.52</td>
</tr>
<tr>
<td>.35</td>
<td>11</td>
<td>.46 2.1</td>
<td>.54</td>
</tr>
<tr>
<td>.36</td>
<td>9.5</td>
<td>.48 1.9</td>
<td>.56</td>
</tr>
<tr>
<td>.37</td>
<td>8.4</td>
<td>.52 1.7</td>
<td>.59</td>
</tr>
<tr>
<td>.38</td>
<td>7.5</td>
<td>.55 1.6</td>
<td>.61</td>
</tr>
<tr>
<td>.39</td>
<td>6.6</td>
<td>.59 1.5</td>
<td>.64</td>
</tr>
<tr>
<td>.40</td>
<td>5.9</td>
<td>.62 1.4</td>
<td>.67</td>
</tr>
<tr>
<td>.42</td>
<td>4.7</td>
<td>.70 1.3</td>
<td>.72</td>
</tr>
<tr>
<td>.44</td>
<td>3.7</td>
<td>.77 1.2</td>
<td>.79</td>
</tr>
<tr>
<td>.46</td>
<td>2.8</td>
<td>.84 1.1</td>
<td>.85</td>
</tr>
<tr>
<td>.48</td>
<td>2.0</td>
<td>.92 1.1</td>
<td>.92</td>
</tr>
<tr>
<td>.5</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>

IV. Complete Solutions

In part I, the method of repeated iteration was used to obtain solutions for preset \( T_A \) values. A similar method can be used if additional response parameter values are available, that is, overall CED (OCED), the time \( t_{max} \) at which the secondary postrotatory nystagmus response shows its maximum SPV, or the maximum itself \( (V_{max}) \).

From equation [15] we obtain

\[ G = VT \]  \hfill [A23]

by substituting infinite time for \( t_{obs} \); \( G \) is a previously defined response parameter \((11, 14-16)\). Likewise, OCED can be derived from G3 in equation [17] by substituting infinite time:

\[ OCED = VT_1(1 - M). \]  \hfill [A24]

Given OCED as a function of \( M \) and \( OCED_{obs} \) as the observed parameter value, Newton's method produces

\[ M = 1 - \frac{OCED_{obs}}{VT_1} \]  \hfill [A25]

as an improved estimate of \( M \), which can be used to restart the iteration of part I, unless \( OCED \) is close enough to \( OCED_{obs} \). The second term in equation [A25] can be multiplied by \( 1 = (VT_1)(1/VT)(T/T_1) \), which by equations [A23] and [11] can be adequately substituted:

\[ M = 1 - \frac{OCED_{obs}(1 - \alpha)}{G}. \]  \hfill [A26]

From equation [5], we obtain

\[ t_{max} = T_A \cdot \ln(\beta C)/((\beta - 1) \ln(\beta C)); \]  \hfill [A27]

and

\[ V_{max} = -(MV/\beta) \exp(-t_{max}/T_A). \]  \hfill [A28]

Invoking equation [A27] for Newton's method, we see it as a function of \( T_A \), and an improved estimate is

\[ T_A = T_{max,obs}(\beta - 1)/\ln(\beta C); \]  \hfill [A29]
from equations [A1] and [A2], we then find
\[ M = T_A \left( \frac{1}{T} - \frac{1}{T_1} \right) \]  
[A30]
as an improved estimate of \( M \) to restart the iteration, unless \( t_{\text{max}} \) is close enough to \( t_{\text{max,obs}} \).

Likewise, equation [A28] can be used as a function of \( M \), and an improved estimate to restart the iteration is
\[ M = \beta \left( \frac{V_{\text{max,obs}}}{V} \right) / \exp(-t_{\text{max}}/T_A), \]  
[A31]
unless \( \left( \frac{V_{\text{max}}}{V} \right) \) is close enough to \( \left( \frac{V_{\text{max,obs}}}{V} \right) \).

We have employed the above 3 methods of repeated iteration to find solutions that fit the precalculated "observed" parameter values for simulated responses. A change by 10% in the value of \( OCED_{\text{obs}} \) caused an error in \( M \) and \( T_A \) of about 10% to 20%. The same change in the corresponding response parameter value caused errors of 50% to 100% in \( M \) and \( T_A \) if \( t_{\text{max,obs}} \) was involved and 10% to 50% if \( V_{\text{max,obs}} \) was involved. Errors in \( T_1 \) were in the range of 1% to 2%. The \( V_{\text{max,obs}} \) parameter is almost useless in electronystagmography, because the SPV values involved are mostly below 10% and fluctuations in the corneoretinal potential and the state of alertness of the subject during the protracted testing periods required may be very disturbing factors (note that \( t_{\text{obs}} \) is virtually insensitive to such fluctuations!). Given these limitations, \( OCED_{\text{obs}} \) is probably the best choice for a parameter to obtain exact solutions in future measurements, especially if a magnetic search coil method can be employed.

V. GW-BASIC programme listing

```
10 REM ADAP#1 -- 200691 -- P.L.M.Huygen
20 CR=.001:INPUT"V, T, to ";V,T,TO
30 PRINT"For a goal value of M, choose (M, 0, 0)"
40 PRINT"For a goal value of TA, choose (0, TA, 0)"
50 PRINT"For a complete solution, choose (0, 0, OCED)"
60 INPUT"M, TA, OCED ";M,TAI,OCI:IF M=0 THEN M=1
70 Q=T/TO:G=T*V:A=.001
90 F=QQ-Q:FA=(QQ/C/A/A-1-1/M)/LC
100 A=A-F/FA:IF ABS(F>A*.1 THEN 80
110 B=M*(1/A-1):C=1/A-1/M:LC=LOG(C)
120 T1=T*(M/B+1):TA=B*T1:TO=T1*LC/(1-1/B)
130 TM=TA*LOG(B*C)/(B-1):VM=-M*V/B*EXP(-TM/TA):OC=V*T1*(1-M)
140 PRINT:PRINT"V, T, to, M, T1, Alfa, Beta, Gamma, Max, OCED ";
150 PRINT V; ",";T; ",";T1; ",";A; ",";TM; ",";VM; ",";OC
160 IF TAI=0 THEN 190
170 IF ABS(TAI-TA)>CR THEN M=TAI/TA*M:GOTO 80
180 IF OCI>0 AND ABS(OCI-OC)>CR THEN GOSUB 210:GOTO 80
190 GOTO 20
200 M=1-OCI/G*(1-A)
210 RETURN
```