

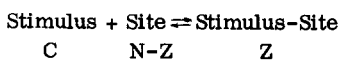
Beidler's taste equation: A correction

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Beidler derived an equation relating the magnitude of neural response to a gustatory stimulus with the concentration of that stimulus. In the derivation, he assumed the amount of stimulating substance removed from the solution by the receptors was small enough not to change the stimulus concentration appreciably. An equation without this assumption is derived, and is evaluated in the light of existing data. The hypothesis for a dissociation reaction in taste inception under some circumstances is given support.

Beidler (1954) has assumed that there are specific receptor sites on the surface of the receptor. A stimulus is adsorbed at these sites with the subsequent excitation of the gustatory system, and the magnitude of the neural response is proportional to the number of receptor sites filled. He further assumed that the mass action law could be applied to the initial adsorption process which could be written as



where Z was the number of sites which combined with the stimulus at this concentration; N was the total number of sites available, so that $N-Z$ was the number of sites unfilled; and C was the concentration of the stimulus. The mass action law could then be written as

$$Z/C (N-Z) = K \quad (1)$$

where K was the equilibrium constant for the reaction. This equation is correct, however, only for very high concentrations of the stimulus when Z is negligible in comparison with C . Although Renqvist (1919) had concluded that such an assumption was reasonable, an inspection of his data has shown that, near the absolute threshold for a salt, about 5% of the salt may be removed from the stimulus solution.

The form of the mass action equation without Beidler's assumption would use $C-Z$ instead of C , so that

$$Z/(C-Z) (N-Z) = K \quad (2)$$

If this equation is expanded and rearranged, the result is

$$1 = CNK/Z - CK - KN + KZ. \quad (3)$$

Beidler's assumption relating the magnitude of the response and the stimulus is $R = aZ$, where a is a constant. With high stimulus concentrations, the maximum response occurs when all the sites are filled,

so that $R_m = aN$. Substitution in Eq. 3 for Z and N , and rearranging to have the constants on the right hand side gives

$$C(R_m - R)/R = -R/a + (a + KR_m)/aK, \quad (4)$$

which shows that if the left hand term of Eq. 4 is plotted against R , the resulting function will be a straight line with negative slope. Equation 4 is somewhat more complicated than Beidler's form, i.e.,

$$C/R = C/R_m + 1/KR_m, \quad (5)$$

but has the advantage of being exact and applicable at all stimulus concentrations.

Because Beidler's equation was developed in an electrophysiological context, a good test of the corrected equation would be to see how well it fits such data. For this test, data were taken from Beidler (1953, Fig. 5). This figure was the record of integrated electrical responses from the chorda tympani nerve of a rat to various concentrations of NaCl. The peak-to-peak deflections from this record were plotted against concentration, and from this plot it appeared that R_m was 29.0. The value of R_m is very important, and should be determined very carefully because the form of the overall curve as a $C(R_m - R)/R$ vs R plot may be somewhat changed with different values of R_m . For convenience in comparing such plots with those for other compounds and from other experiments, R_m may be arbitrarily assigned the value of unity, and other responses treated as fractional values of R_m . Such a plot is given in Fig. 1.

It can be seen that the form of the function is not simply linear, but appears curved. However, the left hand portion is straight, and the function could be interpreted as being made up of two straight lines. These would be a left hand portion with positive slope, and a right hand portion with a lesser, negative slope, as depicted by the two dashed straight lines which were fitted to the data by eye. Such a composite function of two linear branches is often met in chemistry. In those cases, one mechanism may limit the rate or some other aspect of a reaction over a particular range of a variable such as temperature. Over another range of the variable, another mechanism may become more important and, thus, change the rate to a new value. It is assumed that two separate mechanisms are operating in this situation also.

The primary problem is the meaning of the two branches. Because the right hand branch has the expected approximate linearity and negative slope,

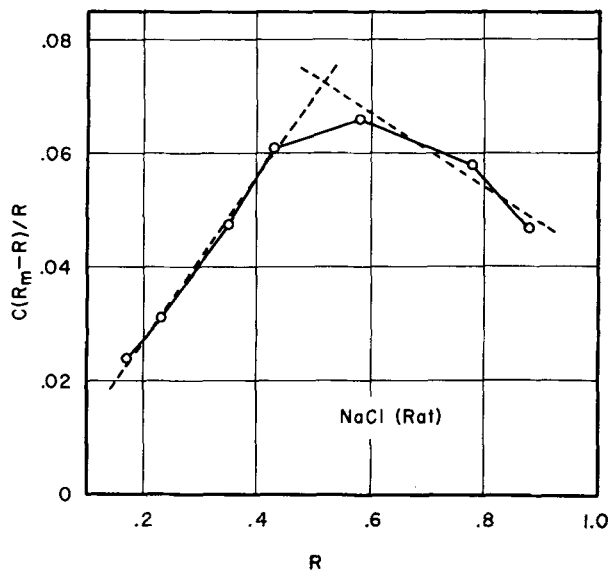


Fig. 1. Electrophysiological data (Beidler, 1953) plotted according to the corrected taste equation. The data are interpreted as being made up of two linear functions, one with a negative slope, and the other with a positive slope. The dotted lines representing these two functions were fitted by eye. The portion of the function with positive slope is interpreted as indicating the dissociation of a stimulus-receptor site combination.

it represents the adsorption reaction originally assumed in the development of the equation. The left hand branch, on the other hand, has a positive slope. This means that the constant a in Eq. 4 must be negative to make the term $-R/a$ positive, because R itself, the response, cannot be negative. The physical significance of having a negative may be found by going back to the assumption that $R = aZ$. If a is negative, the only way that R may remain positive is to have Z negative. This means that a response occurs when a number of receptor sites on the membrane are vacated, rather than filled. In other words, a response is initiated when a dissociation rather than an association reaction occurs at the receptor.

Such a conclusion has support from Cohen, Hagiwara, and Zotterman (1955) who suggested that excitation of the "water" fiber or receptor involved a fundamentally different mechanism from that of the "salt" fiber or receptor. Further, they suggested that the specific mechanism might be the outward flow of the chloride ion from the receptor. These authors also showed that the water fibers stopped their activity at about 0.03 M NaCl and higher concentrations, and the minimum activity of the salt fiber was at about 0.05 M NaCl. Renqvist (1919) has pointed out that, in the human, the quality of NaCl changes from sweet to a salty component at 0.03 M and becomes pure salty at 0.05 M. The change of slope in Fig. 1 occurs between the concentrations of 0.05 and 0.10 M. Beidler (1954) was aware of some discontinuities in his plots, and, apparently for that reason, did not use data obtained with concentrations below 0.1 M.

To check the corrected equation further, values of K , and of the change in free energy (ΔF) were calculated to see if they would agree with the values obtained earlier by Beidler (1958). The calculations in this paper are based on the values of the slopes of the right and left hand line segments as determined separately by graphical means from Fig. 1. The y-axis intercepts of these two line segments were also determined graphically from Fig. 1.

For the right hand segment, the value of K was 28.5, leading to a value of -1.98 kcal/mole for ΔF (Klotz, 1950, p. 144). These values may be compared to 9.8 and -1.37 for K and ΔF , respectively, as determined by Beidler. The values from the corrected equation for the assumed association reaction are seen, thus, to be in general agreement with the values calculated from the restricted equation.

Values of K and ΔF were also calculated for the left hand segment. These were 6.38 and -1.10 for K and ΔF , respectively. The fact that the free energy change is negative here, just as with the association reaction at higher concentrations, implies that the proposed dissociation reaction also precedes spontaneously within its values of stimulus concentration (Fruton & Simmonds, 1953, p. 229).

Much accurate neurophysiological data is needed to confirm the validity of this corrected version of Beidler's taste equation. If the suggested two linear portions of Fig. 1 are a reflection of the change of qualities in NaCl as a function of concentration, then other salts should also exhibit a number of linear segments. For example, Dzendolet and Meiselman (1967) have shown that KCl shifts qualities from sweet, to bitter, to salty as a function of increasing concentration. For LiCl, the shift is from sweet, to sour, and finally to salty. Thus, these salts should each exhibit a function composed of three linear portions. In any such experiment, however, the determination of R_m should be carried out with great care.

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