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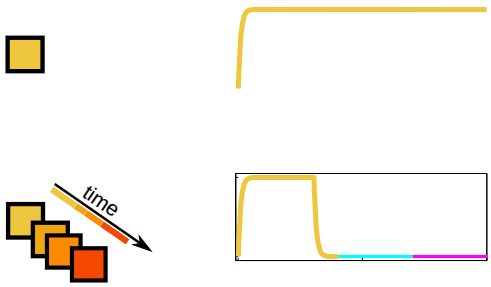
2012). I ; ta t , the te. ; a atte; f the ti. . . -

. **1** Va ; iab e a d a ; a . ete ; ₍ ith thei ; defa . t a . e

S . b	De c ; i ti
Va ; iab e	
I_j	E te ; a ti . . . f ; e citat ; . ati j
u_j	N -di . e i a fi ; i g ; ate f e citat ; . ati j (. a i . . . $u_j = 1$)
v	N -di . e i a fi ; i g ; ate f g ba i hibit ; . ati (. a i . . . $v = 1$)
p_j	Le e f facilitati f a e f ; . . ati j (ba e i e $p_j = 1$)
w_{jk}, w	St ; e gth f e citati f ; . ati k t e citat ; . ati j
T_j, T	D ; ati f ti . . .
Ti . e a ; a . ete ; (defa . t a . e i a ; e the i)	
τ	Ti . e ca e f e ; a fi ; i g (10 . ^{6})
τ_f	Ti . e ca e f h ; t te ; . facilitati (1 ^{4})
τ_w	Ti . e ca e f ea ; i g ; . e (150 ^{1})
τ_a	Ti . e ca e f ada tati (400 . ^{5})
τ_s	Ti . e ca e f a tic i . t f ; . the ; . ati (50 . ^{6})
T_{cue}	D ; ati f ti . . . t t ; igge ; e a (50 . ^{2,3})
D	De a i ; e a tic fi ; i g affecti g c ecti bet ₍ ee . ati (30 . ^{1})
D'	De a i ; e a tic fi ; i g affecti g c ecti ₍ ithi . ati (20 . ^{1})
Othe ; a ; a . ete ; (defa . t a . e i a ; e the i)	
ϕ	Fi ; i g ; ate ; e e f . cti (Hea i ide te f . cti)
θ	Th ; e h d f ; acti ati f e citat ; . ati (0.5)
θ_v	Th ; e h d f ; acti ati f i hibit ; . ati (0.5)
p_{max}	Ma i . . . e e f h ; t te ; . facilitati (2)
Z_k	St ; e gth f e citati f ; . ati k t i hibit ; . ati (0.3)
L	Weight f g ba i hibiti (0.6)
b	St ; e gth f ada tati (1)
M	Lea ; i g ; . e th ; e h d (1)
w_{max}	Ma i . . . a tic ₍ eight bet ₍ ee . ati (0.4852)
w'_{max}	Ma i . . . a tic ₍ eight ₍ ithi . ati (4.1312)
w_{min}	Mi i . . . a tic ₍ eight ₍ ithi . ati (1.3488)
γ_d	St ; e gth f LTD0 6.4598999 194.03999328 369.368985f h hh

a . . ti i. ified the a a i , b. t a t ece a;


time

2.

T g a; a tee that g te; . a ticit ead t a ; e; e c di g f e e t ti. e , it i ece a; that the ea; ed eight, w_{21}^{∞} gi e b E . (6), . atche the de i; ed eight $\mathcal{W}(T)$ gi e b E . (9). Thi ca be achie ed b e . ati g the ; ight ha d ide f E . (6) a d (9), that

(1

(Ke te; et a . 1999; Pfi te; a d Ge; t e; 2006; C ath et a . 2010).

T de t; ate h the ti i g f e e t ca be e c ded i the et ; a; chitect . ; e, e ta; t ith t ati (Fig. 2). D . ; i g t; ai i g, ati 1 a ti . ated f ; T_1 ec d f ed b ti . ati f ati 2 (Fig. 2a). The ti . . a t; g e . gh t d . iate the d a . - ic f the ati ; e e (Secti 2). Whi e the fi; t ti . . a ; e e t, ati 1 a acti e a d LTD d . i ated, dec; ea i g the a tic eight, w_{21}, f; . . - ati 1 t ati 2. Afte; T_1 ec d , the fi; t ti . . e ded, a d the ec d ati a acti ated. H e e;, ati 1 did t bec . e i acti e i ta ta e . , a d f ; . e ti e b th ati 1 a d 2 e; e acti e. D . ; i g thi e; a i d , LTP d . i ated eadi g t a i c; ea e i a tic eight w_{21}. Sh ; t afte; ati 1 beca e i acti e, cha ge i the eight w_{21} cea ed, a a ticit cc . ; he the ; e a tic ati i acti e. The i i- tia a d fi a a tic eight (w_{21}^0 a d w_{21}^1, ; e ecti e) ca be c . . ted i c ed f ; . (Secti 2). Re eated ; e e tati f the t; ai i g e . e ce ead t e . e - tia c e; ge ce f the a tic eight , w_{21}^i (eight afte; *i* th t; ai i g t; ia), t a fi ed a . e (Fig. 2b). O the the; ha d, the a tic eight w_{12} i ea e ed d ; i g each t; ia beca e the ; e a tic ati 2 i a a acti e afte; the t a tic ati 1 (Secti 2). I the ca e f N ati , each eight $w_{k+1,k}$ i c e; ge t a e; a . e a ciated ith T_k, he; ea a the; eight i bec . e eg igib e d ; i g ; e a . Th , the et ; t; . ct ; e e e t . a e c de the ; de; f the e . e ce.

The d ; ati f acti ati i ati 1, T_1, dete; . i e the e . i ib; i . a . e f the a tic eight f; . a- ti 1 t ati 2, w_{21}^{∞} (Secti 2). F ; a; ge; a . e f T_1, LTD a t ge; , ea e i g w_{21} (Fig. 2c). He ce,

; ed a . echa i . f ; ti. e- ee i g (B. . a 2000; D. ; te it 2003; Re. ti. a et a . 2004; Ka . a; a; a d B. . a 2007; Ga ; i et a . 2009). With . t ch a ; ce , c. ed acti it . d ; e . t i a e . e ce ; e a ed i the ; e; de; , b. t i f ; . ati ab . t e e t ti. i g . d be t.

F ; i. icit e f c. t . ati , he; e acti - it f the fi; t . ati ; e ; e e t a ti. ed e e t (Fig. 3). T i. if the a a i , e a a . . ed that a tic eight a; e fi. ed d. ; i g ; e a . Thi a . . ti i t e e tia (Secti 4.4). Afte; . ati l i acti ated ith a b; ief c. e, it ; e. ai acti e d. e t ; ec. ; ; e t e. citati (Secti 2

(i g 20,000 i itia w^0). The a tic $_{V_i}$ eight afte; the *i*th t; ai i g, w_{21}^{i}, i de c; ibed b a ; babi it de it f. c- ti that c e; ge i the i. it f . a t; ai i g t; ia . The ea (. de) f thi di t; ib. ti i the . t i e a . e f the ea; ed a tic $_{V_i}$ eight afte; ; e eated ; e e tati f the e . e ce (Fig. 5c). The a; ia ce f the ea; ed a - tic $_{V_i}$ eight, w_{21}^{∞},

a e ; a ati , ca a the ; e f a , ti. e t ; ac - i g ; ce (Be da a d He ; 2003), i tead f h ; t te ; . faci itati . I c t ; a t t the ca e f h ; t te ; . faci itati , ada tati ca e the effecti e i . t f ; e ati t dec ; ea e e ; ti. e.

I thi ca e ati acti it a de ed b

$$\tau \frac{du_j}{dt} = -u_j + \phi(w_{jj}u_j + s_j - \theta - Lv - a_j),$$

$$\tau_a \frac{da_j}{dt} = -a_j + bu_j,$$

$$\tau_s \frac{ds_j}{dt} = -s_j + \sum_{k \neq j} w_{jk}u_k,$$

$$\tau \frac{dv}{dt} = -v + \phi\left(\sum_{k=1}^{N} Z_k u_k - \theta_v\right),$$

he e a_j de te the ada tati e e f ati j, τ_a i the ti. e ca e f ada tati , a d b i the ada tati t ; e gth. Feedbac bet ee ati a a . ed t be e ; tha feedbac ithi a ati ; th , the t ta i . t f ; ati j a it i t e f-e citati $(w_{jj}u_j)$, a d a tic i . t f ; the ; ati (s_j) ich e ed the ti. e ca e τ_s. N te that i the i. it $\tau_s \to 0$, a e a ; e i ta ta e . .

F ; a itab e ch ice f a ; a. ete ; , g ba i hibiti t ; ac acti it fa te ; tha e citati bet ee ati . The , he a ati bec e i acti e d e t ada - tati , the e e f g ba i hibiti dec ; ea e , a ig . b e . e t ati t bec . e acti e. Thi . ea the eight f e f e citati ca e c de ti. i g. Th , i thi et e . de ed g te ; . a ticit ithi a ati a e . The ea ; i g ; . e f ; w_{jj} a a a g . t w_{jk} ith the additi a a . . ti that i ce w_{jj} ; e ; e e ted the a tic eight ithi a ati , it c d t dec ; ea e be a ce ; tai a . e w_{min}. A , the a ; a. ete ; f ; g te ; . a ticit ithi a ati a ; e a ed t be dif- fe ; e t f ; . the a ; a. ete ; f ; g te ; . a ticit bet ee ati .

The ea ; i g ; . e a the

$$\tau_w \frac{dw_{jj}}{dt} = -\gamma'_d(w_{jj} - w_{min})u_j(t - D')(1 - u_j(t)) - \gamma'_p(w_{jj} - w'_{max})u_j(t - D')u_j(t).$$

Whe the ati a acti ated ($u_1(t) \approx 1$) f ; $t \in [0, T_1]$ (Fig. 7a), the cha ge i the eight w_{11} e ; e g e ; ed b the iece i e diffe ; e tia e ati

$$\frac{dw_{11}}{dt} = \begin{cases} 0, & t \notin [D', T_1 + D'] \\ \frac{\gamma'_p}{\tau_w}(w'_{max} - w_{11}) & t \in [D', T_1] \\ -\frac{\gamma'_d}{\tau_w}(w_{11} - w_{min}) & t \in [T_1, T_1 + D']. \end{cases}$$

The f i g e ati ; e ate the a tic eight at the e d f a ; e e tati , $w_{11}(T_{tot})$, t the a tic eight at the begi i g f the ; e e tati , $w_{11}(0)$:

$$w_{11}(T_{tot}) = w_{11}(0)e^{-T_1\gamma'_p/\tau_w}e^{(\gamma'_p - \gamma'_d)D'/\tau_w} + w'_{max}e^{-D'\gamma'_d/\tau_w}(1 - e^{-(T}$$

Thi ea; i g ; ce i di ti ct f; . the a ; ach . t i ed i (B. . a a d Maa 2009; He e . i et a . 2014), i ce it e t; ai the; ec. ;; e t a; chitect. ; e bet ee - . ati e c di g ti. e; t. i g f a d t; ea. ; ead . t i . ece a; .

.4 f

The; e i a a; ge et f a; a. ete; f ; hich the et ; ca

t cc. ; . Thi a . . e the; e i . e e.te; a ig a i dicati g h acc. ; ate the e . e ce i bei g ; e a ed. F ; i ta ce, h . a e; f ; . a ce f a iece f . . ic ; e ie

F . ; ca. d-T; c. e, N., Ha e , D., Va V; ee v ij , C., & B; . e , N. (2003). H v i e ge e; ati . echa i . dete; . i e the e. - ; a ; e e t f . ct. ati g i . t . *The Journal of Neuroscience*, *23*(37), 11,628 11,640.

Ga; di e; , C.W. (2004). *Handbook of stochastic methods*. Be; i : S ; i ge; .

Ga ; i , J.P., & Bea; , M.F. (2014). Lea; ed ati te. ; a e . e ce ; ec g iti a d ; edicti i ; i. a; i . a c ; te . . *Nature Neuroscience*, *17*(5), 732 737.

Ga ; i , J.P., Sh e; , M.G.H., L e v e tei , Y., Bea; , M.F., & Sh . - a , H.Z. (2009). Lea; i g; e v a; d ti i g i c ; te. th; gh; e v a; d de e de t e . ; e i f a tic a ticit . *Proceedings of the National Academy of Sciences of the United States of America*, *106*(16), 6826 6831.

Ge; t e; , W., & Ki t e; , W.M. (2002). Mathe. atica f ; . . a-

M ;; e, M.C., R , J., & B. ;; , D. (2005). Saccadic e e. e t ca e c . ; e i f ti. e a e a ace. *Nature Neuroscience*, *8*(7), 950 4.

Naba i, S., F , R., P; . , C.D., Li , J.Y., T ie , R.Y., & Ma i , R. (2014). E gi ee; i g a. e. ; ith td a d t . *Nature*, *511*(7509), 348 52.

Oh, M.C., De; ach, V.A., G. i; e, E.S., & S de; i g, T.R. (2006). E t; a a tic. e. b; a e t; affic i g; eg ated b g . ; l e; i e 845 h h ; ati ; i. e a. a; ece t ; f ; g-te; . te tiati . *The Journal of Biological Chemistry*, *281*(2), 752 8.

Oja, E. (1982). Si. ified e. ; . de a a ; i ci a c . e t a a e; . *Journal of Mathematical Biology*, *15*(3), 267 273.

Pe; i , R., Be; ge; , T.K., & Ma; ; a , H. (2011). A a tic ; ga i i g ; i ci e f ; c ; tica e. ; a g; . . *Proceedings of the National Academy of Sciences of the United States of America*, *108*(13), 5419 5424.

Pfi te; , J.P., & Ge; t e; , W. (2006). T; i et f i e i a . de f i e ti. i g-de e de t a ticit . *The Journal of Neuroscience*, *26*(38), 9673 9682.

Pf ; d; e he; , P.Q. (2003). A. dit ; feedbac i . . ic e; f ; . a ce: E ide ce f ; a di ciati f e . ci g a d ti. i g. *Journal of Experimental Psychology: Human Perception and Performance*, *29*(5), 949.

Phi t, B.D., Se ha; , A.K., Sh . a , H.Z., & Bea; , M.F. (2001). Vi . a e. e; ie ce a d de ; i ati bidi; ecti a . dif the c . - iti a d f. cti f NMDA; ece t ; i i . a c ; te . . *Neuron*, *29*(1), 157 169.

P ; i i, C., Na d, R., Me i, S., & Ge; t e; , W. (2013). Te. ; a hite i g b e; - a ada tati i e c ; tica e. ; . . *Nature Neuroscience*, *16*(7), 942 948.

Ra , R.P., & Sej i, T.J. (2001). S i e-ti. i g-de e de t hebbia a ticit a te. ; a diffe; e ce ea; i g. *Neural Computation*, *13*(10), 2221 2237.

Re. ti. a , J., Ya e , V., F i, S., & Se , W. (2004). C i. bi g e. ; a acti it a a e e t-ba ed c ; tica ; e ; e e tati f ti. e. *The Journal of Neuroscience*, *24*(13), 3295 3303.

Sa ai, K., Hi a a, O., Mi a chi, S., Ta i , R., Sa a i, Y., & P. t , B. (1998). T; a iti f b; ai acti ati f; . f; ta t a; ieta a; ea i i . . t ; e . e ce ea; i g. *The Journal of Neuroscience*, *18*(5), 1827 1840.

Shea-B; , E., Ri e , J., Ra iti , B.C., & Ma a a i, C. (2006). A fi; i g; ate . de f a; i ia deficit i i te; a ti. i g. *Brain Research*, *1070*(1), 189 201.

Sh e; , M.G., & Bea; , M.F. (2006). Re a d ti. i g i the ; i a; i . a c ; te . . *Science*, *311*(5767), 1606 1609.

Si e , P., Ba ci, F., C he , J.D., & H . e , P., et a . (2011). A . de f i te; a ti. i g b e. ; a i teg; ati . *Philosophical Transactions of the Royal Society B*, *31*(25), 9238 9253.

Sj t; . , P.J., T. ;; igia , G.G., & Ne , S.B. (2001). Rate, ti. i g, a d c e; ati it j i t dete; . i e c ; tica a tic a ticit . *Neuron*, *32*(6), 1149 1164.

S g, S., Sj t; . , P.J., Reig , M., Ne , S., & Ch ii, D.B. (2005). High ; a d feat. ; e f a tic c ecti it i ca c ; tica ci; c it . *PLoS Biology*, *3*(3), e68.

Ta e chi, T., D ie ic , A.J., & M ;; i , R.G. (2014). The a - tic a ticit a d . e. ; h the i : e c di g, t ; age a d