Opposite effects of tetanic stimulation of the auditory thalamus or auditory cortex on the acoustic startle reflex in awake rats

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Abstract

The amygdala mediates both emotional learning and fear potentiation of startle. The lateral amygdala nucleus (LA) receives auditory inputs from both the auditory thalamus (medial geniculate nucleus; MGN) and auditory association cortex (AAC), and is critical for auditory fear conditioning. The central amygdala nucleus, which has intra-amygdaloid connections with LA, enhances startle magnitude via midbrain connections to the startle circuits. Tetanic stimulation of either MGN or AAC *in vitro* or *in vivo* can induce long-term potentiation in LA. In the present study, behavioural consequences of tetanization of these auditory afferents were investigated in awake rats. The acoustic startle reflex of rats was enhanced by tetanic stimulation of MGN, but suppressed by that of AAC. All the tetanization-induced changes of startle diminished within 24 h. Blockade of $GABA_B$ receptors in the LA area reversed the suppressive effect of tetanic stimulation of AAC on startle but did not change the enhancing effect of tetanic stimulation of MGN. Moreover, transient electrical stimulation of MGN enhanced the acoustic startle reflex when it lagged behind acoustic stimulation, but inhibited the acoustic startle reflex when it preceded acoustic stimulation. The results of the present study indicate that MGN and AAC afferents to LA play different roles in emotional modulation of startle, and AAC afferents are more influenced by inhibitory $GABA_B$ transmission in LA.

Introduction

ã ã . ã y ãã (LA) ã ã y ã (AFC) (H & Dã , 1986; R ã & L D , ã . L - ã (L P) LA, AFC (M K ã & Ŝ -Gã ã , 1997; Q *et al.*, 1995, 1997; R ã & L D , 1995; R ã *et al.*, 1997), ã y ã ã ã MGN AAC ã *in vitro* ã *in vivo* (C ã ã *et al.*, 1990; Bã *et al.*, 2002; C & L D , 1990; R ã & L D , 1995; ããã ã *et al.*, 1995; H ã & Kã , 1998; *et al.*, 1999; ã *et al.*, 2001;

D y *et al.*, 2003; Bã & L D 2004). H ã ã L P ã y (ã *et al.*, 2001; D y *et al.*, 2003) ã y ã y LA ã AFC. B ã ã ã ã ã y ã ã ã .

ã ã (AŜR) ã ã ã ã y ã ã . ã y ãã ã ã ã ã (Dã , 1992; F & Fã , 1999; G & Dã , 2000). O LA ã ã ã ã-ã y ã ã (CE) ã y ãã (P ã & A ãã , 1998; Pã *et al.*, 2004), ã ã (R *et al.*, 1991; K & E , 1993; F *et al.*, 1997) ã y ã ãy ã ã (R & Dã , 1988, 1990; ã & P ã , 1993; F *et al.*, 1994, 1996; F ã ã & ã , 1995; M & Dã , 1999, 2000). Dã ã ã y ãã AŜR (Ŝ ã ã *et al.*, 1996) ã ã ã- ã ã y ãã ã AŜR (F *et al.*, 2000). , ã ã ã ã y LA ãy AŜR.

LA ã ( ) ã ã GABA (Lã & Pã , 1997, 1998; Mã ã y & Ŝã , 1998). I ã ã ã y ã y ã

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E- ã : ã @ . . ; ã @ y . . ã

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GABA$_B$ (H & G , 1994; y *et al*., 2000). I
y,
MGN AAC A R, GABA$_B$
LA .

Materials and methods

Experimental subjects

M (*Rattus norvegicus*), 300 450 ,
C R C (C , Q) y
12- y (07.00). y
A C C ,
C C A C ,
y.

Surgery

D
(L & , 2000). B y,
(60 / , . .; M. .C. P ,
C , ON, C)
(0.4 / . .), (P O ,
R , A, A) - (L
& , 2000) y (I -
, D , IL, A) 62 ,
P & (1997). R ,
LA (AP, −2.8 −3.8 ; ML,
5.4 , D , −7.5). B MGN
MGN (AP,
−5.4 ; ML, 3.2 ; D , −5.9 −6.2).
MGN, , y
y y y-
(L & , 1992),
LA AFC (. . D &
L D , 1999). B AAC
E3 (AP, −5.8 ; ML, 6.5 ; D ,
−5.5). A E3 AAC LA
(M *et al*

LA, y MGN. ($n = 5$) LA, y MGN. E3 LA ($n = 7$) LA, y E3. ($n = 5$) LA, y E3. MGN E3 y E 1. y B GABA$_B$ LA , E 2 F 20 , y. I y , E 1. A R. A , . A A R y , 1 , 24 .

Experiment 3: effects of tetanic stimulation on startle induced by pairing acoustic stimulation with electrical stimulation of MGN or TE3

I , ( ) MGN AAC y y ; ( ) y , y A , ( ) MGN E3 (I), −25, −20, −15, −10, −5, 0, 5, 10, 15, 20 25 (L *et al.*, 1998, 1999; L & , 2000). P I 230 340 µA. E MGN E3 I , y 24 MGN E3 . F I .

Statistical analyses

A y ANOVA, $P < 0.05$.

Histology

A , . L y DC (500 µA 10) , 10% 30% y , 40 µ y (−20 °C).

Results

Histology

F . 1. E 2 F . 2. C MGN E3 P & (1997). I E 1, MGN E3 23 (F . 1A). I E 2, MGN E3 19 (F 1B 2). I E 3, MGN E3 11 (F . 1C). B y , E 2.

Experiment 1: effects of unilateral tetanic stimulation of MGN or TE3

A R , y , 1 24 MGN y ($F_{3,28} = 5.420$, $P < 0.05$) (F . 3A). *Post hoc* , A R , y 1 MGN y ($P < 0.05$). H , 24 ($P > 0.05$). A R , y , 1 24 E3 y ($F_{3,20} = 3.800$, $P < 0.05$; F . 3B). H , MGN, A R E3. *Post hoc* A R y y E3 ($P < 0.05$). A R 1 ($P < 0.05$) 24 ($P > 0.05$).

y MGN ($F_{3,12} = 0.841$, $P > 0.05$) E3 ($F_{3,16} = 0.566$, $P > 0.05$) A R (F . 4), A R y 1 MGN, y E3.

Experiment 2: effects of bilaterally blocking GABA$_B$ receptors in the LA area

F MGN, - y ANOVA A R ($F_{1,35} = 0.383$, $P = 0.542$). A , ($F_{3,35} = 0.968$, $P = 0.424$).

F 5A MGN LA. MGN, MGN y A R

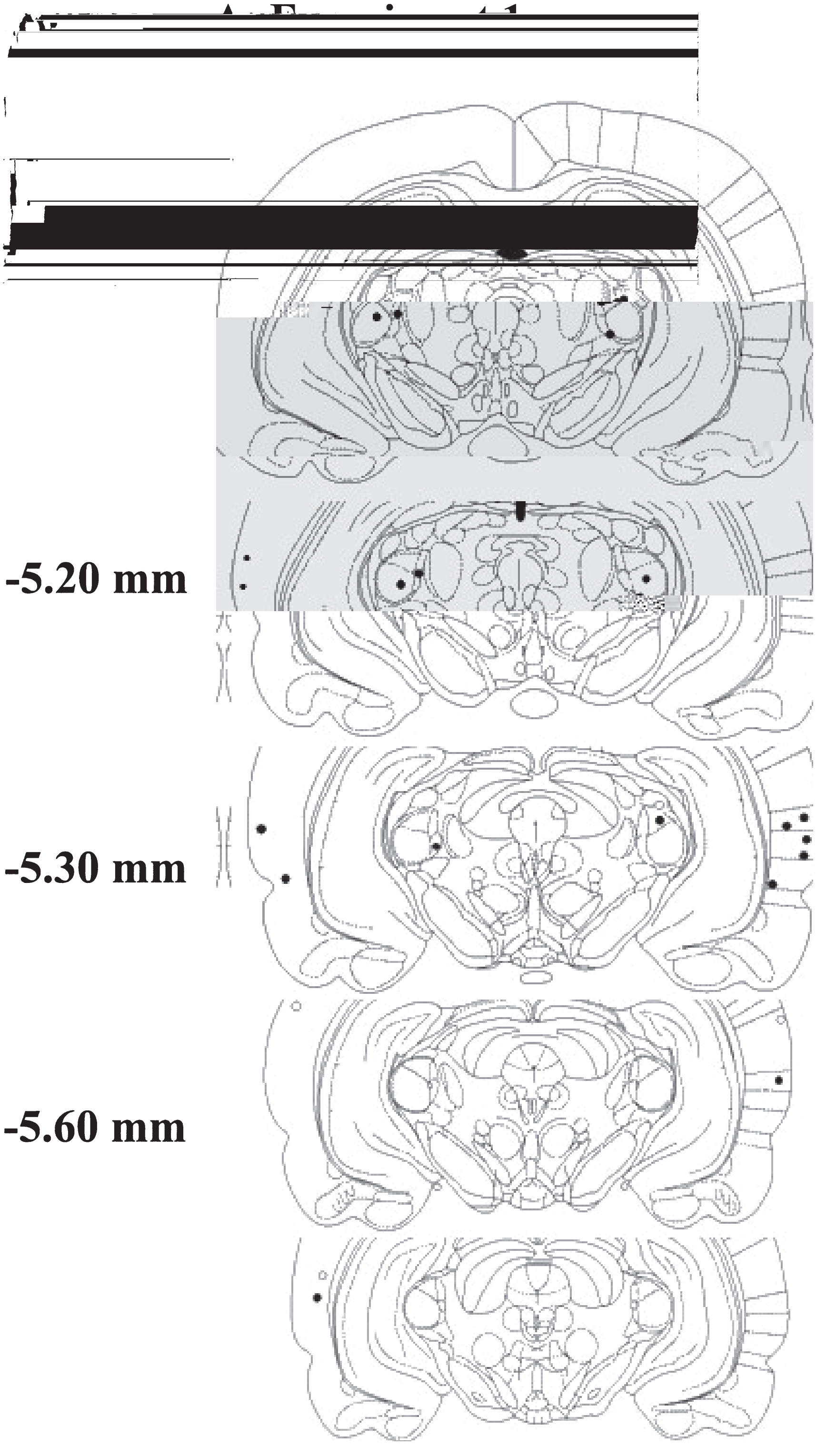


FIG. 1. L … (MGN) … (AAC, … E3) … (P… A, E… 1; P… B, E… 2; P… C, E… 3); ●, … ; ○, … . D … P… & … (1997) …

($F_{3,16} = 4.832$, $P < 0.05$). *Post hoc* … LA, … MGN … LA … MGN … ($F_{3,16} = 4.706$, $P < 0.05$). … A…R ($P < 0.05$). H…, … *Post hoc* … 1 … 24 … ($P > 0.05$). I … MGN, A…R … ($P < 0.05$).

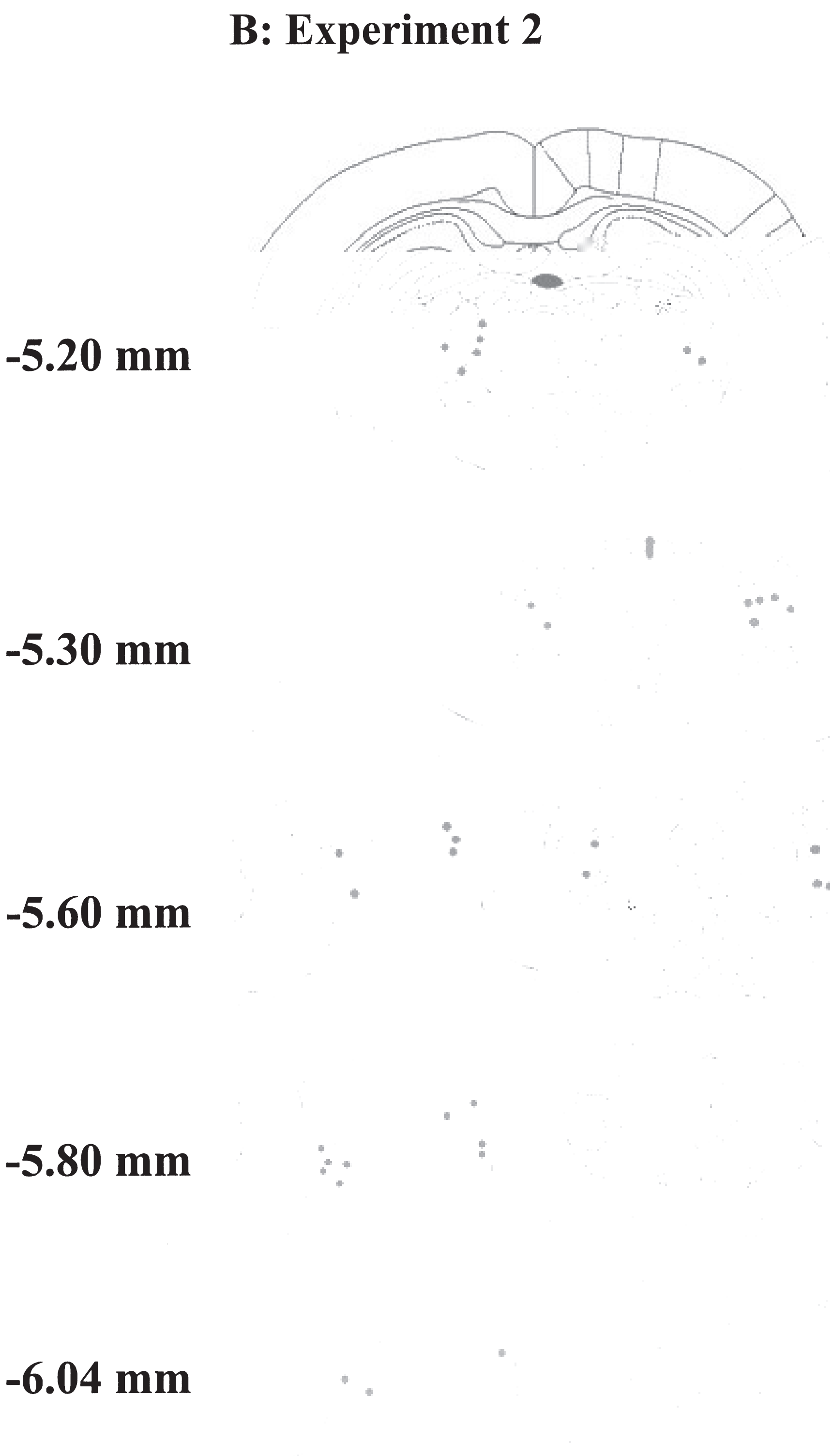
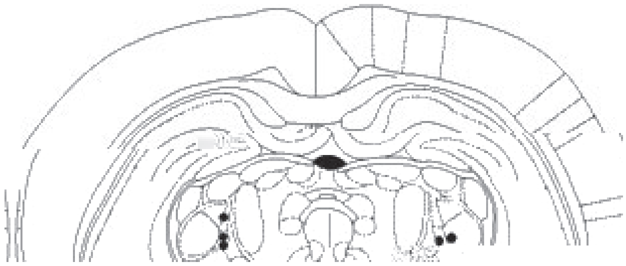


FIG. 1. C

H , 1 24 F E3, ANOVA ($P > 0.05$). E 1 ($F_{1,31} = 14.128$, MGN $P < 0.05$). A , ($F_{1,12} = 0.055$, $P > 0.05$). ($F_{3,35} = 4.593$, $P < 0.05$).

C: Experiment 3

-5.20 mm



-5.30 mm

-5.60 mm

-5.80 mm

-6.04 mm

FIG. 1. C

F 5B E3 1 ($P < 0.05$) E3. LA. 24 ($P > 0.05$). I - E3, y, LA, A R E3 y A R y ($F_{3,16} = 4.130$, $P < 0.05$). ($F_{3,12} = 4.570$, $P < 0.05$). *Post hoc* A R y ($P < 0.05$) 1 ($P < 0.05$) y y ($P < 0.05$) E3. A R

24 . y
E 1
E3 y
($F_{1,12} = 1.228$, $P > 0.05$).
F 6 A R
. I

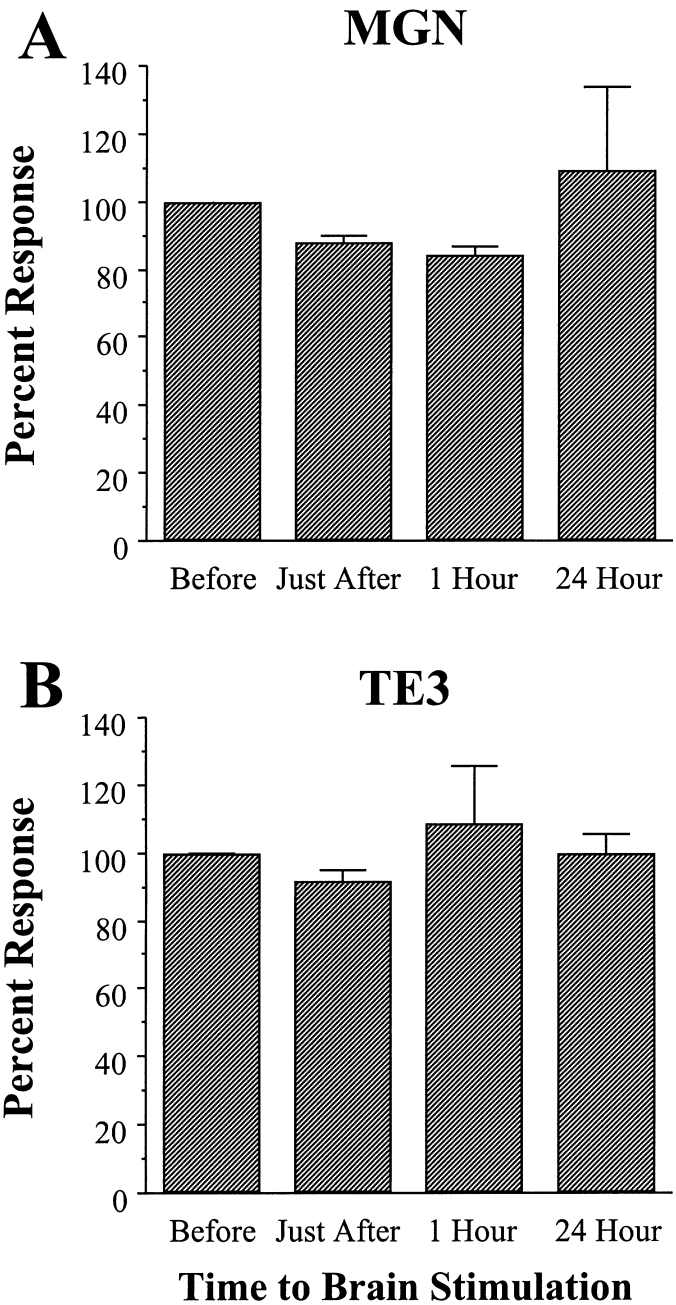


FIG. 4. N a a a a (A R) a y a , 1 a a 24 a a a - y a a MGN (Pa A) E3 (Pa B).

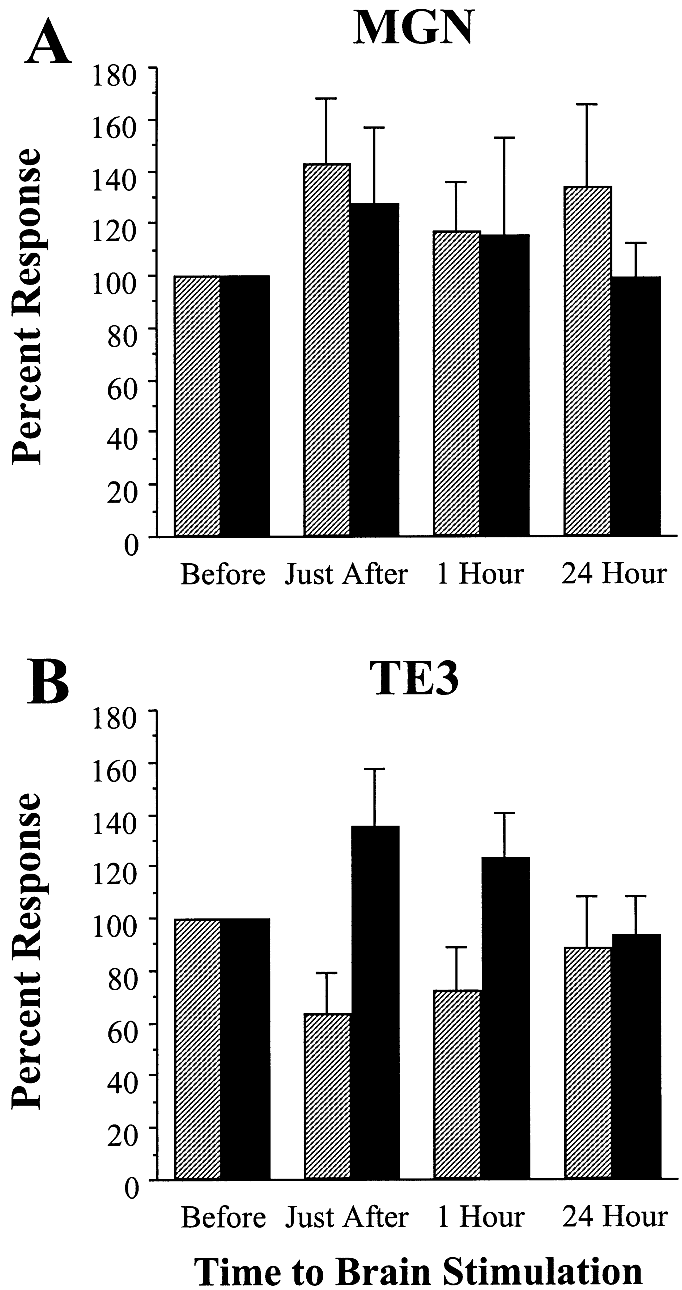


FIG. 5. N a a A R , a y a , 1 a a 24 a a a a a MGN (Pa A) E3 (Pa B). L a a A R a a ; a a a A R a a .

F a a a a MGN, a a a a a a a a I . a a y a a y - a , a a a a a a a a a a a a MGN, a a a a a a a a a a E3 a y I ($F_{10,152} = 1.312$, $P > 0.05$; F . 7, a), a a I a a a a a ($F_{20,185} = 0.339$, $P > 0.05$). H , a a a a a a ($F_{2,152} = 14.659$, $P < 0.05$). F

a a a a E3, a a a a a a y a a I . a y a . y - a a a a a .

Discussion

Behavioural consequences of tetanic stimulation of the two auditory afferents

D y et al. (2003) a a a a a L P y a a a MGN a a

y AAC
. A y AFC (
L D , 2000), D y *et al.* (2003)
y L P LA
y
in vitro . y -
A R D y *et al.* (2003) y
MGN AAC :
A R .
y y
y . y ,
E 2 3
E 1.
A R, y
y .

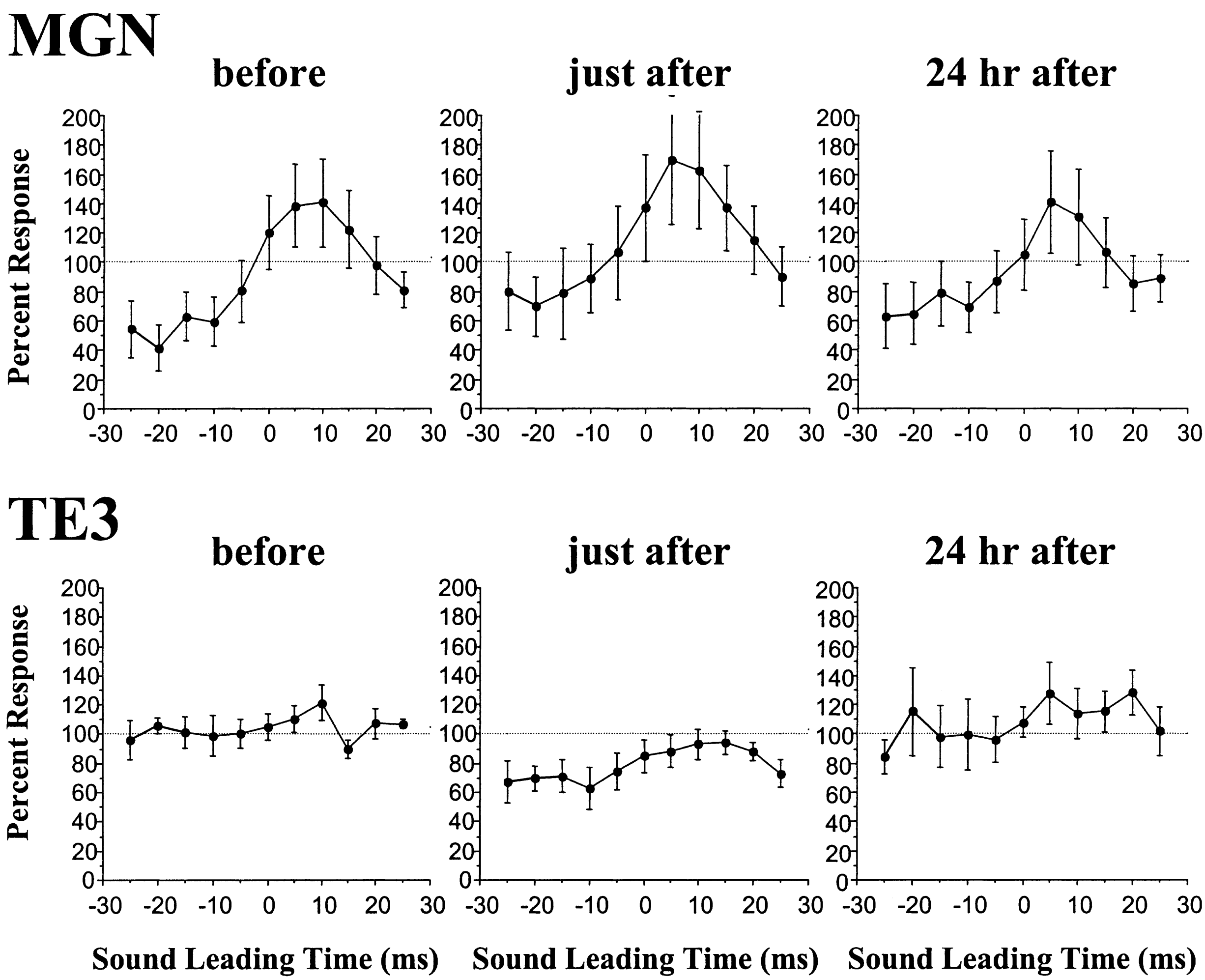


FIG. 7. N . . . MGN ( ) E3 ( ) , y 24 MGN E3. AR .

y (5 10) ; ( ) . AR (−20 F . 7) . M , MGN . y . I . I . MGN y y y (H et al., 2005) . MGN y y . MGN, AAC AR. A MGN, AAC y . I . AAC . MGN AAC .

MGN and AAC afferents to LA principal neurons and interneurons

LA , y (M D , 1982; M & O , 1983; R et al., 1991; & M , 1992; M D & A , 1993; et al., 1993; L & P , 1998; M y & , 1998). B y MGN AAC (L et al., 1996; L & P , 1998; M y & , 1999; y et al., 2000; B & L D , 2004; et al., 2004). A MGN y . y (F & L D , 1997; et al., 2000), y y MGN LA y , , R1 *N*- y -D- (NMDAR) G R1 3 α- -3- y y -5- y -4- (AMPA) (L D et al., 1991; F & L D , 1997). B y LA (M D , 1982; M & O , 1983; N & B -A , 1987) MGN . MGN , y AAC R1 G R1 3 (F & L D , 1999). H , , NMDAR y y MGN , AAC (L et al., 1995, 1996; & L D , 1999; et al., 2001). I y, (M y & , 1998; & A , 2003) LA .

NMDA AMPA
LA
NMDAR
AAC . A
D et al. (2003), AMPA .
NMDA MGN AAC LA
L P
In vitro,
AAC LA, NMDAR- L P LA
LA (M
& , 1998). I
(L &
P , 1998). I
. O
. M
AAC L P
AAC A R (
P et al., 2004).

Tetanic stimulation and fear conditioning

MGN AAC
LA
(C)
( ). H
C LA
. MGN AAC
H , L P
LA L P
A
L P L P LA
. I LA, L P
MGN AAC NMDAR, AP
(H & K , 1998; B & L D , 2004). M
NMDAR LA
R et al. (2001). I
NR2B NMDAR
LA AFC
. I
NMDAR
NR2B AFC.

Behavioural significance of the different effects of thalamic and cortical stimulation

NMDAR
MGN LA . I

MGN, AAC,
NMDAR LA.
MGN AAC
LA ;
(R et al., 2001). A
B et al. (2001),
NMDAR (GCC)
L P.H
LA NMDAR-
GCC- L P LA (H & K , 1998; B et al., 2002), NMDAR GCC
L P. B LA
NMDAR- GCC- L P LA (H &
K , 1998; B et al., 2002),
D et al. (2003)
GCC- L P,
MGN AAC
B AAC MGN
AAC LA
MGN
D AFC, MGN
L P LA
L P L P. D
C , MGN-
AAC
LA
C
. I
AAC (&
C , 1997),
et al., 1984).
MGN (
D et al., 1969). MGN
MGN
(D et al., 2001). H
MGN
MGN
MGN
AAC AFC.
(L D , 1995).

A new model and the inhibitory effect of tetanic stimulation of AAC on startle

R , P et al. (2004) AFC. O
GABA (I C)
CE LA
CE. O I C

Summary

a . A R a a a . a a
a . a MGN AAC. . a a
a a MGN a A R . a a AAC
. A R. . a a AAC
a a y GABA$_B$ a LA a a. .
MGN a AAC ay ay a AFC. Ba
a . . , a . a a ay a
a . a MGN AAC a
F . 8.

Ackamygda1sT oT . gem.,N

y . a I C .
a a a (R y *et al.*, 2000), a
a y a I C . a . a CE
. O. . LA a a y a I C .
. a y a I C . a . y
CE . a . a a a a a
LA a a a CE . . .
I y, a (IL) a a
(PFC), AAC (Ba a *et al.*,
1999) a a a a AFC (Ba *et al.*,
2001), y I C . (a *et al.*, 1989;
M D a *et al.*, 1996; F a *et al.*, 2000). Da a IL a
a a (L & a , 1998) a (M a *et al.*,
1993; Q. *et al.*, 2000). E a . a IL .
CE . . (Q. *et al.*, 2003) a
a (M a *et al.*, 2004). . a a a a a
. a . a AAC A R a
a . a AAC a a :
a a IL . . , a a
a y a I C a CE , a CE
. . a . a y . A R. F. -
a y a , a . a y,
a CE . . y I C
a y GABA$_B$ a .

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