An analysis of the time course of gustatory neural adaptation in the rat

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Smith, David V., John W. Steadman, and C. Norman Rhodine. An analysis of the time course of gustatory neural adaptation in the rat. Am. J. Physiol. 229(4): 1134-1140. 1975.—Neural responses were recorded from the rat chorda tympani nerve following stimulation of the tongue with several concentrations of NaCl. These responses were integrated using a fast time constant (47 ms), and the time course of the decline in neural discharge from the peak of the transient response was computer analyzed. The time course of the adaptation process was described by a constant term and two exponentially decaying components, which most likely reflect the existence of two separate mechanisms contributing to the adaptation process in taste. The constant term and the amplitude of the second gradual exponential decay were correlated with NaCl concentration, whereas the amplitude of the initial rapidly declining exponential component was independent of stimulus intensity. The initial transient response of the chorda tympani nerve may be a function of the rate of stimulus adsorption, whereas the gradual second decline in the neural response may reflect an adaptive mechanism of the taste receptor cell.

taste, chorda tympani, sodium chloride

Integrated responses to NaCl recorded from the rat chorda tympani nerve typically show an initial phasic portion followed by a slowly declining tonic component (14) that is proportional to stimulus concentration. This phasic-tonic response is also characteristic of single chorda tympani neurons (1, 11). There has been some suggestion that the initial phasic burst of activity is particularly important in the representation of gustatory information (5, 7, 8, 20). For example, rats can make taste quality discriminations within the duration of the transient portion of the chorda tympani discharge, and cross-adaptation procedures, which result in a loss of taste sensation in human psychophysical studies (21), have their effect on the phasic portion of the rat chorda tympani response (20). Although the transient portion of the neural discharge appears to be implicated in the representation of sensory information, the mechanisms underlying the production of this phasic burst of activity and the subsequent decline termed adaptation are not well understood.

The time course of the chorda tympani response has received recent attention with regard to its implications for theories of gustatory stimulation (4a, 5, 6, 8). Although neither Beidler’s (2) fundamental taste equation nor Paton’s (13) rate theory of drug-receptor interaction can account for the dynamic character of the gustatory response over a wide range of stimulus intensities, Paton’s rate theory fits the response to any one concentration quite well (4a, 5). In a recently proposed rate theory of gustatory stimulation, Heck and Erickson (8) make the assumption that the chorda tympani discharge is directly proportional to the rate of stimulus adsorption to the taste receptor sites. Consequently, the decline in impulse frequency from the peak of the transient response would be the result of a decrease in the rate of binding as the adsorption process approaches equilibrium. However, rather than attaining an actual steady, or equilibrium, level, the integrated response of the rat chorda tympani nerve continues to exhibit a slow decline over several minutes subsequent to the initial transient discharge (14). This slowly declining “steady-state” response strongly suggests that the time course of the taste response may reflect processes other than, or in addition to, the rate of stimulus adsorption.

In several sensory systems other than taste, multiple factors have been shown to contribute to the decline in the neural response termed adaptation. In the slowly adapting muscle receptor organ (MRO) of the crayfish, for example, adaptation to a constant stimulus reflects several underlying processes. A decrease in impulse frequency in the MRO axon results from viscoelastic properties of the receptor muscle when stretched to a constant length (4), from a decline in the generator potential while the muscle is under constant tension (10), and from properties of the stretch receptor axon, i.e., a decrease in firing rate due to an incremental buildup of hyperpolarization following each impulse (22). Thus, several properties of the crayfish MRO are known to contribute to adaptation in this single sensory neuron. In contrast, although the vertebrate taste system is more complex, involving a synaptic link between receptor cell and first-order neuron, little attention has been given to processes other than binding rate that may contribute to gustatory adaptation. The presence of more than one factor affecting the adaptation process should complicate both the time course of the neural discharge and its mathematical description. In fact, Faull (4a) has demonstrated that the first 2 s of the rat chorda tympani discharge can be fit better with a two-step mathematical model than with either a mass-action formulation or rate theory alone. Since the first 2 s of the neural response do not provide enough data to analyze the slowly declining phase of the adaptation process, we collected neural data elicited by varying concentrations of NaCl presented over 120 s in order to derive a
quantitative description of the time course of gustatory adaptation.

**METHOD**

**Preparation and solutions.** Four adult female Sprague-Dawley rats, ranging in weight from 207 to 295 g, were used. Each animal was deeply anesthetized by intraperitoneal injection of sodium pentobarbital (60 mg/kg). Supplementary injections were given periodically to maintain a deep level of anesthesia. The trachea was cannulated. The rat’s head was held firmly in a clamp and positioned to allow dissection of the left chorda tympani nerve. The nerve trunk was located and freed from surrounding connective tissue under a stereoscopic dissecting microscope. The nerve was cut where it entered the tympanic bulla and placed on a nichrome wire electrode. An indifferent electrode was positioned nearby in the wound and the animal was grounded via the head clamp. Responses of the whole nerve were differentially amplified (Grass P511) and stored on magnetic tape. During recording the neural responses were monitored with an oscilloscope and audiomonitor, then integrated and displayed on a strip-chart recorder. The anterior portion of the rat’s tongue was enclosed in a flow chamber fitted with a rubber dam so that saliva was excluded and solutions were delivered from a system of overhead funnels at a rate of 3 ml/s. Even though the funnel containing the stimulus solution almost emptied during the 120-s stimulation period, the flow rate varied by less than 4% throughout this period. The stimulus solutions, made from reagent grade NaCl and distilled water, were the following: 1.0, 0.6, 0.3, 0.1, 0.06, 0.03, and 0.01 M NaCl. The stimuli were maintained and delivered at room temperature (21°C).

**Experimental procedure.** Each NaCl concentration was presented to the tongue of each preparation for a period of 2 min. During data collection, each stimulus was preceded and followed by at least a 2-min distilled water rinse. Since rather drastic changes can sometimes occur in the responsiveness of a chorda tympani preparation, even though the baseline response appears to be stable, a control stimulus of 0.1 M NaCl was presented for 15 s between stimulus concentrations. The mean responses at each concentration were then computer analyzed to obtain a mathematical description of their time course.

**RESULTS**

Stimulation of the tongue of the rat with NaCl at concentrations ranging from 0.01 to 1.0 M results in a chorda tympani discharge characterized by an initial rapidly declining transient phase followed by a slowly declining steady-state component that is proportional to NaCl concentration. Figure 1 shows the mean integrated response to these NaCl concentrations initially (transient) and at various times following the peak of the transient response. It is evident from Fig. 1 that the response does not attain an “equilibrium” after the transient discharge, but continues to exhibit further adaptation throughout the stimulation period. Neither the transient nor the steady-state response shows a linear relationship to concentration over the entire stimulus range. Both aspects of the response begin to saturate at higher NaCl concentrations, although the transient response does so at lower intensities than the steady-state response. A computer printout of the mean response data as a function of time after the peak of the transient response is shown in Fig. 2, where the response to each succeeding concentration of NaCl is displaced to the right for greater clarity. Here it can be seen that the initial decline from the peak of the phasic response is

**Fig. 1.** Mean integrated responses to 7 concentrations of NaCl at various times beginning with peak of transient response. Integrator time constant was 47 ms.
quite rapid and that the adaptation process appears quite similar to a decaying exponential, as would be predicted by the rate theory (8).

If the decline in the chorda tympani response were exponential as suggested by Heck and Erickson (8), then the response should show a linear relationship to time in a semilogarithmic plot. Since initial inspection of such a plot of the response data suggested not one but two exponentially decaying processes, such a model was employed to describe the integrated chorda tympani response as a function of time after the peak of the transient response. This two-exponential model is described by the equation:

\[ R(t) = A_0 + A_1 e^{-t/\tau_1} + A_2 e^{-t/\tau_2} \]  

where \( R(t) \) is the integrated chorda tympani response, \( A_0 \) is a constant equal to the steady-state value of \( R(t) \) at \( t = 120 \) s, and \( A_1 \) and \( A_2 \) are amplitude coefficients associated with the time constants of decay, \( \tau_1 \) and \( \tau_2 \). The meaning of the amplitude and time constant parameters \( (A_0, A_1, A_2, \tau_1, \tau_2) \) and the manner in which they combine to influence the total response as a function of time are graphically illustrated in Fig. 3. The time course of the neural response after the peak of the transient burst of activity, according to the model shown in Fig. 3, would be the sum of a constant term, \( A_0 \), and two decaying exponentials, \( A_1 \) and \( A_2 \), which are characterized by the time constants, \( \tau_1 \) and \( \tau_2 \).

For each of the NaCl concentrations, these parameters were independently varied in a computer analysis until values were obtained that produced a minimum mean square error between the model and the mean response data. The computer routine used for the fitting of the mean response data to the model was based on the Gram-Schmidt orthonormalization procedure (16, 23). The ratio of the integral mean square error, minimized by iteration through a number of possible sets of parameter values, to the integral of the square of the observed response, expressed as a percentage, was used as the measure of the goodness of fit between the data and the model. The resulting parameters of the model for each NaCl concentration and the percentage of fit using these parameters at each concentration are shown in Table 1. The high value of the percent fit for each NaCl concentration demonstrates that the two-exponential mathematical model adequately describes the time course of gustatory adaptation. It would be possible to use a single exponential term and a constant term in a mathematical model of this response (see Discussion, equation 14).

![Fig. 2. Computer printout of mean integrated responses of rat chorda tympani nerve to 7 concentrations of NaCl. Time 0 is time of peak of transient response. Integrator time constant was 47 ms. Record for each successive concentration is displaced to right for greater clarity.](http://ajplegacy.physiology.org/doi/abs/10.1152/ajpgi.1986.254.12.1136)

![Fig. 3. Graphical representation of 2-exponential model showing how model parameters combine to influence time course of adaptation process. Ordinate: amplitude, values of coefficients \( A_0 \), \( A_1 \), and \( A_2 \) being maximum amplitudes of curves so labeled (dashed lines). Abscissa: time and time constants, \( \tau_1 \) and \( \tau_2 \), of 2 exponentials, \( A_1 \) and \( A_2 \). Solid line shows time course of function composed of 2 exponentials, \( A_1 \) and \( A_2 \), and constant, \( A_0 \). Values of parameters shown here are those calculated for 0.1 M NaCl, as shown in Table 1.](http://ajplegacy.physiology.org/doi/abs/10.1152/ajpgi.1986.254.12.1136)

<table>
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<tr>
<th>NaCl Conc. (M)</th>
<th>Percent Fit</th>
<th>( \tau_1 )</th>
<th>( \tau_2 )</th>
<th>( A_1 )</th>
<th>( A_2 )</th>
<th>( A_0 )</th>
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<td>38</td>
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<td>7.38</td>
<td>14.5</td>
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\( \tau_1 = 0.504 \)  
\( \tau_2 = 0.607 \)  
\( t = 1.49 \)  
\( t = 1.71 \)  
\( r_p = -0.322 \)  
\( r_p = 0.763 \)  
\( r_p = 0.917 \)  
\( t = 5.14^* \)  

* \( P < .05 \).
short time constant ($A_0 e^{-t/T_1}$) with the constant results in 3.13 times as much error as that in the two-exponential model. Including only the long time constant ($A_2 e^{-t/T_2}$) with the constant results in 5.13 times as much error. Thus, the two-exponential model is significantly better in describing the time course of the response than the single-exponential model.

In order to determine whether the amplitude coefficients, $A_0$, $A_1$, and $A_2$, and the time constants, $T_1$ and $T_2$, are dependent on NaCl concentration, correlation coefficients were computed between each of the model parameters and NaCl concentration. The product-moment correlation coefficient ($r_p$) was calculated between each amplitude parameter ($A_0$, $A_1$, and $A_2$) and NaCl concentration. Since the time constants ($T_1$ and $T_2$) do not satisfy the assumption of product-moment correlation that a linear regression equation relates the two variables, a rank correlation coefficient ($r_p$) was calculated for the time constant parameters. Even in the Heck and Erickson model (8), the time constant would be inversely related to the concentration plus another constant. Thus, relative magnitudes of these unknown constants would determine whether the inverse of the time constant should satisfy the necessary linear regression assumption. Statistical analysis of these correlation coefficients indicated that for step changes in NaCl concentration the amplitude coefficients, $A_0$ and $A_2$, are positively correlated with NaCl concentration, while $A_1$ and the time constants, $T_1$ and $T_2$, are independent of stimulus intensity. The correlation coefficients and the corresponding values of $t$ for each model parameter are shown in Table 1. Thus, the stronger the NaCl concentration the greater the amplitude of both the gradual second decline of the adaptation process and the steady-state value of the response. However, the amplitude of the initial rapidly declining exponential is independent of stimulus intensity.

**DISCUSSION**

The results of these analyses suggest that adaptation of the chorda tympani response reflects at least two underlying processes. While it is perhaps inappropriate to make inferences about specific receptor mechanisms from integrated whole-nerve responses, correlations between these data and other relevant literature can provide support for certain hypotheses regarding the nature of the transduction process in taste. For example, the rate of solution flow has been shown to have an effect on both the amplitude of the transient portion of the chorda tympani response (19, 22a) and human estimates of taste intensity (9). These findings support the idea that the initial phasic burst of chorda tympani activity reflects the rate of stimulus adsorption (8), which could vary directly with the rate of solution flow. These considerations from the literature led to the consideration of the following physical model of the taste receptor system. First, it is assumed that there is a diffusion process that must take place in order for the chemical to reach the receptor, and second, that the change in chemical concentration at the surface of the tongue may be described as shown in Fig. 4. This model allows one to include the effect of flow rate on the response since the time, $T_1$, required to reach the final concentration, $K$, will be smaller for higher flow rates. For notational simplicity in the following mathematical development, the slope of the rise in concentration is defined as $m = K/T_1$, which will be proportional to flow rate. Finally, it is assumed that the response is proportional to the rate of complex formation, as in the model proposed by Heck and Erickson (8). All of this development is similar to that discussed by Beidler (3) and by Faull (4a). While Beidler assumed, as in the present discussion, that the diffusing material cannot go further than the thickness of the “slab,” Faull made the assumption that the material could continue to diffuse further. The present results do not distinguish between these two assumptions, but do support the validity of this physical model. Neither Beidler’s nor Faull’s theoretical development includes the rate of change in concentration of the solution flowed over the tongue as is done here (see Fig. 4). Since the present development includes flow rate, it allows prediction of the relationship of the coefficients to flow rate as well as concentration.

The described one-dimensional diffusion problem may be concisely stated mathematically as:

$$\frac{\partial^2 C(x, t)}{\partial x^2} - \frac{\partial C(x, t)}{\partial t} = 0$$

subject to boundary conditions:

$$C(0, t) = f(t)$$

where $f(t)$ is as shown in Fig. 4, and

$$C(x, 0) = 0$$

**Equation 2** is simply the diffusion equation in one dimension, here called $x$. **Equation 3** is the description of the time course of the change in the concentration flowed over the tongue. **Equation 4** specifies that the material may not diffuse into the tongue, whereas **equation 3** states that the initial concentration in the region of interest is zero. The solution to this set of equations is given by:

$$C(x, t) = C_0(x, t) - u(t - T_1)C_0(x, t - T_1)$$
where

\[ C_0(x, t) = mt + \frac{m}{2}(\alpha a)^2 \]

\[ + \frac{2m}{2a^2} \sum_{n=1}^{\infty} \sin \left( \frac{\alpha_n x}{\lambda_n} \right) \exp \left( -\lambda_n^2 t \right) \]  

and

\[ \lambda_n = \frac{(2n - 1)\pi}{2a} \]

\[ u(t - T_1) = \begin{cases} 0 & t \leq T_1 \\ 1 & t > T_1 \end{cases} \]

In this study, we are interested in the concentration at the receptor, C(a, t). Then \( C_0(a, t) \) simplifies to:

\[ C_0(a, t) = mt - \frac{m}{2}(\alpha a)^2 \]

\[ + \frac{2m}{2a^2} \sum_{n=1}^{\infty} \sin \left( \frac{\alpha_n x}{\lambda_n} \right) \exp \left( -\lambda_n^2 t \right) \]

Thus, the physical model leads to the following mathematical model for the concentration of solute at the receptor:

\[ C(a, t) = mt - \frac{m}{2}(\alpha a)^2 \]

\[ + \frac{16m(\alpha a)^2}{\pi^3} \sum_{n=1}^{\infty} \frac{(-1)^{n+1} \exp \left( -\lambda_n^2 t \right)}{(2n - 1)^3} \]

\[ 0 \leq t < T_1 \]

and

\[ C(a, t) = mT_1 + \frac{16m(\alpha a)^2}{\pi^3} \sum_{n=1}^{\infty} \frac{(-1)^{n+1} \exp \left( -\lambda_n^2 t \right)}{(2n - 1)^3} \]

\[ \cdot \left[ 1 - \exp \left( +\lambda_n^2 T_1 \right) \right] \]

\[ T_1 \leq t \]

where

\[ \lambda_n = \frac{(2n - 1)\pi}{2a} \]

The following observations may be made about the solution described by equations 11 and 12: 
1) for \( t \geq T_1 \), equation 12 is a constant depending on the concentration, \( K = mT_1 \) plus a sum of exponentials. 2) The coefficients of the exponential terms are inversely proportional to \( n^4 \), making the first term far larger than any other. 3) The time constants \( (1/\lambda_n^2) \) are inversely proportional to \( n^2 \), making the first term last far longer than any others. If equation 12 is used in conjunction with the Heck and Erickson model, the predicted response is given by:

\[ aR(t) = A_0 + A_1 e^{-\gamma_1 t} + \sum_{n=1}^{\infty} B_n e^{-\gamma_n t} \]  

where

\[ \gamma_n = \frac{(2n - 1)\pi}{2a} \]

1) \( A_0 \) should be proportional to the rate of the solution used to bathe the tongue \( (m T_1 = K) \). 2) \( A_1 \) should be a function of both concentration and rate of stimulus onset \( (m) \), i.e., the flow rate of the solution. Thus, it will not be simply proportional to either parameter. 3) \( B_n \) should be proportional to the rate of onset, \( m \). 4) \( B_0 \) and higher terms are inversely proportional to \( n^4 \), making their contribution to the total response small compared to that of the first three terms, \( A_0 \), \( A_1 \), and \( B_1 \). 5) Time constant \( \tau_1 \) characterizes the chemical dynamics of the complex formation, as given in the Heck and Erickson development. As shown there, it is not directly proportional to concentration. Rather it is of the form: \( \tau_1 = 1/(b_0 K + b_2) \). 6) Time constants \( \gamma_n \) characterize the diffusion process and are independent of concentration or rate of stimulus onset. For reasonable assumptions about the diffusion properties, the time constants \( \gamma_n \) are all very small compared to \( \tau_1 \), making these terms essentially zero (see ref. 4a, p. 77). The consequence of equation 13 and the properties of the coefficients and time constants is a model of the response having the form:

\[ aR(t) = A_0 + A_1 e^{-\gamma_1 t} \]  

Since equation 13 consists of a series of exponential terms, it does not permit making any statements about supporting Beidler’s (2) equation or Paton’s (13) theory. Such a comparison would be possible only if numerical values were available for all the constants involved, including many which are simply not known. These include the slope, \( m \), the diffusion constant, \( a^2 \), and the diffusion distance, \( \chi \).

Initial analysis of the data collected in this study suggested that two exponential terms were present in addition to the constant term. This is easily confirmed by a semilogarithmic plot of the data. Mathematical models using a constant plus two exponentials have been used to describe the response of other sensory systems (15). If some sort of neural adaptation were proposed as the mechanism underlying the second exponential decay, two properties could reasonably be hypothesized for this function. First, the amount (amplitude) of adaptation could be expected to be positively correlated with the concentration of the stimulus, and second, the time constant would be expected to be much larger than that associated with the initial response. Thus, the initial transient development leads to the proposed mathematical model consisting of three terms, \( A_0 \) and \( A_1 e^{-\gamma_1 t} \), reflecting chemical dynamics of the system and \( A_2 e^{-\gamma_2 t} \), reflecting neural adaptation.

In the mathematical model proposed, the amplitude of the initial transient response is equal to the sum of the values of \( A_0 \), \( A_1 \), \( A_2 \). The values of \( A_0 \) and \( A_2 \) are correlated with NaCl concentration, as predicted by the theoretical considerations. Thus, the maximum transient response magnitude \( (A_0 + A_1 + A_2) \) is correlated with stimulus concentration in agreement with the results reported by Halpern and Marowitz (6). Further, \( A_1 \) is not correlated with NaCl concentration, on which the mathematical model. The value of \( A_1 \) is equal to the initial response value minus the sum of \( A_0 \) and \( A_2 \), both of which increase with increasing NaCl concentration. If the initial transient response were a function of the rate of stimulus adsorption \( (8) \), then the amplitude \( (A_1) \) of the initial exponential might be expected to show a decrease with increasing NaCl concentration. For example, if the initial rate of binding were to approach its maximum more rapidly than did the equilibrium rate, then the phasic portion of the response would show a decrease relative to the tonic component at higher stimulus concentrations. In fact, Fig. 1 shows that the...
transient portion of the response does begin to saturate at lower NaCl concentrations than the steady-state response. Thus, the characteristics of the initial exponential component of the adaptation process are consistent with the suggestion that the transient burst of activity reflects the rate (m) of stimulus-receptor complex formation (8). In addition, it has been shown that the rate of stimulus onset has an effect on the transient portion of the chorda tympani response but not the steady-state component (19, 22a).

Although the initial transient adaptation may reflect the rate-sensitivity of the gustatory system, the gradual decline that occurs during the steady-state portion of the response is most likely due to other factors. Adaptation of the taste receptor potential of the frog (18) and the rat (12) consists of a gradual decline in the receptor potential after the maximum response with a time course similar to the slow decline (τ2) demonstrated by the present analysis. In addition, there is greater adaptation of the rat taste receptor potential with greater NaCl concentrations (12), which implies that γ2 should be positively correlated with concentration. As may be seen in Table 1, the amplitude of the gradual decay (γ2) in the chorda tympani response is positively correlated with NaCl intensity. Thus, it appears that over a relatively extensive period of time, when the stimulus-receptor adsorption process has presumably long since attained equilibrium, there is a gradual decline in both the taste receptor potential and the consequent first-order neural impulse frequency. The mechanisms underlying this gradual decay are not known, although both the correlation of γ2 with concentration and the magnitude of 29 (29 s) are consistent with a hypothesis that the gradual decay reflects a neural adaptation process.

While recordings from the first-order nerve typically show a transient phase, those of vertebrate taste receptor potentials show only the gradual decline characteristic of the steady-state phase of the first-order nerve response and not an initial rapidly declining transient phase. Consequently, Sato (17) has argued that the transient response and its subsequent decline seen in the glossopharyngeal nerve of the frog is generated by synaptic mechanisms or by properties of the first-order nerve rather than by the receptor cell. However, if the initial transient response is sensitive to the rate of stimulus adsorption, the very slow rates of solution application used in vertebrate taste cell studies would seriously distort or eliminate any transient phase that might otherwise be present in the receptor potential. Whether or not the taste receptor exhibits a transient response awaits further research in which the rate of stimulus onset (m) is carefully controlled.

Since both the initial phasic portion of the vertebrate taste nerve discharge and the gradual decay during the steady-state phase of the response contribute separate exponentially decaying components to the adaptation process, they most likely result from different underlying mechanisms. Current literature (8, 9, 19, 22a) strongly suggests that the initial transient discharge and its decline may be a function of the rate of stimulus adsorption, whereas the later phase of the adaptation process may reflect an adaptive mechanism of the taste receptor cell (12). The results of the mathematical analysis and statistical tests of the coefficients confirm each of the hypotheses made about the expected dependence of A0, A1, A2, and τ1 on the concentration of the solution flowed over the tongue. The results further suggest that the time constant of the second gradual adaptation process (τ2) is independent of concentration, although no hypothesis was made concerning this dependence based on theoretical considerations. While the present mathematical analysis has illustrated the double-exponential nature of the adaptation process in taste, further work is needed to clarify the specific mechanisms underlying these processes.

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