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Do Neocortical Pyramidal Neurons Display Stochastic Resonance?

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Abstract. Neocortical pyramidal neurons in vivo are subject to an intense synaptic background activity that has a significant impact on various electrophysiological properties and dendritic integration. Using detailed biophysical models of a morphologically reconstructed neocortical pyramidal neuron, in which synaptic background activity was simulated according to recent measurements in cat parietal cortex in vivo, we show that the responsiveness of the cell to additional periodic subthreshold stimuli can be significantly enhanced through mechanisms similar to stochastic resonance. We compare several paradigms leading to stochastic resonance-like behavior, such as varying the strength or the correlation in the background activity. A new type of resonance-like behavior was obtained when the correlation was varied, in which case the responsiveness is sensitive to the statistics rather than the strength of the noise. We suggest that this type of resonance may be relevant to information processing in the cerebral cortex.

Keywords: cerebral cortex, synaptic background activity, neocortex, noise, computational models

1. Introduction

Over the last two decades, phenomena like the amplification of weak signals or the improvement of signal detection and reliability of information transfer in nonlinear dynamical systems in the presence of a certain nonzero noise level were subject of an increasing number of theoretical and experimental investigations. They became well known and are now well established under the term *stochastic resonance* (SR). Since its first appearance as a possible explanation of the periodicity of Earth's ice ages (Benzi et al., 1981; Nicolis, 1982), SR has shown to be an inherit property of many physical, chemical and biological systems. For a comprehensive review and up-to-date summary of the basic theoretical principles underlying SR, experimental verifications, and applications, we refer to Gammaitoni et al. (1998) and references therein.

Neurons provide particularly favorable conditions for displaying SR—namely, they are strongly excitable and nonlinear, and often they are subject to noisy environments. Indeed, evidence for SR was found in neurons, both theoretically (e.g., Bezrukov and Vodyanoy, 1997; Bulsara et al., 1991; Capurro et al., 1998; Chow et al., 1998; Huber et al., 1998; Lee et al., 1998; Lee and Kim, 1999; Longtin, 1993; Longtin and Chialvo, 1998; Mar et al., 1999; Mato, 1998; Neiman et al., 1999a, 1999b; Shimokawa et al., 1999; Wang et al., 1998; Wiesenfeld and Moss, 1995) and experimentally (e.g., Chialvo and Apkarian, 1993; Collins et al., 1995, 1996; Denk and Webb, 1989; Douglas et al., 1993; Ivey et al., 1998; Jaramillo and Wiesenfeld, 1998; Levin and Miller, 1996; Pei et al., 1996; Richardson et al.,

1998; [illegible], 1997; [illegible] 1999). [illegible] fi- [illegible] CA1 [illegible] 2000). [illegible] fi[illegible] (C[illegible] 1997; [illegible], 1996; [illegible] 1995b; [illegible] 1998; [illegible] 1994), [illegible]

[illegible] (C[illegible] 1967; D[illegible] 1992; [illegible], 1974; [illegible] 1965). [illegible] fi[illegible] 5 to 20 [illegible] (E[illegible] 1964; [illegible] 1959; [illegible], 1988; [illegible] 1978; [illegible], 2001), [illegible] fl[illegible] (e.g. A[illegible] 1999; C[illegible], 1996; D[illegible] P[illegible] é, 1999; H[illegible] D[illegible] 2000; [illegible], 1999; [illegible], 1988; [illegible], 1997; P[illegible] é [illegible], 1998). [illegible] fl[illegible] (D[illegible] P[illegible] é, 1999; P[illegible] é [illegible], 1998). [illegible] "[illegible]" ([illegible]

[illegible] ([illegible] D[illegible] 2000).

2. Methods

2.1. Model Settings

C[illegible] a [illegible] (Fig. 1A) [illegible] (C[illegible], 1997). [illegible] 45% [illegible] (D[illegible] F[illegible] 1992). [illegible] (D[illegible] P[illegible] é, 1999).

F[illegible] (I_{Na}, [illegible] fi[illegible] I_{Kd} [illegible] V_m-[illegible] I_M) [illegible] (H[illegible] 2). [illegible] (H[illegible] 1991) [illegible] 10 [illegible], 1988). [illegible] a_{dc}. [illegible] a [illegible] $a_{dc} = 0.4$, [illegible] ("[illegible]") [illegible] $a_{dc} = 0.7$, [illegible] ([illegible] 1995a), [illegible] $a_{dc} = 1$). [illegible] Ca^{2+}-[illegible] (C-[illegible] I_{KCa} ([illegible], 1989; [illegible] 1 [illegible]$^{-2}$), [illegible] Ca^{2+}-[illegible]

Table 1. [illegible] E_{rev}, [illegible] R_{in}, [illegible] g_{L}, [illegible] C [illegible]

g_{L} = 0.02 mS cm^{-2}	C_{m} = 0.04 μF cm^{-2}	E_{L} = −80 mV
g_{Lm} = 4.52 · 10^{-5} mS cm^{-2}	C_{m} = 1.449 μF cm^{-2}	R_{i} = 250 Ωcm
g_{Ld} = 6.5495 · 10^{-5} mS cm^{-2}	C_{d} = 1 μF cm^{-2}	

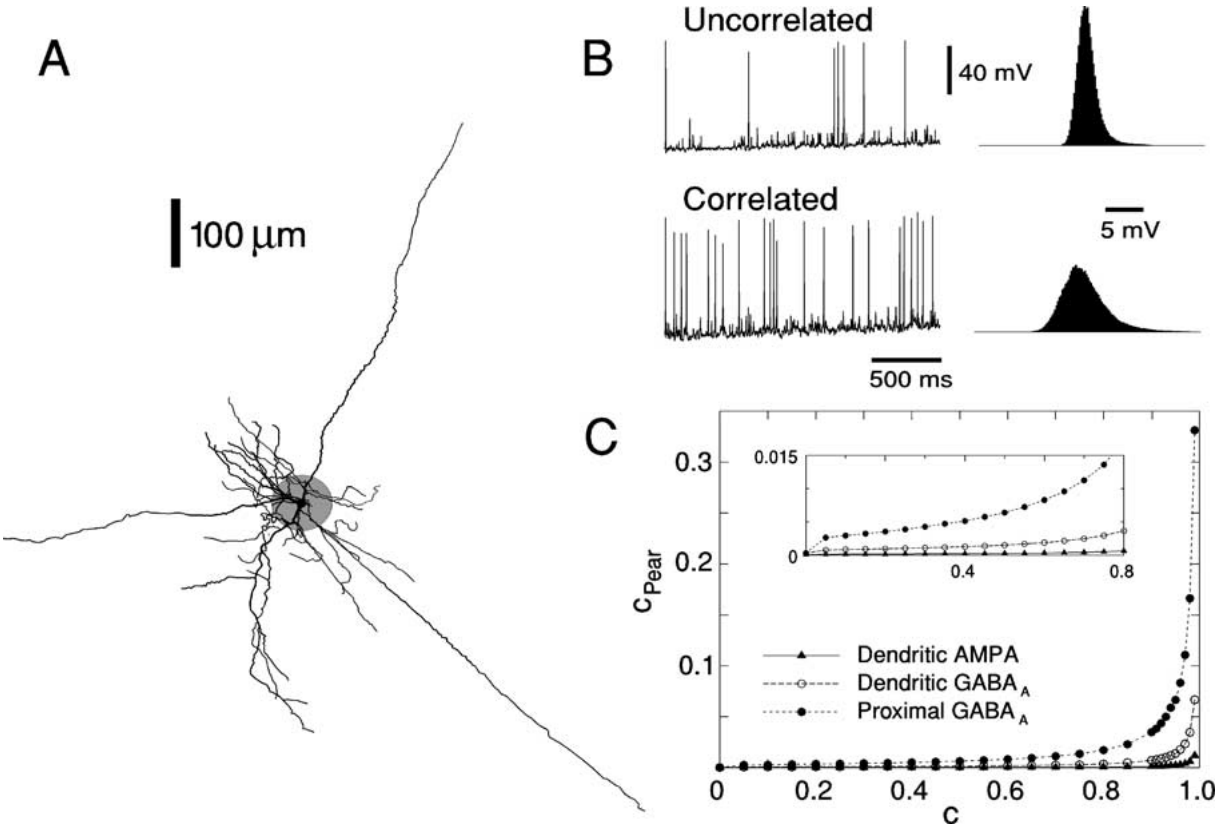

Figure 1. [illegible] **A:** [illegible] 100 μm [illegible] **B:** V_m [illegible] **C:** [illegible] V_m [illegible] c_{Pear} [illegible] c [illegible]

I_{CaL} [illegible] $^{-2}$ [illegible] $^{-2}$ [illegible] I_{NaP} [illegible] I_{Na}, I_{Kdr} [illegible] I_{KA} [illegible]

[illegible] α-[illegible] γ-[illegible] A ($GABA_A$) [illegible]

[illegible] (DeFelipe, 1992; [illegible] 1991; [illegible] 1989), [illegible] 6,563 [illegible] 3,376 $GABA_A$ [illegible] (2,818 [illegible] 558 [illegible] (Gulledge, 1996) [illegible] [illegible] (Destexhe, 1999; Pare, 1998), [illegible]

Table 2. [illegible] E, [illegible] $\bar{g}$). [illegible] a_c [illegible] (s[illegible] 2, [illegible]M

F[illegible] I_N[illegible]	D[illegible]	[illegible] I_K[illegible]	V_m-D[illegible] I_M
E_N[illegible] $= 50$ [illegible]		$E_K = -90$ [illegible]	
$\bar{g}$[illegible] $= a_c \cdot 516$ [illegible] $^{-2}$		$\bar{g}$[illegible] $= a_c \cdot 100$ [illegible] $^{-2}$	
$\bar{g}$[illegible] $= a_c \cdot 51.6$ [illegible] $^{-2}$		$\bar{g}$[illegible] $= a_c \cdot 10$ [illegible] $^{-2}$	$\bar{g}$[illegible] $= a_c \cdot 0.5$ [illegible] $^{-2}$
$\bar{g}$[illegible] $= a_c \cdot 74.8$ [illegible] $^{-2}$		$\bar{g}$[illegible] $= a_c \cdot 14.5$ [illegible] $^{-2}$	$\bar{g}$[illegible] $= a_c \cdot 0.725$ [illegible] $^{-2}$

Table 3. [illegible] a_s [illegible] (s[illegible] 2, [illegible]M F[illegible] D[illegible] (1998).

GABA$_A$ [illegible]	AMPA [illegible]	[illegible] AMPA [illegible]
$\alpha_{GABAa} = 5$ [illegible]$^{-1}$ [illegible]$^{-1}$	α[illegible] $= 1.1$ [illegible]$^{-1}$ [illegible]$^{-1}$	α_{AMPA}[illegible] $= 1.1$[illegible]$^{-1}$ [illegible]$^{-1}$
$\beta_{GABAa} = 0.1$ [illegible]$^{-1}$	β[illegible] $= 0.67$ [illegible]$^{-1}$	β_{AMPA}[illegible] $= 0.19$ [illegible]$^{-1}$
$C_{max\,GABAa} = 1$ [illegible]	C_{max}[illegible] $= 1$ [illegible]	$C_{max\,AMPA}$[illegible] $= 1$ [illegible]
$C_{dur\,GABAa} = 1$ [illegible]	C_{dur}[illegible] $= 1$ [illegible]	$C_{dur\,AMPA}$[illegible] $= 1$ [illegible]
$E_{rev\,GABAa} = -75$ [illegible]	E_{rev}[illegible] $= 0$ [illegible]	$R_{rev\,AMPA}$[illegible] $= 0$ [illegible]
		$E_{pre\,thres\,AMPA}$[illegible] $= 0$ [illegible]
		$T_{dead\,AMPA}$[illegible] $= 1$ [illegible]
g_{GABA}[illegible] $= a_s \cdot 869.4$ [illegible]	g_{AMPA}[illegible] $= a_s \cdot 1738.8$ [illegible]	g_{AMPA}[illegible] $= 0.1$ [illegible]$^{-2}$
g_{GABA}[illegible] $= a_s \cdot 600$ [illegible]		
N_{GABA}[illegible] $= 2818$	N_{AMPA}[illegible] $= 16563$	N_{AMPA}[illegible] $= 197$
N_{GABA}[illegible] $= 558$		

[illegible] $\nu_h = 5.5$ [illegible] GABA$_A$ [illegible] ν[illegible] $= 1.0$ [illegible] AMPA [illegible] a [illegible] in [illegible] At [illegible] $N_0 = N + \sqrt{c}\,(1 - N)$ [illegible] N [illegible] F[illegible] $N_0 < N$ [illegible] (“[illegible]”) [illegible] N [illegible] N_0, [illegible]

[illegible] D[illegible] D[illegible] P[illegible] é (1999). [illegible] c [illegible] P[illegible]’s[illegible] fi[illegible] GABA$_A$ [illegible] AMPA [illegible] c [illegible] c[illegible], [illegible] Fig 1C.

[illegible] AMPA [illegible] 197 [illegible] B). [illegible] a [illegible] AMPA [illegible] fi[illegible] fi[illegible] T[illegible] $= 100$ [illegible]

[illegible] T_{isi} [illegible] 5 [illegible] 20 [illegible] (H [illegible] Dkr 2000).

[illegible] (H [illegible] Ch 1997), [illegible] 60 [illegible] 600 [illegible] F [illegible] fi [illegible] 30 s [illegible] 0.1 [illegible] V_m [illegible]

A [illegible] DEL [illegible] 00 (D [illegible] C [illegible] C [illegible]) [illegible] N [illegible]

2.2. Data Analysis and Measures of Response Coherence

[illegible] 0.1 [illegible] fi [illegible] B [illegible] 2 [illegible] 5 [illegible] 0.5 [illegible] 0.1 [illegible] F [illegible] 1993) [illegible] 10,000 [illegible] $^{19} = 524,288$ [illegible] ^{18} [illegible] 60 [illegible] 2 [illegible] 30 [illegible] 0.038 [illegible] 0.019 [illegible]

[illegible] 1998).

2.2.1. Power Spectral Analysis.

[illegible] (N [illegible]) s A [illegible] "[illegible]" [illegible] ν_0 [illegible] (e.g. F [illegible] 1993; [illegible] 1999; [illegible] 1995; [illegible] 1990), [illegible] fi [illegible]

$$\text{SNR} = 10 \cdot \log_{10}\left[N(\nu_0)^{-1}\int_{\nu_0-\Delta\nu}^{\nu_0+\Delta\nu} \mathrm{d}\nu\, P(\nu)\right], \quad (1)$$

[illegible] $P(\nu)$ [illegible] $N(\nu)$ [illegible] ν [illegible] D [illegible] fi [illegible] $\Delta\nu \to 0$ [illegible] fi [illegible] $\cdot \Delta\nu = 0.1$ [illegible] fi [illegible]

B [illegible] V_m [illegible] "[illegible]" [illegible] (1) [illegible] fi [illegible]

2.2.2. ISI Distribution.

A [illegible] 1993; [illegible] 1995) [illegible] (e.g. D [illegible] 1993; [illegible] 1998), [illegible] T_0, [illegible] T_{isi}. [illegible] D [illegible] 1993) [illegible] fi [illegible]

[illegible]

(2)

[illegible]

2.2.3. Coherence Between Output and Stimulus.

[illegible] (1993):

(3)

[illegible]

2.2.4. Probability for Evoking Spikes.

[illegible]

(4)

[illegible] 2000). [illegible]

σ_V [illegible]

(5)

[illegible] 10 [illegible] 20 [illegible]

[illegible] $P_2(x)$ [illegible] $(-(x-a)^2/b^2)$, $\frac{P_2(x)}{x^2}$ [illegible] (a/x) [illegible] $\frac{P_2(x)}{x^2}$ [illegible] $(-ax)$, [illegible] $P_2(x)$ [illegible] $a\,\mathrm{e}^{-bx}$. [illegible]

3. Results

[illegible]

[illegible] 1999) [illegible] 1998). [illegible]

[illegible] (D[illegible] P[illegible], 1999; P[illegible] et al., 1998), [illegible] V_m [illegible] −65 [illegible] [illegible] V_m [illegible] [illegible] (Fig. [illegible] $\sigma_V \sim 4$ [illegible] 5 [illegible] 20 Hz (see Fig. 1B). [illegible] c [illegible] (see [illegible] 2, [illegible] P[illegible]'s [illegible] c_R [illegible] Fig. 1C. [illegible] et al., 1994).

3.1. Conductance Study: The Impact of Background Conductance Density

We first [illegible] a_s, [illegible] *strength* [illegible] a_s [illegible] $0.50 \leq a_s \leq 1.95$ [illegible] $\Delta a_s = 0.05$. [illegible] $c = 0.0$ [illegible] $c = 0.7$ [illegible] A[illegible] 2, [illegible]

A [illegible] a_s [illegible] V_m. F[illegible] −67 mV [illegible] $a_s = 0.5$ [illegible] −64 mV [illegible] $a_s = 1.95$ [illegible] (see Fig. 2A). [illegible] V_m [illegible] σ_V, [illegible] mV $\leq \sigma_V \leq 3$ mV [illegible] $c = 0.0$ [illegible] 2 mV $\leq \sigma_V \leq 4$ mV [illegible] $c = 0.7$ (Fig. 2B). [illegible] V_m [illegible] a_s [illegible] $c = 0.7$, [illegible] V_m [illegible]

[illegible] in σ_V [illegible] 2 mV [illegible] a_s [illegible] V_m [illegible] σ_V [illegible] A[illegible] a_s [illegible] F[illegible] in [illegible] σ_V, [illegible]

[illegible] F[illegible] $c = 0.0$ [illegible] V_m [illegible] A[illegible] V_m [illegible] 0.5 [illegible] a_s. D[illegible] σ_V, [illegible] $c = 0.7$. [illegible] a_s, [illegible] 7 [illegible] 8 Hz [illegible]

[illegible] 10 Hz (Fig. 2E). B[illegible] a_s. [illegible] a_s. [illegible] $c = 0.0$, [illegible] σ_V [illegible]

[illegible] V_m [illegible] (Fig. 2C). [illegible] "[illegible]" [illegible]

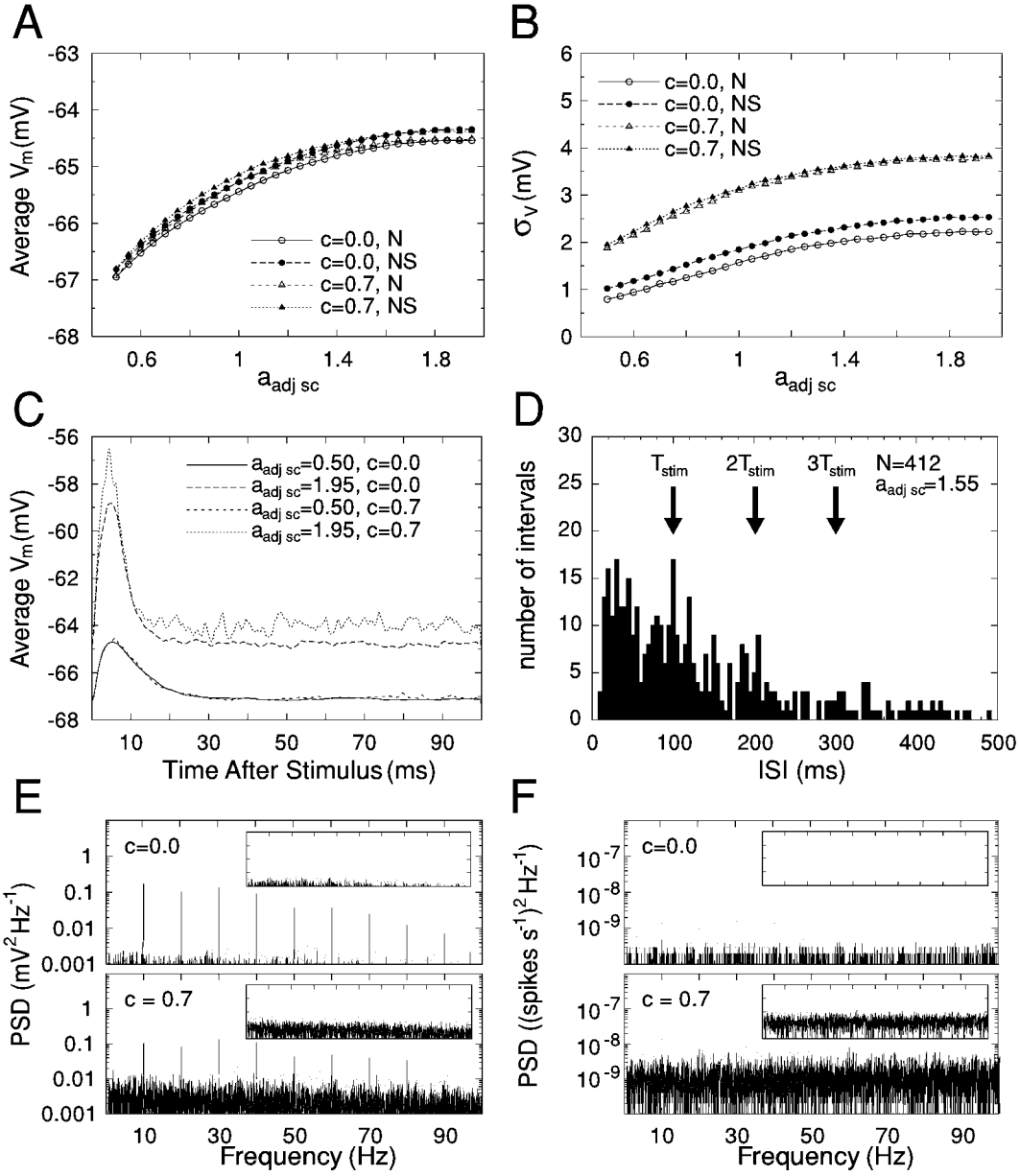

Figure 2. B[illegible]

A: [illegible] V_m [illegible]

B: [illegible] σ_V [illegible] V_m [illegible] a_{ε} [illegible]

C: A[illegible] V_m [illegible]

D: [illegible] $a_{\varepsilon} = 1.55$ [illegible] $c = 0.7$. [illegible] $T_{\text{in}} = 100$ [illegible]

E [illegible] **F:** [illegible] (E) [illegible] (F) [illegible] $a_{\varepsilon} = 1.50$. [illegible] 10 Hz [illegible]

a_s .

$c = 0.0$. A

$c = 0.7$

$T_{in} = 100$

a_s

a_s

a_s . A

$c = 0.7$. A

$c = 0.7$

a_s

σ_V

T_{in})

$a_s =$

3.0

σ_V

σ_V,

* (Fig3C).

V_m

V_m

P_s

*. F

*. *

$c = 0.7$ $a_s \sim 0.5$ $\sigma_V \sim 1.7$ M

(Fig4A),

a_s

a_s σ_V.

(Fig4B).

V_m

“ ”

σ_V.

3.2. *Frequency Study: The Impact of Excitatory Background Firing Rates*

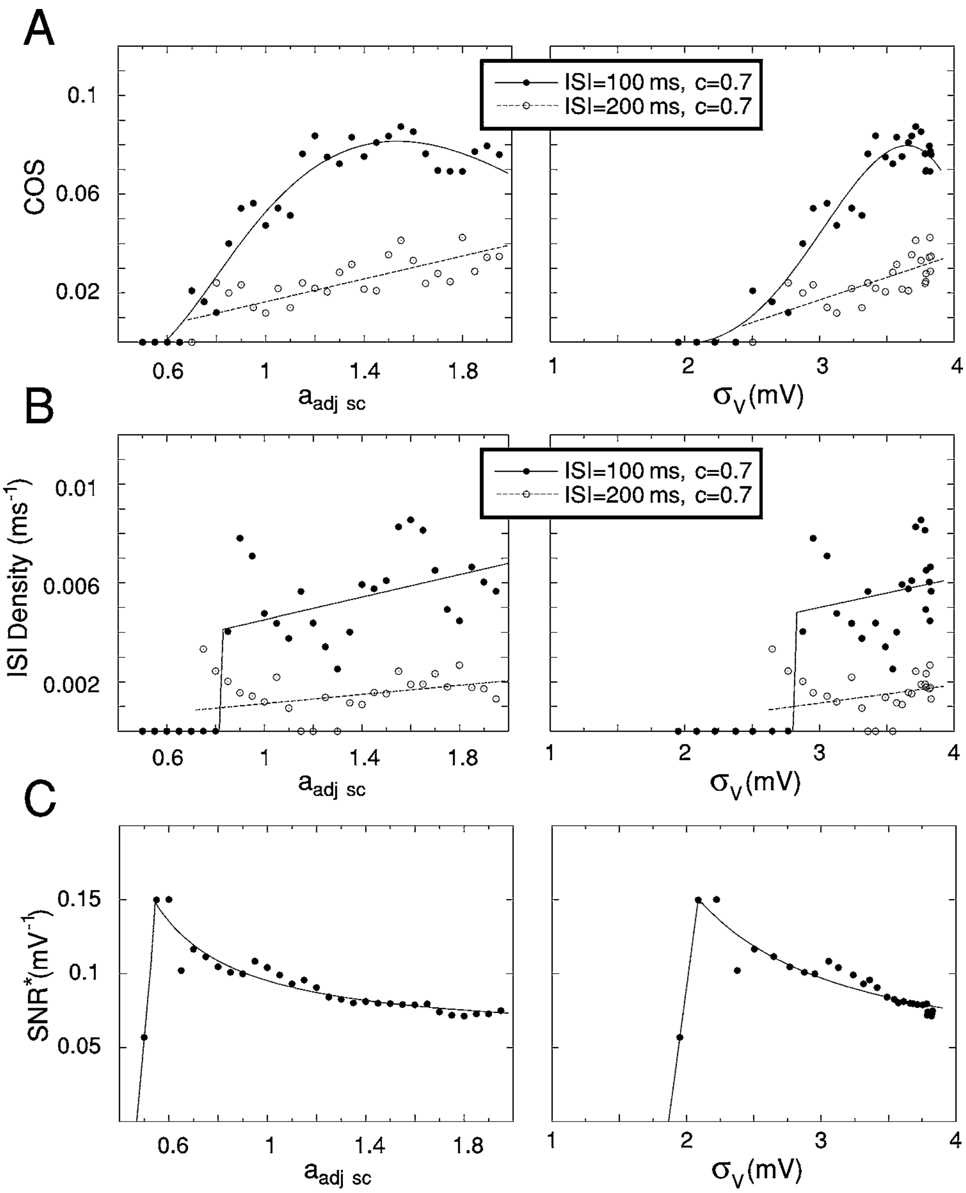

Figure 3. C[illegible] $c = 0.7$. [illegible] a_s. [illegible] σ_V [illegible] **A:** C[illegible] fi[illegible] 100 [illegible] 200 [illegible] 5 [illegible] **B:** [illegible] 100 [illegible] 200 [illegible] 5 [illegible] fi[illegible] 2, [illegible] **C:** [illegible] * [illegible] 10 [illegible] *.

[illegible] A[illegible] T[illegible] fi[illegible] 0.5 [illegible] $\leq \nu_s \leq 2.0$ [illegible] 6 [illegible] $\Delta\nu_s =$ 0.1 [illegible] ν_h [illegible] fi[illegible] 5.5 [illegible] As [illegible]

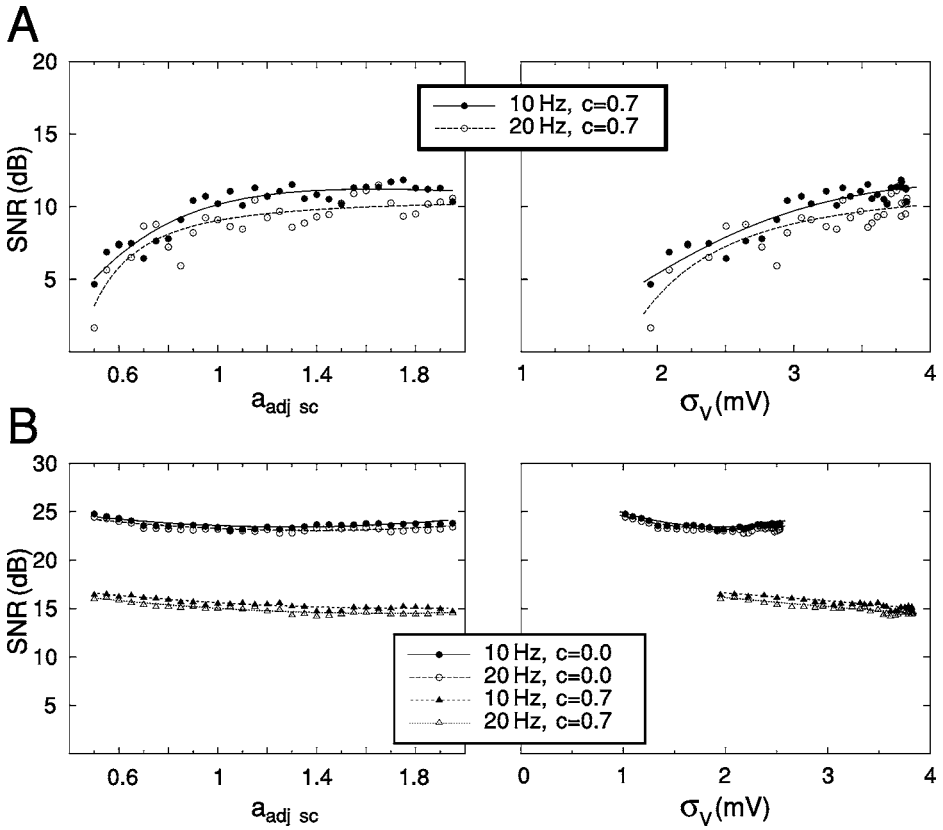

Figure 4. **A:** **B:** $c = 0.7$. **B:** $c = 0.0$ $c = 0.7$ V_m

$c = 0.0$ $c = 0.7$. ν_e V_m -70 mV -58 mV $c = 0.0$, -70 mV -60 mV $c = 0.7$). V_m ν_e . V_m (1 mV $\leq \sigma_V \leq$ 3 mV $c = 0.0$, 2 mV $\leq \sigma_V \leq$ 3.5 mV $c = 0.7$, Fig. 5A). σ_V

For σ_V ν_e . V_m σ_V ν_e $c = 0.0$ ~ 0.9 Hz $c = 0.7$ $\nu_e =$ 2.0 Hz,

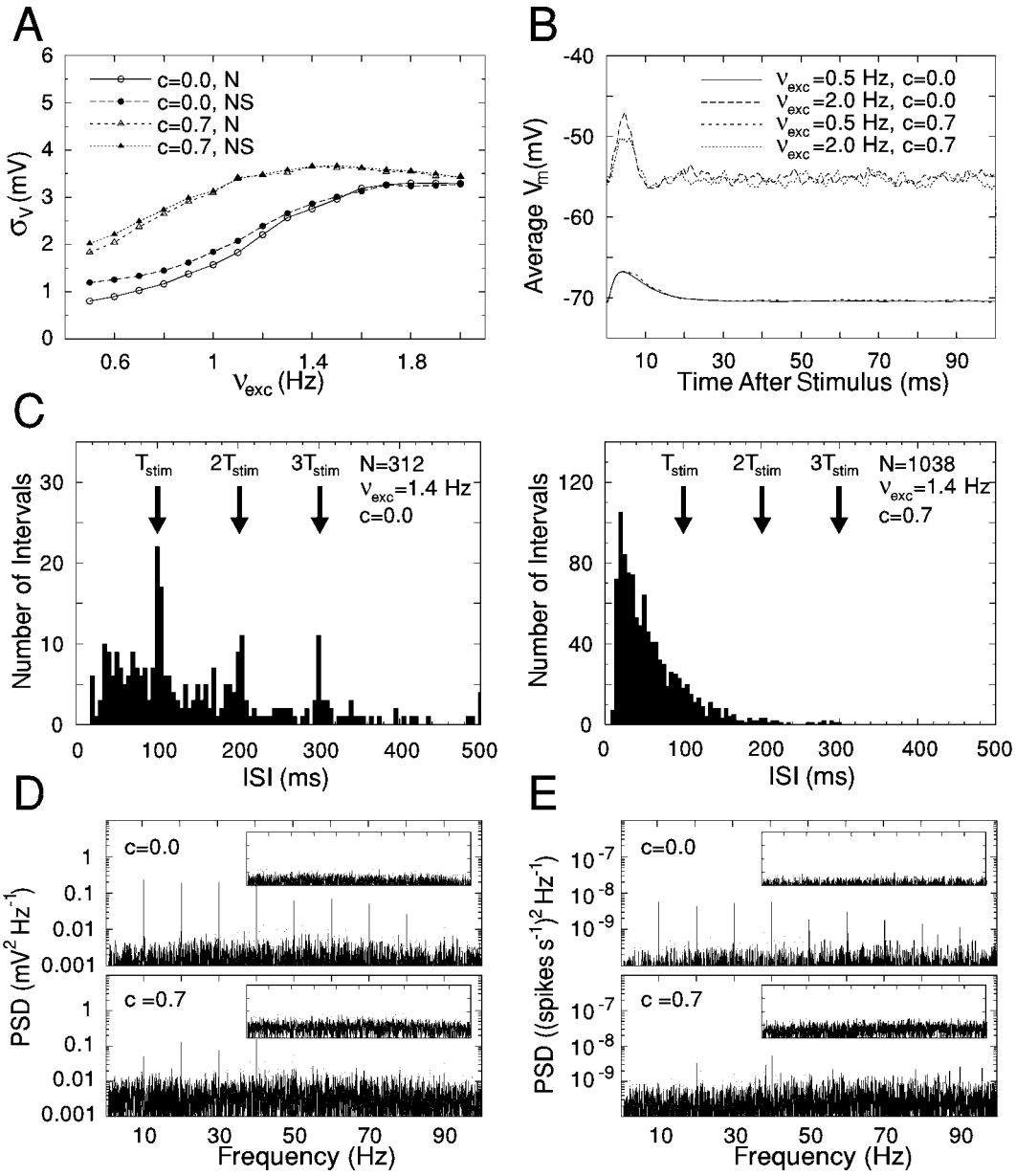

Figure 5. B[illegible] **A:** [illegible] fig[illegible] [illegible] V_m fl[illegible] σ_V s[illegible] ν_e [illegible] [illegible] $c = 0.0$ [illegible] $c = 0.7$. **B:** A[illegible] V_m [illegible] $\nu_e = 1.4$ [illegible] $c = 0.0$ ([illegible] $c = 0.7$. **C:** [illegible] [illegible] 100 s[illegible] [illegible] **D** [illegible] **E:** [illegible] (D) [illegible] (E) [illegible] $\nu_e = 1.4$ [illegible]

[illegible] $c = 0.0$ [illegible] [illegible] ν_e [illegible] (Fig 5C, [illegible] $c = 0.7$ [illegible] (Fig 5C, [illegible]

F[illegible] (Fig. 5D and E) [illegible] ν_{exc} [illegible] ν_{exc}, [illegible] $c = 0.7$. [illegible]

[illegible] ν_{exc}.

[illegible] (Fig. 6 [illegible]). [illegible]

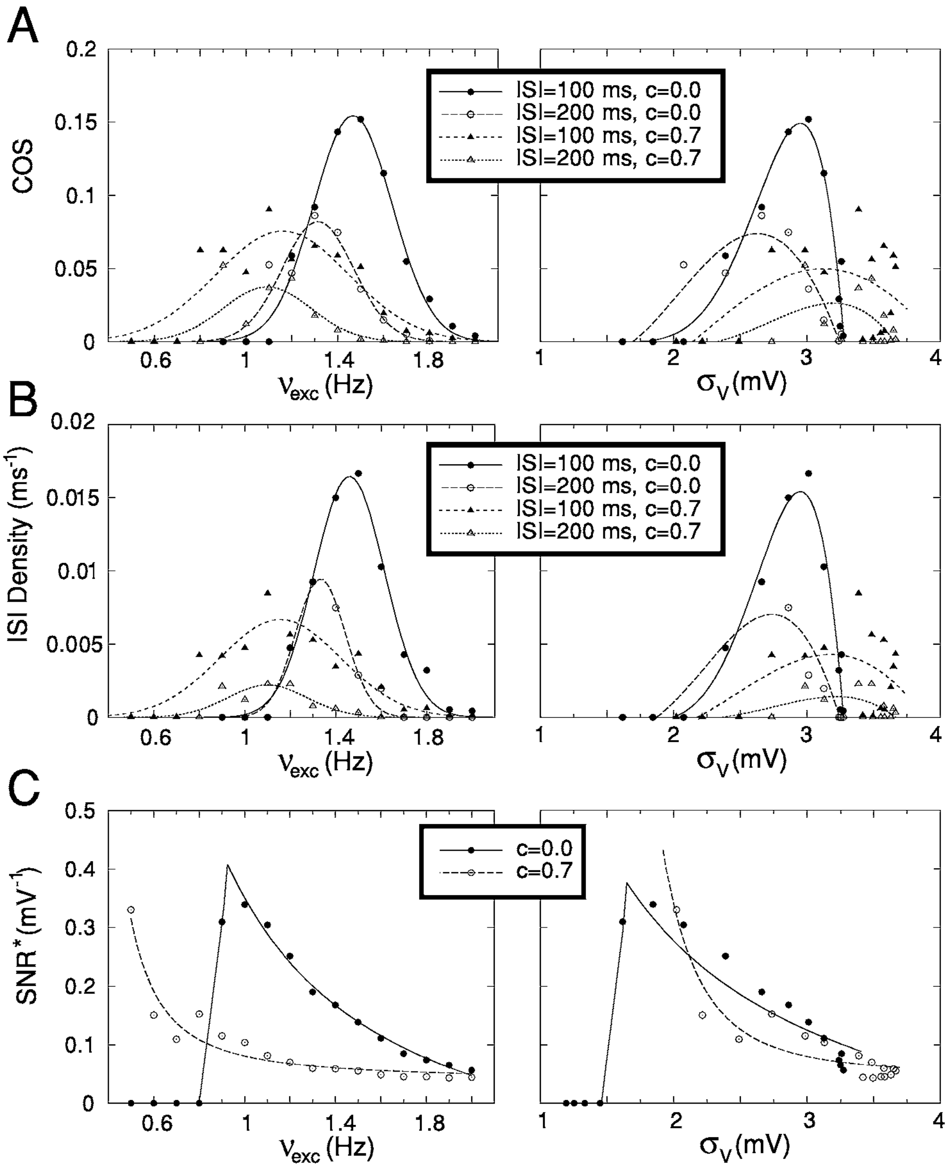

Figure 6. C[illegible] ν_{exc}. [illegible] 6 V_m [illegible] **A:** C[illegible] 100 [illegible] 200 [illegible] 15 [illegible] **B:** [illegible] 100 [illegible] 200 [illegible] 5 [illegible] **C:** [illegible] * [illegible]

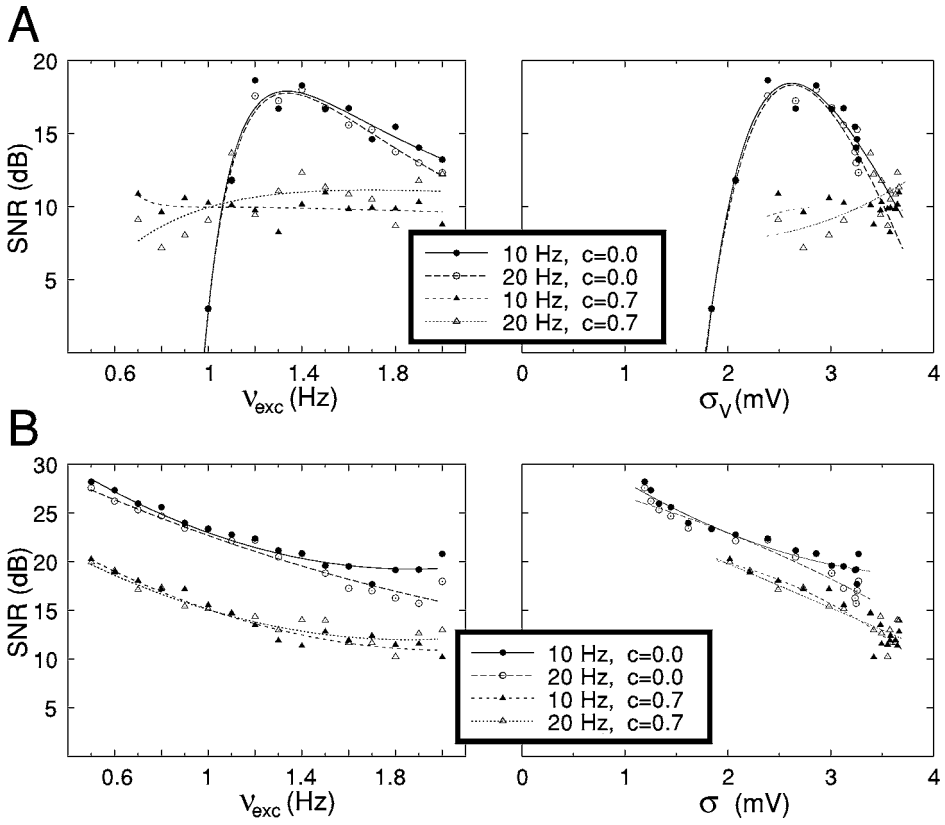

Figure 7. D
B
w $c = 0.0$ d $c = 0.7$. **A:**
B:
V_m

T_{in} .
$c = 0.7$
ν_e ~ 1.5 $\sigma_V \sim 3.0$ $c = 0.0$,
ν_e ~ 1.2 $\sigma_V \sim 3.5$ $c = 0.7$.
σ_V
F
$c = 0.0$,
ν_e ~ 0.8
V_m ($\sigma_V \sim 1.5$
σ_V d ν_e (Fig5A),
σ_V
—
ν_e
ν_e
ν_e
*

$\sigma_V \sim 1.7$

$c = 0.0$

V_m

3.3. *Correlation Study: The Impact of the Background Statistics*

V_m

c $0.0 \le c \le 0.99$ $\Delta c = 0.05$ $c \le 0.90$ $\Delta c = 0.01$ $c > 0.90$.

($a_c = 0.7$) ($a_c = 1.0$).

V_m

c. $c \sim 0.9$, V_m -65

c.

V_m

(Fig 8A). Fig 8B V_m

V_m

V_m $1 \le \sigma_V \le 7.5$

$.5 \le \sigma_V \le 6.5$

$2 \le \sigma_V \le 5.5$

σ_V.

σ_V 0.5

c.

σ_V,

$c \sim 0.65$,

0.1 45

4 50

Fig 8C.

c.

(Fig 8D and E)

c.

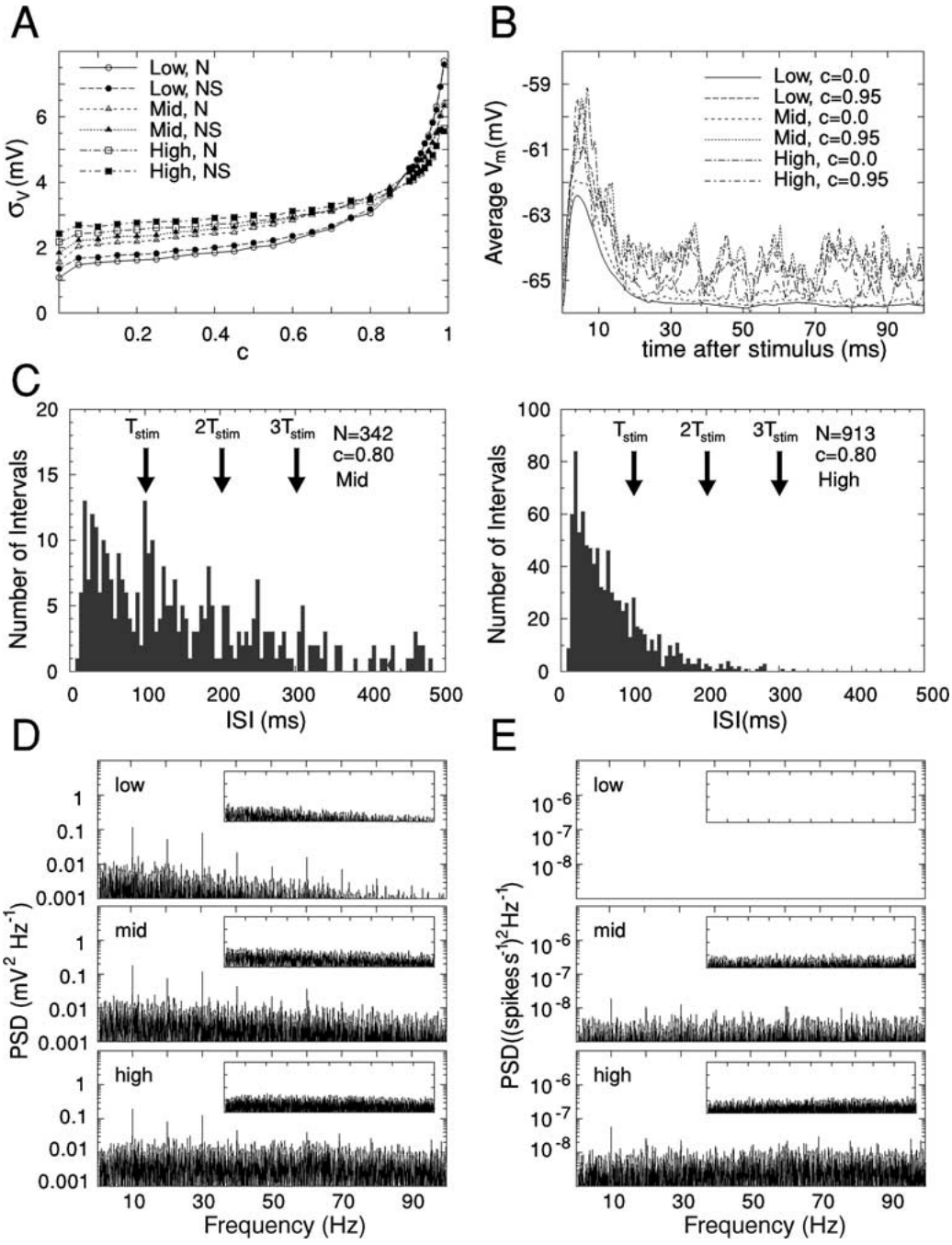

Figure 8. B[illegible]

A: [illegible] V_m [illegible] σ_V. [illegible] σ_V [illegible] c [illegible]

B: A[illegible] V_m [illegible] $c = 0.8$ [illegible]

C: [illegible]

D [illegible] **E:** [illegible]s $c = 0.8$ [illegible]

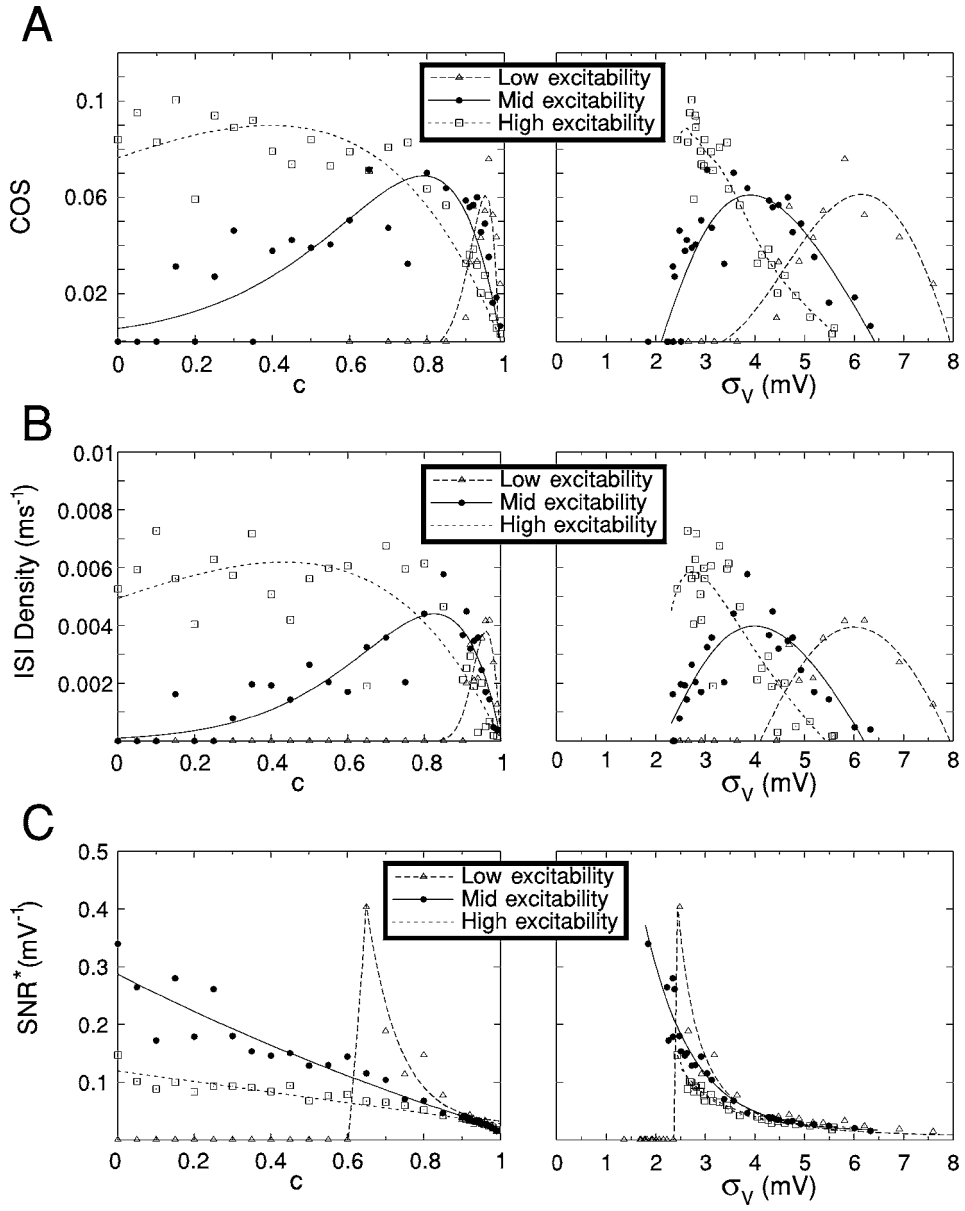

Figure 9.
c.
σ_V
A:
B:
C:
*.
c.
σ_V.
$c \sim 0.95$
$\sigma_V \sim 6$
$c \sim 0.75$
$\sigma_V \sim 4$

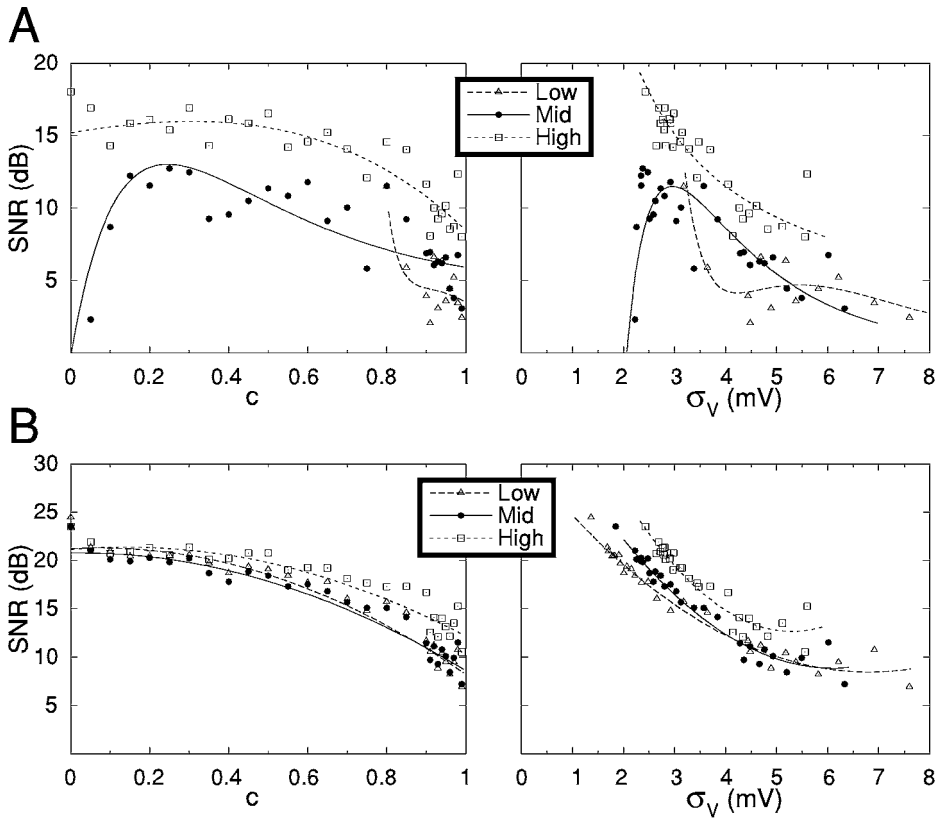

Figure 10. **A:** **B:** V_m σ_V. **A:** c, **B:** V_m

σ_V V_m Fig10A). Fig10C). $c \sim 0.6$, $\sigma_V \sim 2.5$ mV (Fig 10B)

3.4. Robustness of Stochastic Resonance-Like Behavior

I_{CaL}

V_m

$\leq \sigma_V \leq 11$

I_N,

I_K, and I_M

I_{CaL} (a

$\sigma_V \sim 6$

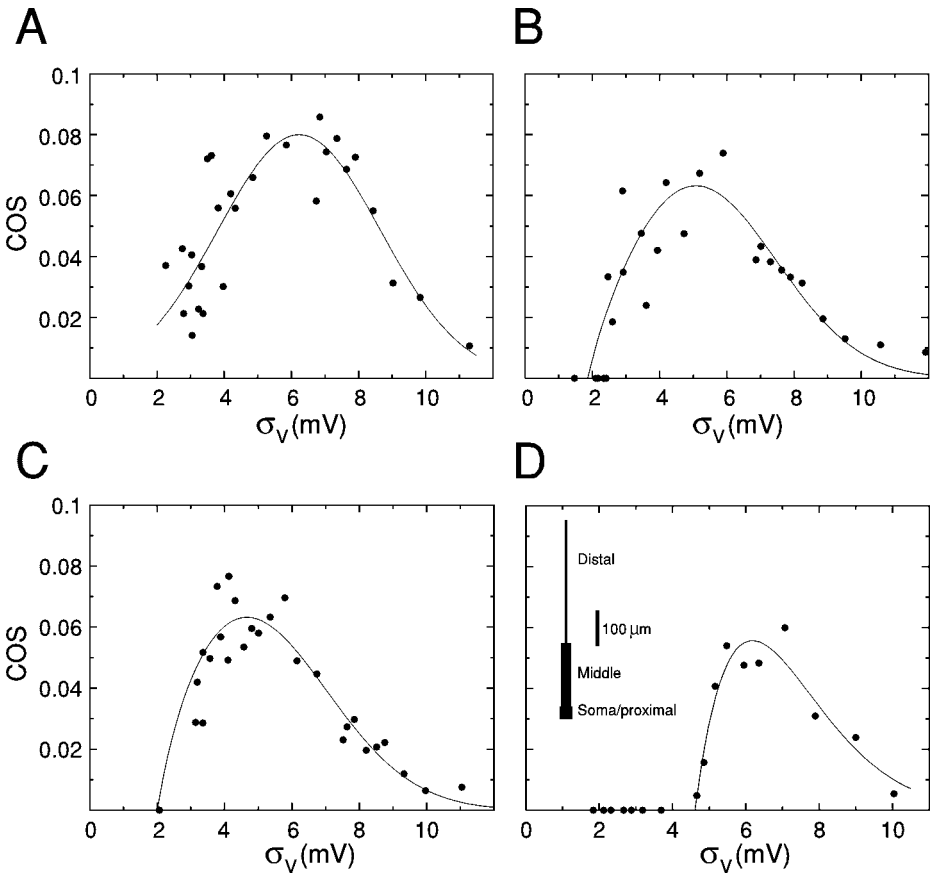

Figure 11.

A:

I_N, I_K, and I_M

$\sigma_V \sim 6$

B:

I_K

V_m

C:

D:

σ_V.

I_{KA} V_m $\leq \sigma_V \leq$ $\sigma_V \sim 5$ $\sigma_V \sim 6$

4. Discussion

4.1. Measures of Response Coherence and Their Applicability

(Eq(2)) (Eq(3)) (Eq(1)) ~2% P_s (Eq(4)), * (Eq(5)), V_m

4.2. "Classical" Stochastic Resonance in Pyramidal Neurons

[illegible]
[illegible]
(B[illegible], 1981; F[illegible] 1993; [illegible], 1991).

[illegible] (Fig 3A [illegible] B). [illegible] σ_V [illegible] V_m fl[illegible] a fi[illegible] (Fig 2B). F[illegible] s [illegible] (Fig 4B). [illegible] V_m [illegible] fl[illegible]

[illegible] V_m fl[illegible] (Fig 5A), a[illegible] ν_e [illegible] (Fig 6A [illegible] B). [illegible] $c = 0.0$ [illegible] CS[illegible] $c = 0.7$. [illegible] σ_V, [illegible] $c = 0.0$ [illegible] $c = 0.7$ [illegible] CS[illegible] σ_V, [illegible] (Fig 7A). F[illegible] $c = 0.7$ [illegible] ν_e [illegible] s (Fig 7B) [illegible]

[illegible] fi[illegible] CA1 [illegible] D[illegible] 2000), [illegible]

[illegible] R [illegible]

4.3. “Nonclassical” Stochastic Resonance

A [illegible] ’s [illegible] A[illegible] fl[illegible] (e.g. C[illegible], 1998; [illegible], 1989; [illegible], 1999; [illegible] 1998), [illegible] R [illegible]

[illegible] (Fig 8A [illegible] B). [illegible] c [illegible] fl[illegible] F[illegible] σ_V [illegible] A [illegible] s (Fig 10A). [illegible] (Fig 10B) [illegible]

4.4. Possible Functional Consequences

[illegible] V_m fl[illegible] — [illegible] .5 [illegible] $\leq \sigma_V \leq 4$ [illegible] fl[illegible] — [illegible] $\sigma_V = 4.0 \pm 2.0$ [illegible] (D[illegible] P[illegible] é 1999). [illegible]

[illegible] (H[illegible] 2000): [illegible] V_m [illegible] dynamical resonance.

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[illegible] CNRS [illegible] (13724) [illegible] (R01-[illegible]7711). [illegible] NIH [illegible]

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