

The Rule of Choice of Equations for Calculation of Constants of Enzyme Inhibition and Activation

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ABSTRACT

The rule of choice of equations for calculation of constants of enzyme inhibition and activation is proposed to prevent the unjustified use of these equations and expand the possibilities of their application for non-trivial data analysis in enzyme kinetics. Examples of use of equations are given.

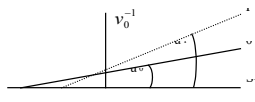
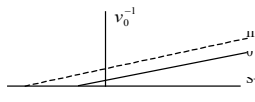
Keywords: The rule of choice of equations for K_i and K_a constants calculation

Introduction

In previous works [1-5] the possibility of construction of L vectors of enzymatic reactions in the three-dimensional (packed) $K_m V I$ rectangular coordinate system (Figure 1) is considered. The taking into account of properties of L vectors, such as: symmetric position in the $K_m V I$ coordinate system and the ratio of l lengths of orthogonal projections on the coincident (Pa, i) semi-axis to the ratio of the L vector projection on the semi-axis in basic s_0 plane (Figure 2) permitted to construct a parametrical classification of

the types of enzymatic reactions (Table 1) and correct the equations for calculation of the K_i and K_a constants of enzyme inhibition and activation, respectively, which now includes fourteen equations: 7 equations s for calculation of constants and 7 equations for calculation of K_a constants. It turned out that some of the obtained equations have similar algebraic forms, which required to consider the rule of choice of these equations to prevent their unjustified use and also for expansion of the possibilities of their application at data analysis in enzyme kinetics.

Table 1: Parametric classification of the types of enzymatic reactions.

No	Effect	Type of Effect	Correlation between the K'_m and V' parameters	Graphs in the $(v^{-1}; S^{-1})$ coordinates
1	Inhibition ($i > 0$)	I_i	$K'_m > K_m^0, V' < V^0$	
2		II_i	$K'_m < K_m^0, V' < V^0$ $tg \omega' = tg \omega^0$	

3		III _i	$K'_m = K_m^0, V' < V^0$	
4		IV _i	$K'_m > K_m^0, V' = V^0$	
5		V _i	$K'_m > K_m^0, V' > V^0$	
6		VI _i	$K'_m < K_m^0, V' < V^0, tg \omega' > tg \omega^0$	
7		VII _i	$K'_m < K_m^0, V' < V^0, tg \omega' < tg \omega^0$	
8	None	I ₀	$K'_m = K_m^0, V' = V^0$	
9	Activation (a > 0)	VII _a	$K'_m > K_m^0, V' > V^0, g \omega' > g \omega^0$	
10		VI _a	$K'_m > K_m^0, V' > V^0, g \omega' < g \omega^0$	
11		V _a	$K'_m < K_m^0, V' < V^0$	
12		IV _a	$K'_m < K_m^0, V' = V^0$	
13		III _a	$K'_m = K_m^0, V' > V^0$	
14		II _a	$K'_m > K_m^0, V' > V^0, g \omega' = g \omega^0$	
*15		I _a	$K'_m < K_m^0, V' > V^0$	

Note: *The symbol of a graph in corresponds to the type of reaction under study. For example: the line (0) characterizes the position of initial (nonactivated) enzymatic reaction, line I – the position of a graph representing the I_a type of activated enzymatic reaction etc.

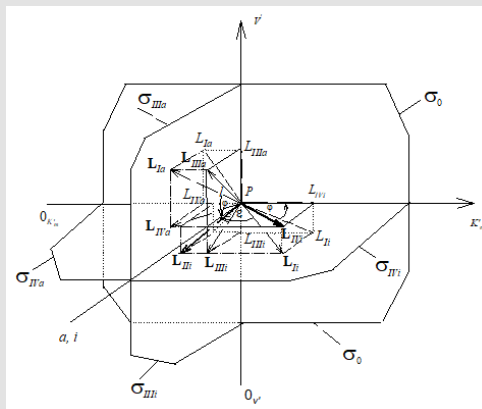


Figure 1: Three-dimensional (packed) $K_m V I$ system of rectangular coordinates with coincident P_i and P_a semiaxes ($P_{a,i}$) molar concentrations of inhibitor i and activator a . The symbols of kinetic parameters: K_m, V, K_m^0, \dots , three-dimensional vectors: $L_{i'}, L_{iV_i}, \dots, L_{i'a'}, L_{i'V_a}$ and their projections $L_{i'}, L_{iV_i}, \dots, L_{i'a'}, L_{i'V_a}$ on the basic s_0 plane as well as the symbols of projections of directing planes $\sigma_{i'V_i}, \sigma_{i'V_a}, \sigma_{i'a'}, \sigma_{i'a}$ on the $PK_m, PO_{V'}, PO_{K_m}$ and PV coordinate semiaxes the same as in the text and in [1-3].

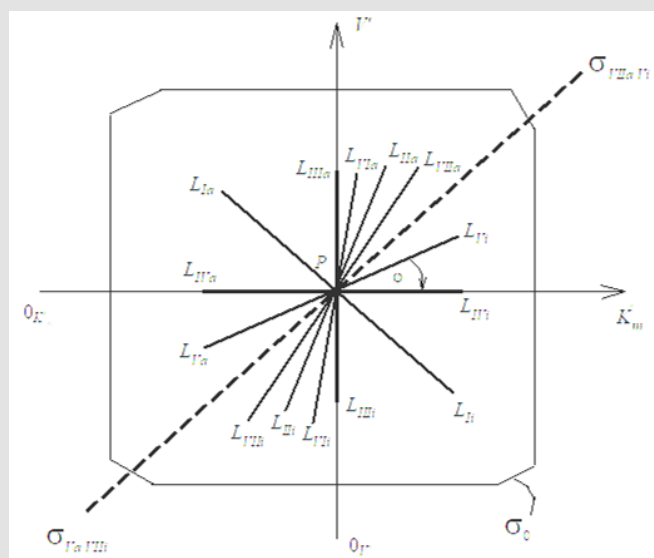


Figure 2: Two-dimensional (scalar) $K_m V I$ coordinate system. The symbols of kinetic parameters: K_m, V, K_m^0, \dots , the projections $L_{i'}, L_{iV_i}, \dots, L_{i'a'}, L_{i'V_a}$ of three-dimensional vectors: $L_{i'}, L_{iV_i}, \dots, L_{i'a'}, L_{i'V_a}$ on the basic s_0 plane and symbols of $PK_m, PO_{V'}, PO_{K_m}$ and PV coordinate semiaxes the same as in Figure 1 and in the text.

The rule of choice is considered in this work, and the examples of using these equations for non-trivial data analysis in enzyme kinetics are given, namely:

- a) The cases, when the values of K_m^0 and V^0 parameters of initial reaction are absent
- b) The cases, when there is possibility to use other equations (similar in the form) for calculation of K_i and K_a constants and
- c) The cases, when equations for calculation of mono-parametrical constants of enzyme inhibition are used for calculation of bi-parametrical types of enzyme inhibition.

Materials and Methods

Calf alkaline phosphatase (EC 3.1.3.1.) - a preparation of Sigma (USA). Substrate: p-Nitrophenylphosphate - 2CHA salt (pNPP) - a preparation of Serva (Germany). Enzyme inhibitor: Sodium molybdate ($Na_2MoO_4 \cdot 2H_2O$) - a crystalline salt of high purity grade of domestic make. The cleavage of pNPP was recorded on a two-beam CF-4 DR spectrophotometer (Optica Milano, Italy). Reactions were carried out in 0.05M Tris-HCl buffer (pH 9.0) of ionic strength 0.1 by NaCl of high purity at constant mixing [1] in a thermostat at 37 °C. The curves of a course of reactions were registered by absorption increment ($+\Delta A_{400}$) of a solution containing the substrate,

enzyme and inhibitor against the solution of the same composition, but without the enzyme. The concentration of pNPP was changed $0.294 \cdot 10^{-4} - 0.98 \cdot 10^{-4} \text{M}$, the enzyme concentration was 1.96mg/ml (Figure 3A). The initial reaction rates (v) were determined by the slope angle of tangents to initial segments of curves of the course of a reaction in not less than 5 parallel experiments. The kinetic and parameters were calculated by plots in the $(v^{-1} S^{-1})$ coordinates

by Lineweaver-Burk using the program SigmaPlot, version 2000 (USA). The isolation of vacuolar polyphosphate hydrolase from *N. crassa* (EC 3.6.11) and the study of effect of arginine-containing activator (ArgA) on initial rates of P9 polyphosphate by this enzyme (Figure 3A) are given in [6]. Root-mean-square deviation at five-fold determination was: $v = \pm 2,5\%$, K_m and $V = \pm 7,5\%$, K_i and $K_a = \pm 10\%$.

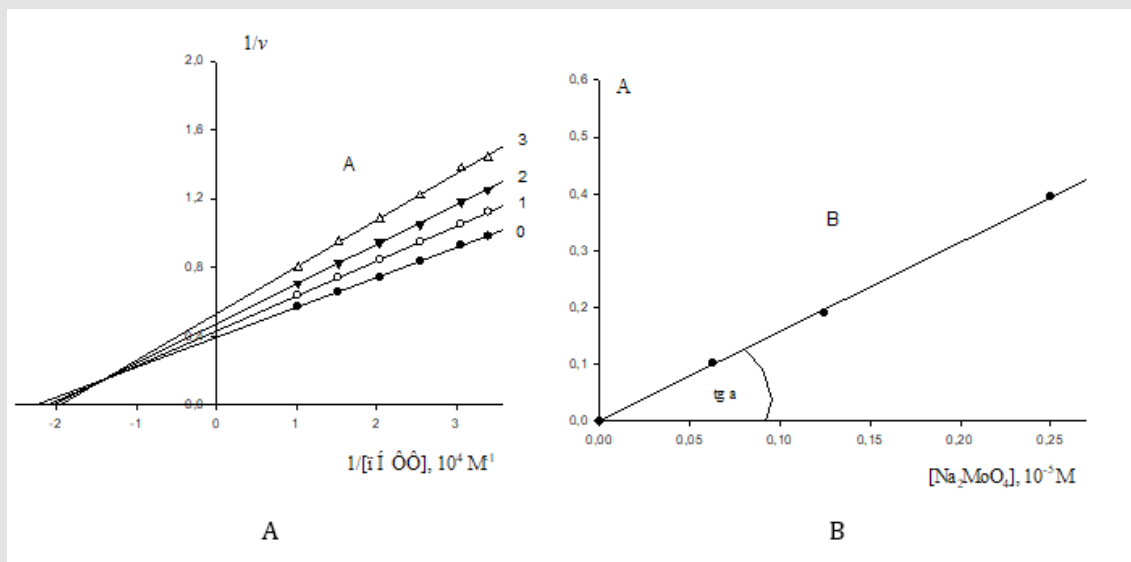


Figure 3:

A. Lineweaver-Burk plots of inhibitory effect of anions MoO_4^{2-} (10^{-5}M): 0.0625 – line 1; 0.125 – line 2 and 0.25 – line 3 on initial rates of pNPP by calf alkaline phosphatase. Line 0 – the inhibitor is absent. Designation v , $\text{mmol}/(\text{min} \times \text{per mg of enzyme})$.

B. Dependence of change in values of (A) denominator of Eq. (1) (Table 1) upon increasing concentrations of Na_2MoO_4 in coordinates (A; i). The concentration of Na_2MoO_4 (10^{-5}M): 0.0625, 0.125 and 0.25: 0.0625, 0.125 and 0.25, respectively.

Results and Discussion

Example 1

As seen in Table 1, the rule of choice of equations for calculation of constants of enzyme inhibition and activation presupposes the construction of experimental dependencies of change of v_i initial rates of inhibited (or activated v_a) reactions upon concentrations of substrate cleaved S obtained in the presence of inhibitor i (or activator a) relative to the same rates of v_o initial (uninhibited $i = 0$ and non-activated $a = 0$) reaction in the $v^{-1} S^{-1}$ coordinates. The type of reaction is determined by the position of obtained plots and according to the type – the equation for calculation of the respective constant. However, great difficulties arise in the following cases according to the forms of equations of Table 1, to calculate the constants of enzyme activation,

1) It is necessary to obtain the values of not only K_m and V parameters of activated (or inhibited) reaction, but also the values

of K_m^0 and V^0 parameters of initial (non-activated $a = 0$) reaction. It can evoke difficulties at using equations of such data analysis, because in some studies the values of K_m^0 and V^0 parameters are absent, for example, due to bad capability of the enzyme to cleave substrate in the absence of activator. Such cases are often found in laboratory practice [6-11], see, for example, the results of study of activating effect of arginine-containing activator ArgA on initial rates of P_9 polyphosphate cleavage by vacuolar polyphosphate hydrolase of *N. crassa* (Figure 3A). From these data it ease to see, that the values of K_m^0 and V^0 parameters of initial reaction in this case are not determined. In some other cases the values of K_m^0 and V^0 parameters of activated reactions there are ability to determine [12-14]. The same situation also occurs at calculation of K_i constants of enzyme inhibition, if the values of K_m^0 and V^0 parameters of initial reaction are not determined [8,15]. Let us examine Figures 3A & 3B devoted to study of enzyme inhibition by

calf alkaline phosphatase (EC 3.13.1.) by increasing concentrations of MoO_4^{2-} .

The values of K_m^0 and V^0 parameters were not determined in this case. According to the parametrical classification (Table 1, line1) the data of Figure 3A correspond to the, I_i , type of enzyme inhibition [2, 3]. Using Eq. (1 of Table 1), the values of constants of enzyme inhibition were calculated by each of 3 concentrations of MoO_4^{2-} and the average value of $K_{li} = 0.628 \times 10^{-5} M$ constant of alkaline phosphatase inhibition was estimated by the slope angle (tg a) of experimental line (Figure 3B) to the abscissa axis in the coordinates (A; i):

$$K_{li} = i / A = 1 / (A / i) = 1 / \text{tga}, \quad (1)$$

where (A) is the denominator of Eq. (1, Table 1). As easily seen in Figure 3B, the value of constants of alkaline phosphatase inhibition can also be calculated by any intervals of inhibitor concentrations, i.e. by the slope angle (tg a) to the abscissa axis of respective segments of the experimental line without introduction of additional symbols to K_m^i , K_m^0 , V^i и V^0 parameters of Eq. (1)

(Table 1), namely, by having determined the values of K_m^i and V^i parameters obtained, for example, by the 1st concentration of inhibitor $0.0625 \cdot 10^{-5} M$ and substituted them in Eq. (1) (instead of K_m^0 and V^0 parameters), and the values of K_m^i and V^i parameters obtained by the 2nd concentration of enzyme inhibitor $0.125 \cdot 10^{-5} M$ – instead of K_m^i and V^i parameters (already available in the equation). In this case, we shall obtain that for the interval of inhibitor concentrations $i_2 - i_1 = \Delta i = (0.1255 - 0.0625) \cdot 10^{-5} M = 0.0625 \cdot 10^{-5} M$

$$K_{li} = \frac{0.0625 \cdot 10^{-5} M}{\left(\frac{4,91 - 4,75}{4,75} + \left(\frac{2,33 - 2,13}{2,13} \right)^2 \right)^{0,5}} = 0.628 \cdot 10^{-5} M. \quad (2)$$

Yet, here it is more advisable to calculate the K_{li} constant of enzyme inhibition by the slope angle of the plot (Figure 3B) to the abscissa axis ($K_{li} = 0.6291 \cdot 10^{-5} M$). As seen in (the Figure 3B), the removal of the zero point ($K_m^0 = 0$ и $V^0 = 0$) on the plot in this case (the absence of really great deviation in the values of denominators of Eq. (1) (Table 1) will be not exhibited by any change of the slope angle of the plot to the abscissa axis.

Example 2

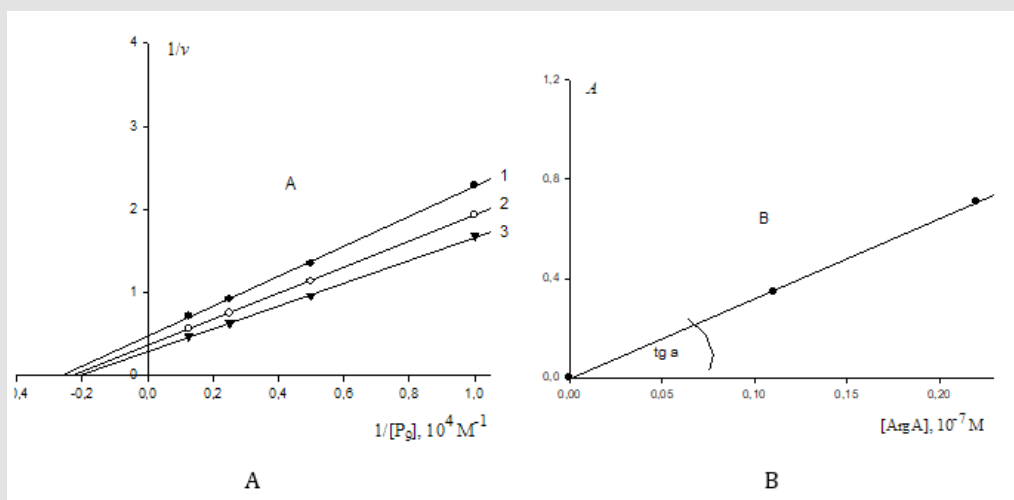


Figure 4:

A. Activating effect of ArgA on initial rates V_{Vla} of P_9 polyphosphate cleavage catalyzed by vacuolar polyphosphatase from *N. crassa*: lines 1, 2 and 3 – the concentration of ArgA is: $1.1 \mu M$ – line 1; $2.2 \mu M$ – line 2 and $3.3 \mu M$ – line 3. Designation: $v - \mu E/min$.

B. Dependence of change in the A denominators of Eq. (6) (Table 1) upon increasing concentrations of ArgA in the coordinates (A;). The intervals of ArgA concentrations are $1.1 \mu M$ and $2.2 \mu M$, respectively.

Use of this technique (Example 1) to data analysis (Figure 4A), which now taking into account the above-said can be referred to the V_{Ia} type of polyphosphate hydrolase activation – leads to calculation of the following values of the constants of enzyme

activation (Eq. 6, Table 1): $K_{Vla} = 3.182 (\mu M)$ – by the interval ArgA ($2.2 - 1.1 = 1,1 \mu M$) and $K_{Vla} = 3.103 \mu M$ – by the interval ArgA ($3.3 - 1.1 = 2.2 \mu M$). The construction of dependencies of A denominators

(Eq. 6) upon the intervals of ArgA concentrations in the coordinates (A, Δa) (Figure 4B), where the slope angle (tg a) of the plot to the abscissa axis according to Eq. (6, Table 1) is connected with the value of K_{IIa} constant of enzyme activation by a ratio:

$$K_{II} = a / A = 1(A / a) = 1 / \text{tga} \quad (3)$$

Bearing in mind that the parameter b(1) of the computing program Statistics (SigmaPlot, version 2000) characterizes the value of the same slope angle (tg a) of the plot (Figure 4B) to the abscissa axis, one can calculate the value of the target constant of enzyme activation by a ratio:

$$K_{II} = 1 / b(1) = 1 / 3.2227(\mu M)^{-1} = 0.3103 \mu M. \quad (4)$$

Example 3

Calculation of constant activation. The activating effect of Guanosine (Guo) on canine alkaline phosphatase (Figure 5) shows that in the presence of $1 \times 10^{-3} M$ Guo the parameters of initial reaction of pNPP cleavage, i. e. = $4.69 \times 10^{-5} M$, $V^0 = 2.921 \text{ mmol/min per mg protein}$, change as follows: $K_m' = 5.67 \cdot 10^{-5} M$, $V = 3.3527 \text{ mmol/min}$

per mg protein. This corresponds to the II_a type of an associative enzyme activation. Hence, to calculate the constant of enzyme activation, one should use Eq. (14, Table 1). Substitution of the obtained values of parameters in this equation allows calculation of this constant of enzyme activation:

$$K_{IIa} = a / \left(\left(\frac{K_m' - K_m^0}{K_m^0} \right)^2 + \left(\frac{V - V^0}{V^0} \right)^2 \right)^{0.5} = 10^{-3} / \sqrt{0.0655} = 3.91 \cdot 10^{-3} M. \quad (5)$$

Substitution of the: $K_{IIi} = 4.785 \cdot 10^{-3} M$, $K_{IIa} = 6.76 \cdot 10^{-3} M$ parameters of this experiment (Figure 5) in (Eq. 14, [16]), result in to:

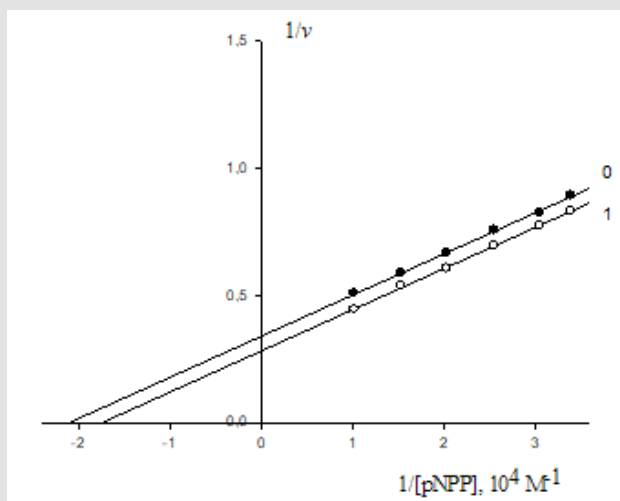
$$K_{IIa} = \left(\frac{6.76^2 \cdot 4.785^2}{6.76^2 + 4.785^2} \right)^{0.5} = (15.254)^{0.5} = 3.906 \cdot 10^{-3} M \quad (6)$$

substitution in (Eq. 6), rewritten to the form:

$$\left(\frac{1}{K_{IIa}} \right)^2 = \left(\frac{1}{K_{IIa}} \right)^2 + \left(\frac{1}{K_{IIi}} \right)^2 = \left(\frac{1}{22.896} + \frac{1}{45.698} \right) = (0.0656 \cdot 10^6 M^{-2})^{0.5} \quad (7)$$

result in to the same value of activation constant:

$$K_{IIa} = \frac{1}{\sqrt{0.0656 \cdot 10^6 M^2}} = \frac{1}{0.2561} \cdot 10^{-3} M = 3.90410^{-3} M. \quad (8)$$



Note: line 1 - the concentration of Guo is $1 \cdot 10^{-3} M$; line (0) - the activator is absent.

Figure 5: Activating effect of Guo on the initial rate V_0 , $\mu\text{mol/min per } \mu\text{g}$ protein of pNPP cleavage by canine alkaline phosphatase.

From the length parts of equations: (6) и (7) may to see that all they obeys to the signs of Pifagor's theorem and this may be used as for calculation any of the three constants by the two others known already and for correction the constants, determined by using any other equations. For example for calculation any of the third constants by the two others known already, or for correction the constants, determined by using any other equations. This extremely convenient in many other cases. Namely, from (Eq. 8) it follows that:

$$K_{IIi} = \left(\frac{K_{IIi}^2 \cdot K_{IIa}^2}{K_{IIi}^2 - K_{IIa}^2} \right)^{0.5} \quad (9)$$

Having substituting the all necessary parameters in Eq. (9), we will become that,

$$K_{IIi} = \left(\frac{45.7 \cdot 15.24}{45.7 - 15.24} \right)^{0.5} = \left(\frac{696.52}{30.46} \right)^{0.5} = (22.75)^{0.5} = 4.78210^{-3} M \quad (10)$$

and as it was to be expected, this result in to the same value of constant ($K_{IVi} = 4.785 \cdot 10^{-3}M$). But by use $K_{IIIa} = 6.76 \cdot 10^{-3}M$, (consider that $K'_m = K_m^0$) [17-21] $K_{IVi} = 4.785 \cdot 10^{-3}M$ (consider that $V' = V^0$) [21-23], or we shall become $K_{IVi} / K_{IIa} = 4.785/3.904$, more than 22%; $K_{IIIa} / K_{IIa} = 6.76/3.904$ more than 72%.

Discussion

As easily to see by comparison of Eqs. (4, 1 and 5) (Table 1) that the value of K_{IVi} constant of enzyme inhibition can be estimated not only using Eq. (4), but also by Eq. (1) and Eq. (5 of Table 1), which (if the ratio of parameters $K'_m = K_m^0$) will be simplified to Eq. (4). To explain the above situation, it is convenient to consider Figure 2, where the positions of $L_{IV'}$, L_{IV} and L_{VI} projections of respective vectors of reaction under study on the basic s_0 plane of Figure 1 are given. As seen in Figure 2, the $K'_m = K_m^0$ projection of L_{IV} of vector and L_{IV} projection of L_{VI} of vector will occupy the place of L_{IVi} projection of L_{IVi} vector of inhibited reaction at the ratio of parameters ..., i.e. the mono-parametrical, IV_i type, of

enzyme inhibition is transient between I_i and V_i bi-parametrical types of enzyme inhibition. Evidently use of Eqs. (1 or 5 of Table 1) for calculation of the constant of enzyme inhibition will lead to correct calculation of their values. It is not recommended to make such substitution of equations due to the following reasons:

- 1) Substitution of Eq. (4) by Eqs. (1 or 5) will not simplify the calculation of K_{IVi} constant, but
- 2) The form of equation and the symbol of constant, if not corrected, may disorient the reader and orient to choose type IV_i instead type I_i of enzyme inhibition.

It is analogous in the case of using the other equations for calculation of K_{Ia} and K_{IIa} , K_{Va} , K_{VIIa} and K_{VIIIa} bi-parametrical constants activation: see Eqs. (15, 14, 11, 10 and 9 of Tables 1 & 2) and the positions of respective bi-parametrical: L_{Ia} , L_{IIa} , L_{Va} ... projections of three-dimensional L_{Ia} , L_{IIa} , L_{Va} ... vectors relatively to L_{IVa} , L_{IIIa} , L_{VI} and L_{VII} projections of (two-parametrical L_{IVa} , L_{IIIa} , L_{VI} and L_{VII} vectors) among their surroundings (Figures 1 & 2).

Table 2: Equations for calculation of the K_i and K_a constants.

Type of effect	New name of the types of enzymatic reactions	Traditional name	Corrected equation for calculation of the K_i and K_a constants
I_i	Bi-parametrically coordinated inhibition	Mixed Inhibition	$K_I = i / \left(\left(\frac{K'_m - K_m^0}{K_m^0} \right)^2 + \left(\frac{V^0 - V'}{V'} \right)^2 \right)^{0.5}$
	Un associative Inhibition	Uncompetitive Inhibition	$K_{III} = i / \left(\left(\frac{K_m^0 - K'_m}{K'_m} \right)^2 + \left(\frac{V^0 - V'}{V'} \right)^2 \right)^{0.5}$
III_i	Catalytic Inhibition	Noncompetitive Inhibition	$K_{IIIi} = \frac{i}{V^0 / V' - 1}$
IV_i	Associative Inhibition	Competitive Inhibition	$K_{IVi} = \frac{i}{K'_m / K_m^0 - 1}$
V_i	Pseudo inhibition		$K_V = i / \left(\left(\frac{K'_m - K_m^0}{K_m^0} \right)^2 + \left(\frac{V' - V^0}{V^0} \right)^2 \right)^{0.5}$
V_i	Dis coordinated Inhibition		$K_{VII} = i / \left(\left(\frac{K_m^0 - K'_m}{K'_m} \right)^2 + \left(\frac{V^0 - V'}{V'} \right)^2 \right)^{0.5}$
VII_i	Transient Inhibition		$K_{VIIi} = i / \left(\left(\frac{K_m^0 - K'_m}{K'_m} \right)^2 + \left(\frac{V^0 - V'}{V'} \right)^2 \right)^{0.5}$

I_0	Initial (uninhibited $i = 0$ and non-activated $a = 0$) enzymatic reaction		
VII_a	Transient Activation		$K_{VIIa} = a / \left(\left(\frac{K'_m - K_m^0}{K_m^0} \right)^2 + \left(\frac{V' - V^0}{V^0} \right)^2 \right)^{0.5}$
V_a	Dis coordinated Activation		$K_{Va} = a / \left(\left(\frac{K'_m - K_m^0}{K_m^0} \right)^2 + \left(\frac{V' - V^0}{V^0} \right)^2 \right)^{0.5}$
V_a	Pseudo activation		$K_{\tilde{v}} = a / \left(\left(\frac{K_m^0 - K'_m}{K'_m} \right)^2 + \left(\frac{V^0 - V'}{V'} \right)^2 \right)^{0.5}$
IV_a	Associative Activation	Competitive Activation	$K_{IVa} = \frac{a}{K_m^0 / K'_m - 1}$
III_a	Catalytic Activation	Noncompetitive Activation	$K_{IIIa} = \frac{a}{V' / V^0 - 1}$
I_a	Unassociative Activation	Uncompetitive Activation	$K_{Ia} = a / \left(\left(\frac{K'_m - K_m^0}{K_m^0} \right)^2 + \left(\frac{V' - V^0}{V^0} \right)^2 \right)^{0.5}$
I_a	Bi-Parametrically Coordinated Activation*	Mixed Activation	$K_{\tilde{i}} = a / \left(\left(\frac{K_m^0 - K'_m}{K'_m} \right)^2 + \left(\frac{V' - V^0}{V^0} \right)^2 \right)^{0.5}$

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