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BRAIN RESEARCH

Research Report

Non-sensory cortical and subcortical connections of the primary auditory cortex in Mongolian gerbils: Bottom-up and top-down processing of neuronal information *via* field AI

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ABSTRACT

In the present study, we will provide further anatomical evidence that the primary auditory cortex (field AI) is not only involved in sensory processing of its own modality, but also in complex bottom-up and top-down processing of multimodal information. We have recently shown that AI in the Mongolian gerbil (*Meriones unguiculatus*) has substantial connections with non-auditory sensory and multisensory brain structures [Budinger, E., Heil, P., Hess, A., Scheich, H., 2006. Multisensory processing via early cortical stages: Connections of the primary auditory cortical field with other sensory systems. Neuroscience 143, 1065–1083]. Here we will report about the direct connections of AI with non-sensory cortical areas and subcortical structures. We approached this issue by means of the axonal transport of the sensitive bidirectional neuronal tracers fluorescein-labelled (FD) and tetramethylrhodamine-labelled dextran (TMRD), which were simultaneously injected into different frequency regions of the gerbil's AI. Of the total number of retrogradely labelled cell bodies found in non-sensory brain areas, which identify cells of origin of direct projections to AI, approximately 24% were in cortical areas and 76% in subcortical structures. Of the cell bodies in the cortical areas, about 4.4% were located in the orbital, 11.1% in the infralimbic medial prefrontal (areas DPC, IL), 18.2% in the cingulate (3.2% in CG1, 2.9% in CG2, 12.1% in CG3), 9.5% in the frontal association (area Fr2), 12.0% in the insular (areas AI, DI), 10.8% in the retrosplenial, and 34.0% in the perirhinal cortex. The cortical regions with retrogradely labelled cells, as well as the entorhinal cortex, also contained anterogradely labelled axons and their terminations, which means that they are also target areas of direct projections from AI. The laminar pattern of corticocortical connections indicates that AI receives primarily cortical feedback-type inputs and projects in a feedforward manner to its target areas. The high number of double-labelled somata, the non-topographic distribution of single FD- and

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Nomenclature

Auditory cortex

AI	primary auditory field (A1)
AAF	anterior auditory field
AC	auditory cortex
AV	anteroventral auditory field
D	dorsal auditory field
DP	dorsoposterior auditory field
V	ventral auditory field
VM	ventromedial auditory field
VP	ventroposterior auditory field

Other brain structures

3V	third ventricle
ac	anterior commissure
Acb(C, S)	nucleus accumbens (core, shell)
AH	anterior hypothalamic area
AI	agranular insular cortex (Ai)
Aq	aqueduct
AStr	amygdalo-striatal transition area
BF	barrel field of S1
BL	basolateral amygdala
BM	basomedial amygdala
CA	central amygdala
CB	cerebellum
cc	corpus callosum
CG (1–3)	cingulate cortex (areas 1–3)
Cl	claustrum
cp	cerebral peduncle
CPu	caudate–putamen
DH	dorsal hypothalamic area
DI	dysgranular insular cortex
DLG	dorsal lateral geniculate nucleus
DMH	dorsomedial hypothalamic area
DPC	dorsal peduncular cortex
DR(d, v)	dorsal raphe nuclei (dorsal part, ventral part)
ec	external capsule
En	endopiriform nucleus
Ent	entorhinal cortex
fmi	forceps minor corpus callosum
Fr(1,2)	frontal cortex (area 1, 2)
GI	granular insular cortex
GP	globus pallidus
HA	hypothalamic area
Hb	habenula
HF	hippocampal formation
HL	hindlimb area of S1
ic	internal capsule
icv	inferior cerebral vein
IL	infralimbic cortex
LA	lateral amygdala
LC	locus coeruleus
LD	laterodorsal thalamic nucleus
LH	lateral hypothalamic area
LO	lateral orbital cortex
LP	lateral posterior thalamic nucleus
LV	lateral ventricle
M1(2)	primary (secondary) motor cortex
mca	middle cerebral artery
MG(d,m,v)	medial geniculate nucleus (dorsal, medial, ventral division)
mlf	medial longitudinal fasciculus
MO	medial orbital cortex
mPFC	medial prefrontal cortex
MZMGB	marginal zone of the medial geniculate body
NB	basal nucleus of Meynert
OB	olfactory bulb
OC	orbital cortex
Oc(1,2)	occipital cortex (area 1, 2)
Olf1	primary olfactory cortex (Pir)
PAG	periaqueductal grey
Par(1,2)	parietal cortex (area 1, 2)
PH	posterior hypothalamic area
PIN	posterior intralaminar thalamic nucleus
Pir	piriform cortex (Olf1)
PLi	posterior limitans thalamic nucleus
Po	posterior thalamic nucleus
PP	peripeduncular nucleus
PPC	posterior parietal cortex
PRh	perirhinal cortex
PVP	paraventricular thalamic nucleus, posterior part
RS(A,G)	retrosplenial cortex (agranular, granular)
Rt	reticular thalamic nucleus
S1(2)	primary (secondary) somatosensory cortex
SC	superior colliculus
SG	suprageniculate nucleus
SN(C, R)	substantia nigra (*pars compacta, pars reticularis*)
Te1	temporal area 1 (rat auditory core)
Tr	trunk area of S1
V1(2)	primary (secondary) visual cortex
VL	ventrolateral thalamic nucleus
VLG	ventral lateral geniculate nucleus
VLO	ventrolateral orbital cortex
VLPAG	ventrolateral periaqueductal grey
VO	ventral orbital cortex
VPa	ventral pallidum
VTA	ventral tegmental area
ZI	zona incerta

Others

I–VI	cortical cell layers I–VI
BF	best frequency
c	caudal
d	dorsal
FD	fluorescein-labelled dextran
hf	high frequency
l	lateral
lf	low frequency
m	medial
r	rostral
TMRD	tetramethylrhodamine-labelled dextran
v	ventral