Influence of the intensity of NaCl solutions on adaptation degree and recovery time course

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The degree of adaptation and the time course of recovery after adaptation to NaCl solutions of various intensities were examined by magnitude estimation and simple sensory reaction time using a test stimulus of constant intensity. The results show that the degree of adaptation increased with the adapting concentration following a negatively accelerated function. Similarly, all recovery curves were negatively accelerated functions of the recovery time. The relation between the recovery constant (time necessary to attain two-thirds of normal responsivity) and adapting concentration approximates with both criteria more or less a linear function. Thus the recovery constant is a positively accelerated function of the degree of adaptation. The relationship between concentration and degree of adaptation can be approximated by Beidler's equation of taste stimulation, while the time course of recovery can be expressed by an exponential equation that can also be related to Beidler's theory. The two criteria used showed similar deteriorating effects of taste adaptation, indicating that reaction time can also be a useful criterion of the level of sensory responsivity.

Prolonged steady stimulation of taste receptors results in changes in the response level of the gustatory system. These changes, known as adaptation phenomena, generally consist of some reduction in the taste response, and are therefore used as criteria of adaptation effects. The criteria are various: threshold values, sensation intensity, time necessary for the disappearance of taste, total taste effect, reaction time, and speed of recovery. With the neurophysiological approach, taste adaptation was assessed according to changes in the transient and tonic portions of the integrated response of the gustatory nerves, threshold values, and single-fiber preparation, according to the frequency of afferent impulses (e.g., Bartoshuk, 1980; Marks, 1974).

Several psychophysical taste studies have mentioned the influence of the intensity of the adapting stimulus on some adaptation effects (Abrahams, Krakauer, & Dallenbach, 1937; Bujas, 1953; Bujas, Ajduković, Szabo, Mayer, & Vodanović, 1994; DuBose, Meiselman, Hunt, & Waterman, 1977; Ganzevles & Kroeze, 1987; Gent, 1979; Gent & McBurney, 1978; Krakauer & Dallenbach, 1937). However, only one systematic study, which used change in

threshold as the adaptation criterion, discusses the relationship between intensity of the adapting concentration and the rate of recovery after adaptation (Hahn, 1934). For this reason, the aim of the present research was to investigate the influence of an NaCl adapting solution of various intensities on the degree of adaptation and the time course of recovery.

The degrees of adaptation and levels of recovery were evaluated using magnitude estimation (ME) and reaction time (RT) as criteria. Classical psychophysics was principally based on threshold measurement. After it was found that taste threshold values often failed to predict suprathreshold sensory effects (Bartoshuk & Marks, 1986; Bujas, 1953; Moskowitz, 1977) and that the matching procedure was time consuming, in the "new" psychophysics, the effects of suprathreshold stimuli have mostly been evaluated by using magnitude estimations (Stevens, 1961). Unfortunately, however, magnitude estimates can be affected by intersubject differences and intrasubject changes in terms of the general evaluation criterion and be biased by the subject's knowledge and control of his/her estimations (Jones & Marcus, 1961; Poulton, 1968; Szabo-Stipetić, 1967; Teghtsoonian & Teghtsoonian, 1971; Warren & Warren, 1963). For this reason, we tried to follow the adaptation effects and recovery processes using, in addition, changes in simple RT, which has the advantage

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of being, in this respect, a more objective and reliable approach. RT data, however, are obviously not a substitute for magnitude estimations. RT correlates somewhat with stimulus intensity, and therefore also with sensation intensity, but only in the range in which RT decreases with stimulus intensity toward a constant value of K (the irreducible part of RT). As the irreducible part is not correlated with sensation intensity, after Piéron (1914, 1922, 1959), several authors (Aikin, 1974; Banks, 1973; Bujas, Szabo, Ajduković, Mayer, & Vodanović, 1988a, 1988b; Galifret & Piéron, 1949; Luce & Green, 1972; McGill, 1961; Vaughan, Costa, & Gilden, 1966) tried to use, as a measure of sensation intensity, the reciprocal value of RT from which the irreducible part of RT was subtracted [$1/(RT - K)$]. Unfortunately, Piéron's reaction speed values, and consequently the derived psychophysical functions, are greatly influenced by the K value, which is difficult to determine in a sufficiently accurate and reliable manner (Banks, 1973; Mayer, Bujas, Szabo, Ajduković, & Vodanović, 1988).

In using RT data, our aim was to test whether, along with direct sensory evaluations, simple taste RT, measured directly and without further adjustment, could serve as an additional criterion of the level of taste responsivity.

METHOD

Subjects

Four subjects, familiarized with psychophysical taste measurements, participated in the experiments. The subjects, 3 males and 1 female with a median age of 35 years, were laboratory employees.

Stimuli and Apparatus

Six NaCl solutions, made in distilled water in concentrations from 0.05 to 1.6 M in equal log steps, were used as the adapting stimuli. All stimuli elicited pure taste sensations without any side effects. The test stimulus used to assess the adaptation effects and levels of recovery was a solution of 0.2 M NaCl. In control measurements, instead of the supraliminal adapting stimulus, a weak, clearly subliminal solution of 0.005 M NaCl was applied. This subliminal solution, similar in NaCl concentration to saliva, was used instead of distilled water, because, as determined in preliminary experiments, the prolonged flow of distilled water itself causes a decrease in test stimulus effects. All solutions and the rinsing water were kept in a water bath at 38°C.

The stimuli were delivered to the anterior part of the tongue by a gravity-open flow system. A siphon container with a delivery tube was fixed above an outlet glass channel. During stimulation, the subject's tongue, placed on the channel, was immobilized by a plastic arch such that the exposed part of the tongue was just below the delivery tube. The stimulated tongue area was approximately 7 cm², and the solution flowed at a rate of 6 ml/sec.

RT was recorded via an electronic chronometer. On the outflow of the solution delivery tube, two thin wire electrodes were attached. Upon its flow to the tongue, the solution connected the electrodes, thereby causing a weak and short condenser discharge. The condenser discharge activated the chronometer. At the moment of experiencing the taste of the solution, the subject stopped the chronometer by manually releasing a switch. The condenser discharge did not provoke any sensation.

Procedure

The adapting solution flowed over the tongue for 22 sec, after which a recovery period followed. The recovery periods lasted 5, 10,

30, and 90 sec and, using RT, also 270 sec. The test stimulus, which lasted 5 sec, was presented after adaptation in the experiments with RT; in the experiments with ME, the test stimulus was given prior to adaptation and then again after adaptation. Throughout the whole 5- and 10-sec recovery periods, the tongue was rinsed with water. In longer recovery periods, the tongue was rinsed during the initial 5 sec of recovery and during the 5 sec preceding the presentation of the test stimulus. For the two extreme concentrations (0.05 and 1.6 M NaCl), only the adaptation degree after 5 sec of recovery was assessed.

To assess the full adaptation degree provoked by 22 sec of stimulation with a given concentration, it would obviously be necessary to present the test solution immediately after the adapting stimulus. However, this is partly permissible only in using ME, in which case the inevitable mixture of the traces of the adapting solution and the test solution does not substantially alter the subsequent ME. On the contrary, to enable the subject to react to the appearance of the taste of the test solution after adaptation, it is necessary to produce a clear discontinuity between the taste of the adapting solution and the taste of the test stimulus. The interposed 5-sec water rinse evidently reduced the adaptation effect. However, although adaptation to all concentrations was partial and in addition reduced by the 5-sec water rinse, the remaining degree of adaptation, as further recovery values showed, was high enough to permit a follow-up of its decrease in the course of the recovery times.

A diagram of the experimental procedure using the RT criterion is shown in Figure 1.

In control trials, the procedure was equal in all details, with the previously mentioned exception that instead of the adapting solution a tasteless 0.005 M NaCl solution was applied for 22 sec.

In the RT-data analysis, the degree of adaptation and the course of recovery were evaluated by comparing the RT to the test stimulus following adaptation (RT_A) with the RT to the test in corresponding control trials (RT_0).

In the experiments using ME, a modulus equal to 10 was assigned to the perceived taste intensity of the first test stimulus (T_1) in experimental as well as in control trials (Figure 2). The subject's task was to estimate the magnitude of the second test stimulus (T_2), presented after adaptation or after the tasteless solution flow, relative to the taste intensity of the preceding first test stimulus ($T_1 = 10$).

In the ME-data analysis, the effects of adaptation and recovery were evaluated by comparing the ME of the second test in the experimental trials (ME_A) with the magnitude estimation of the second test in corresponding control trials (ME_0).

The experiments using RT and ME were conducted in separate sessions. In each session, an equal number of experimental and control trials were run. The mean values of each subject are based on at least 10 measurements of RT for each concentration and each re-

Figure 1. Sequence of stimuli in measurements of the degree of adaptation and recovery using reaction time as criterion. A, adapting stimulus; W, water; T, test stimulus. In control trials, instead of A, a tasteless NaCl solution flowed.

Figure 2. Sequence of stimuli in measurements with magnitude estimation. a, experimental trial; b, control trial; A, adapting stimulus; W, water; T, test stimulus. Diagram shows the sequence only after 5 sec of recovery.

covery time and on at least six MEs. The rest between experimental trials was about 5 min, and data were collected in about eight sessions per subject.

RESULTS

Relationship Between Intensity of Adapting Solution and Degree of Adaptation

The results showed that, after adaptation, the perceived intensity of the test stimulus decreased while RT was prolonged.

Those adaptation effects can be expressed in terms of the degree of responsivity (S), which indicates the percentage of the normal responsivity remaining after adaptation: $S_{ME} = (ME_A/ME_0)100$; and $S_{RT} = (RT_0/RT_A)100$, where ME_A = magnitude estimation of the test stimulus after adaptation, ME_0 = magnitude estimation of the test stimulus in control trials, RT_A = reaction time to the test stimulus after adaptation, RT_0 = reaction time to the test in control trials.

The complement to 100% of S gives the degree of adaptation (D), showing in percentages how much adaptation has depressed normal responsivity (100%):

$$D_{ME} = 100 - [(ME_A/ME_0)100];$$

$$D_{RT} = 100 - [(RT_0/RT_A)100].$$

When $ME_A = ME_0$ and $RT_A = RT_0$, the adaptation degree is zero ($D = 0$), and when $ME_A = 0$ and $RT_A \gg RT_0$, the degree of adaptation is practically complete ($D \approx 100\%$).

The average values (arithmetic means) for the 4 subjects are presented in Figure 3 (based on ME) and in Figure 4 (based on RT). All individual curves exhibited the same form as the average curves.

The adaptation degree, assessed according to both criteria, increases with the adapting concentration following a negatively accelerated function.

For descriptive purposes, a logarithmic function can be fitted to both curves. Thus, the degree of adaptation, measured by using a common test stimulus 5 sec after the end of adaptation, can be described as a linear function of the logarithm of the adapting concentration. The mean difference between observed and calculated data is 6.3% for D_{ME} , and 4.9% for D_{RT} . As a further test of goodness of fit, the proportion of explained variance—the coefficient U —as suggested by Eisler and Roskam (1977), was calculated. For D_{ME} data, $U = 0.989$; for D_{RT} data, $U = 0.961$.

Time Course of Recovery

The time course of recovery may be followed by observing the return of responsivity toward the normal value (100%). The degree of recovery (R) for the ME criterion is $R_{ME} = (ME_t/ME_0)100$ and for the RT criterion, $R_{RT} = (RT_0/RT_t)100$, where ME_t and RT_t are values obtained after a given recovery time (t).

Figure 3. Relationship between intensity of adapting solution (abscissa) and the degree of adaptation (ordinate). Data based on magnitude estimation.

Figure 4. Relationship between intensity of adapting solution (abscissa) and the degree of adaptation (ordinate). Data based on reaction time.

Figure 5 shows the obtained curves averaged across 4 subjects.

The subjects differed in their levels of recovery but not in the general form of the time course of recovery. All recovery curves were negatively accelerated, indicating that recovery was fastest at the beginning and progressed with diminished speed as full recovery (100%) was approached. The stronger the adapting solution, the slower the recovery process. After adaptation, ME remained depressed and RT remained prolonged over a rather long period. According to both criteria, within the 90-sec recovery period, complete recovery was attained only after adaptation to 0.1 M. Recovery was also complete within this period

after adaptation to 0.2 M, but only according to the ME criterion. For all other adapting concentrations, the period of diminished responsivity exceeded 90 sec.

When assessed according to RT, the recovery was significantly slower than when ME served as the criterion. For example, with RT as the criterion, 2/3 of complete recovery from adaptation to 0.4 M NaCl was reached after 48.5 sec, whereas with ME the same recovery level was attained after only 27.5 sec. The difference between these two recovery curves is significant at the $< .01$ level (Wilcoxon's test for paired observations).

For descriptive purposes, the recovery data according to both criteria can also be approximated with logarithmic

Figure 5. Left panel: recovery time course after adaptation to four NaCl concentrations. Data based on reaction time. Right panel: course of recovery time evaluated by magnitude estimation. Abscissa: recovery time in seconds. Ordinate: degree of recovery.

mic functions. The mean difference between observed and calculated data range from 0.4% to 2.6%, and the U coefficients range from 0.999 to 0.931.

The recovery speed following adaptation to concentrations of varying intensity may be assessed by using the constant τ , corresponding to the recovery time needed to attain 67% ($2/3$) of preadaptation efficiency. The left panel of Figure 6 shows the relationship between adapting concentration and the recovery speed constants determined from the recovery curves.

The time needed to attain the 67% recovery level is more or less proportional to the adapting concentration. However, this "linear" relation is not preserved when, instead of the adapting concentration, the degree of adaptation is considered. Given that the degree of adaptation increases more slowly than the adapting concentration, the relationship between the degree of adaptation and the recovery constant should be a positively accelerated function. As the right panel of Figure 6 shows, with the increase in degree of adaptation, an unproportionally longer and longer rest is needed to attain the same percentage of recovery.

DISCUSSION

The intensity of the adapting solution has a significant influence on the responsivity of the sensory system of taste. The more intense the concentration of the adapting solution, the greater the increment in RT and the decrement in sensation magnitude. With the increase in the concentration of the adapting solution, the sensation magnitude decreases and the RT increases, initially at a rapid rate; then the changes gradually slow down.

The logarithmic function, used solely for describing the relationship between the concentration of the adapting

solution and the degree of adaptation, does not correspond with the facts that when the concentration has a zero value, the degree of adaptation is also zero, and that, for very strong concentrations, the degree of adaptation has a definite limit. The relationship between the concentration (C) of the adapting solution and the degree (D) of adaptation can, according to both criteria, be satisfactorily expressed by Beidler's (1954) taste equation, with the difference being that, in the case of adaptation, the equation operates with the number of inactivated receptor sites instead of with the number of bound sites.

The cessation of prolonged stimulation is followed by the recovery process, that is, a gradual return of the taste system's responsivity to its preadapted level. Adaptation to stronger stimuli is followed by slower recovery. Regardless of the intensity of the previous adapting stimulus, the recovery process follows a negatively accelerated function. Recovery progresses rather slowly, and, in this respect, it is similar to the slow rate of the time course of adaptation. That the mechanism of adaptation and recovery are opposite but symmetrical is in agreement with the possibility of approximating the adaptation and recovery data with the same type of exponential equation. This similarity in the time course of adaptation to NaCl and the following recovery was observed early by Hahn (1934), who used the absolute threshold as the criterion. Hahn approximated NaCl-adaptation data by the equation $C_n - C = Be^{-\beta t}$, where C = threshold at moment t , C_n = terminal threshold, t = adaptation time, and B , β = constants. Similarly, the recovery data were approximated by $C - C_0 = De^{-\delta t}$, where C_0 = threshold value before adaptation, and D , δ = constants.

For the time course of recovery, too, the logarithmic functions do not account for two facts. First, the recovery immediately after adaptation (recovery at the moment

Figure 6. Left panel: relationship between adapting concentration (abscissa) and the recovery constant (ordinate). Right panel: relationship between degree of adaptation (abscissa) and recovery constant (ordinate). Values based on reaction time and magnitude estimation criteria.

$t = 0$) does not start from zero, because 22 sec of stimulation, even with the strongest concentration, resulted in only partial adaptation as measured by a common test stimulus. Second, the recovery, after a more or less long rest period, reaches a definite plateau that corresponds to complete recovery. These conditions can be satisfied by the exponential function, which, in addition, can be related to Beidler's (1954) theory of taste stimulation.

Analogously to adaptation, during which the number of activated receptor sites progressively decreases, during the recovery period the number of previously inactivated sites (A_i) progressively diminishes. In agreement with the law of mass action, the rate of this reactivation is proportional to the number of inactivated sites during adaptation: $dA_i/dt = -KA_i$, where K is a proportionality constant. This equation can be rewritten as $A_i = Be^{-Kt}$, where B is the number of inactivated sites at the start of recovery ($t = 0$). Since the total number of sites, which, after complete recovery, can be activated again, is proportional to the plateau value ($= 100$), the exponential equation corresponding to the recovery data (R) can be written as

$$R = 100 - Be^{-Kt}.$$

Applying this equation to, for example, the recovery curve obtained after adaptation to 0.4 M NaCl, for ME data $B = 60.4$ and $K = 0.019$. For the eight recovery curves based on both criteria, the mean difference between observed and calculated values ranges from 0.5% to 3.8%, and the proportions of explained variance range from $U = .994$ to $U = .944$.

The general relationships observed in gustatory adaptation and recovery processes are similar to those already found in most sensory systems. However, in different systems, the changes provoked by adaptation or recovery can follow trends with different rates. Moreover, particularly in the taste system, these functional relationships can depend on the type of criterion used, on the procedure of stimulus delivery, and upon the particular compound used as stimulus.

Among the variety of indices of the functional level of the taste system, sensory RT was used in very few taste-adaptation investigations (Bujas, Ajduković, et al., 1994; Bujas, Szabo, Ajduković, & Mayer, 1991a; Yamamoto & Kawamura, 1984). However, taking into account some advantages of the RT approach, it seems that RT measurement can be useful in the study of changes in the functional level of the sensory system. Sensation latency time provides information that is situated between the threshold and full sensation magnitude and can serve as a control of and supplement to data obtained with other indicators.

Also scarce are investigations of taste adaptation that have taken psychophysical functions into account. In the equation relating to changes of response magnitude during adaptation, Gent and McBurney (1978) considered, instead of the adapting stimulus, the stimulus raised to a power n of the corresponding psychophysical function. Using the same subjects who participated in the present investigation, Bujas, Ajduković, et al. (1994) investigated the influence of adaptation to NaCl on psychophysical

functions on the basis of ME and Piéron's reaction speed. The exponents n in the potential functions were 0.63 for ME and 0.72 for $1/(RT - K)$. In agreement with some other authors (Bartoshuk, 1968; Bartoshuk & Marks, 1986; McBurney, 1966), it was found that, after adaptation, the slopes of both psychophysical functions were steeper.

According to our results, recovery estimated by the magnitude-estimation procedure is faster than that estimated by reaction time. This finding may be attributable to the possibility that recovery of the peak receptor response, corresponding to the full sensation magnitude, is faster than the recovery of latency time and buildup rate, which determine reaction time (Bujas, Szabo, Ajduković, & Mayer, 1991b; Smith, Bealer, & van Buskirk, 1977).

Our results concur with neurophysiological data. Smith and Bealer (1976) measured the excitability of rat chorda tympani following adaptation to NaCl solutions of varied intensities by observing the recovery of the transient portion of the integrated neural response. Stronger adapting stimuli produced considerably longer periods of post-excitatory depression, and the recovery curves were a logarithmic function of the recovery time. And Smith et al. (1977) reported that the recovery of the steady-state response of rat chorda tympani followed a time course that was the inverse of the slow decline in response to the adapting stimulus. In one other study Wang and Bernard (1970), using as the criterion the changes in the peak response in the integrated activity of the cat chorda tympani, reported that under the influence of adaptation not only was the magnitude of response reduced, but—and this concerns reaction time—the rate of the rise of the integrated response was decreased by increased adaptation. In addition, they found that recovery increased following a logarithmic function of the rinse time.

Obviously, our results concerning the dependence of adaptation and recovery on the intensity of the adapting solution hold for the NaCl salty taste and cannot be warrantably generalized to other taste compounds.

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