

TABLE II

*Variables and parameters of the activation model of phototransduction*

In the definition of  $t_{\text{eff}}$ ,  $t_{\text{R}}$ ,  $t_{\text{G}}$  and  $t_{\text{P}}$  are delays associated with Rh\*, G\* and PDE\* production respectively;  $t_r$  is a possible delay associated with radial cGMP equilibration;  $t_{\text{chan}}$  is a delay in cGMP channel closure. The symbol  $t_{\text{eff}}$  is defined somewhat differently in Ref. 112, where it is used to refer solely to the first three delay steps. In cases where the electrical recording technique does not voltage-clamp the photoreceptor, an additional delay,  $t_{\text{m}}$  is contributed by the membrane time constant.

Symbol	Description	Unit <sup>b</sup>	Typical value or range in rods	
			amphibian	mammalian (approximate)
<b>Variables<sup>a</sup></b>				
$\Phi$	Number of photoisomerizations produced by a brief flash (at $t = 0$ )	-		
$f_{\Phi}$	Fraction of photopigment isomerized by a brief flash	-		
$Rh^*(t)$	Number of photoactivated rhodopsin molecules per outer segment	-		
$G^*(t)$	Number of activated G-protein molecules per outer segment	-		
$PDE^*(t)$	Number of activated PDE catalytic subunits per outer segment	-		
$cG(t)$	Concentration of free cGMP in the outer segment	$\mu\text{M}$	0.5-4	0.5-4
$F(t)$	cGMP-activated current as fraction of resting (dark) level	-	0-1	0-1
$R(t)$	$1 - F(t)$ ; normalized photoresponse			
<b>Parameters</b>				
$\nu_{\text{RG}}$	Rate of production of G* by a single Rh*	$\text{s}^{-1}$	4000	12500
$\nu_{\text{enc}}$	2-d diffusion limit to $\nu_{\text{RG}}$ ; Eqn. 2	$\text{s}^{-1}$	7000	17000
$c_{\text{GP}}$	Coupling gain of the activation of PDE* by G*	-	0.8-0.9	0.8-0.9
$\nu_{\text{RP}}$	$c_{\text{GP}}\nu_{\text{RG}}$ ; Rate of production of PDE* due to a single Rh*	$\text{s}^{-1}$	3500	10000
$V_{\text{cyto}}$	Volume of the outer segment cytoplasm	pl	1.0	0.04
$2k_{\text{cat}}$	turnover number of PDE with two fully activated catalytic subunits	$\text{s}^{-1}$	2000	4000
$K_{\text{m}}$	Michaelis constant of fully activated PDE	$\mu\text{M}$	150	100
$BP$	Buffering power of the cytoplasm for cGMP	-	1-2	1-2
$\beta_{\text{sub}}$	Rate constant of a single catalytic subunit of PDE in a well-stirred volume equal to $V_{\text{cyto}}$ ; Eqn. 12	$\text{s}^{-1}$	$6 \cdot 10^{-6}$	$4 \cdot 10^{-4}$
$n$	Hill coefficient of opening of the cGMP-activated channel	-	3	3
$A$	$\nu_{\text{RP}}\beta_{\text{sub}}n$ ; Amplification constant; eqns (20) and (21)	$\text{s}^{-2}$	0.08	12.0
$t_{\text{eff}}$	$t_{\text{R}} + t_{\text{G}} + t_{\text{P}} + t_r + t_{\text{chan}}$ ; Effective delay time	ms	15-25	2-5
$t'_{\text{eff}}$	$t_{\text{eff}} + t_{\text{m}}$ (unclamped cells) + uncorrected delay in signal processing	ms		

<sup>a</sup> Italicized symbols are used throughout to refer to *variables* or parameters specified by the model; Roman symbols (e.g., Rh\*) refer to the individual protein entities.

<sup>b</sup> '-' as a table entry in this column indicates a dimensionless quantity.