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2-1) イントロ

ヒトの大脳皮質には 100 億個を超える (最近では 200 億個とされています) ニューロンが存在しているとされます。これらの大脳皮質ニューロンは興奮性神経伝達物質としては主にグルタミン酸を使用し、抑制性物質としては GABA を用いると考えられています。グルタミン酸と GABA の生合成と代謝についてはニューロンとアストログリアの間で代謝回路が存在することが知られており、ニューロン・グリア関連 neuron-glia interaction の重要な一側面です (図 2-1)。まず、神経伝達物質としてのグルタミン酸は中性アミノ酸であるグルタミンから主に作られることが知られています。この酵素反応は非 ATP 要求性にニューロンの中で行われるのに対して、放出されたグルタミン酸は主にアストログリアに取り込まれてそこで、ATP を消費しながらグルタミンに変えられます。こうして合成されたグルタミンはグリアから放出され細胞

外液に 0.5 mM 程度のグルタミンプールを形成して、グルタミン酸作動性ニューロンの利用に供されます。この代謝の流れはグルタミン回路と呼ばれて、ニューロンとグリアの主要な代謝カップリングの一つです。

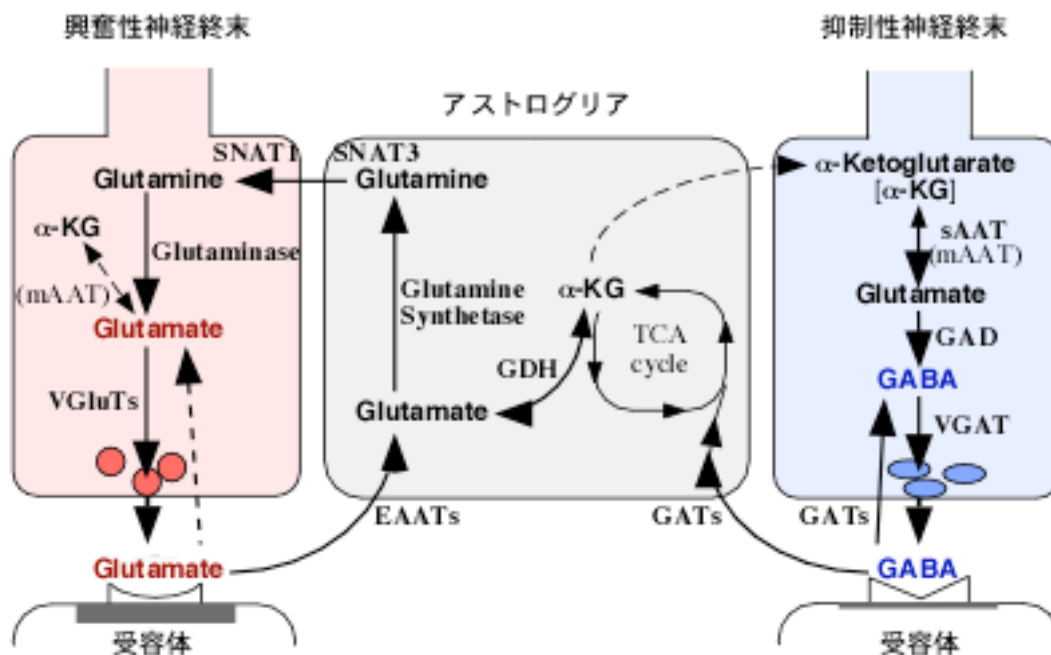


図 2-1

EAAT, excitatory amino acid transporter; GAD, glutamic acid decarboxylase; GAT, GABA transporter; mAAT, mitochondrial aspartate aminotransferase; sAAT, soluble aspartate aminotransferase; SNAT, neutral amino acid transporter; VGAT, vesicular GABA transporter; VGluT, vesicular glutamate transporter.

一方でGABA はグルタミン酸を原料としてグルタミン酸脱炭酸酵素 glutamic acid decarboxylase により、抑制性のGABA作動性ニューロンで合成されます。シナプス間隙に放出された GABA はシナプス終末あるいはアストログリアによって取り込まれ、再利用されるか代謝されると考えられています。

大脳皮質のニューロンをこうした神経伝達物質等の化学的な側面から分類すると表 2-1 のようになります：

表 2-1. 大脳皮質ニューロンの化学的分類

Glutamatergic ... [Spiny cell, Excitatory, 66~88%]

[Pyramidal cell] Cholecystinin

layer II/III; Calbindin

layer IV; ROR β

layer V; ER81, NK3 receptor

layer VI; neurotensin receptor 1

[Spiny stellate cell]

GABAergic ... [Aspiny/smooth non-pyramidal cell, Inhibitory, 10~30%]

Group I: Parvalbumin, Kv3.1b [Basket cell, Chandelier cell]

Small subgroup; Preprotachykinin A (Substance P), Cortistatin, NK1 receptor(+)
 Group II: Somatostatin, Preprodynorphin, mGluR1 α [Martinotti cell, Double bouquet cell]
 Small subgroup; Neuropeptide Y, NO synthase, NK1 receptor(++)
 Group III: [Bipolar cell, Double bouquet cell, Chandelier cell]
 Choline acetyltransferase, Catecholamine, Calretinin, Vesicular glutamate transporter 3
 Vasoactive intestinal polypeptide, Corticotropin releasing factor, Cholecystokinin
 Preproenkephalin, Preprotachykinin B (Neurokinin B), μ -Opioid receptor
 Group IV: [Neurogliaform cell = spider web cell]
 α -actinin2
 Others: L1 horizontal cell, Cajal-Rezius cell

多種類のニューロンが脳皮質には存在していますが、脳皮質のそれぞれの領野が多様な機能をこなしている割には、領野間には構成要素であるニューロンの種類に大きな違いが見られず、何らかの構成原則なり作動原理なりを皮質領野は共有していることが示唆されます。さて、脳皮質の構成ニューロンのうち 62 ~ 88%が興奮性のグルタミン酸作動性ニューロンで、形態学的には錐体ニューロン pyramidal neuron と有棘星状ニューロン spiny stellate neuron に分類されます (表 2-1)。これらのニューロンの樹状突起は棘突起という小さな突起が密集して分布していて、そこには主に興奮性シナプスが形成されます。有棘星状ニューロンは細胞体周囲に多極性に樹状突起を伸ばし、主に細胞体の所属する皮質層への入力を受け取る。錐体ニューロンも細胞体周囲に同様の樹状突起 (基底樹状突起 basal dendrite とよばれる) を多数持ちますが、これに加えて細胞体から表層に伸びる 1 本の尖状樹状突起 apical dendrite をもつところが特徴です。したがって錐体ニューロンは有棘星状ニューロンと同じように細胞体が所属する層で基底樹状突起に入力を受け取りますが、所属する層より上の皮質層でも、典型的には皮質第 I 層などでも尖状樹状突起に入力を受けていることとなります。ある意味、錐体ニューロンの apical dendrite は I 層への入力を受け取るためにあるといっても良いかもしれません。

残りの 12 ~ 38%が抑制性介在ニューロンで、無棘性あるいは棘突起が少ない樹状突起を持ちます。下記は皮質における **GABA neurons** の割合についてのデータのまとめです。

表 2-2. 脳皮質における GABA ニューロンの割合

rat	visual cortex	GAD(+)/total neurons=15%	Lin et al JCN 244:369, 1986
rat	visual cortex	GABA(+)/total neurons = 12-16%	Meinecke and Peters, JCN 261:388, 1987
rat	occipital cortex	GABA(+)/total neurons = 15%	Beaulieu (1993) BR 609: 284
	parietal cortex	GABA(+)/total neurons = 15%	
	frontal cortex	GABA(+)/total neurons = 15%	
rat	area 24b,25,32	GABA(+)/total neurons = 14.8-17.2%	Gabbott et al (1997) JCN 377:465
rat	S1 barrel (P60)	GABA(+)/total neurons = 14%	Micheva, Beaulieu (1995) EJM 7:419
cat	area 17; layer II-VI	GABA(+)/total neurons = 20.6%	Gabbott & Somogyi, EBR 61:323, 1986
	area 17; layer I	GABA(+)/total neurons = 95%	
cat	S1 area 3b	GABA(+)/total neurons = 29.8%	Li, Schwark (1994) JCN 343:353
	S1 area 2	GABA(+)/total neurons = 22.6%	
cat	A1 L1	GABA(+)/total neurons = 94.2%	Prieto et al (1994) JCN 344:349
	A1 L2-6	GABA(+)/total neurons = 16.1-27.1%	
monkey	neocortex	GABA(+)/total neurons = 19-25%	Hendry et al., JNsci 7:1503, 1987
monkey	striate cortex	GABA or GAD(+)/total neurons \geq 15%	Fitzpatrick et al (1987) JCN 264:73

	L1	GABA or GAD(+) / total neurons = 77-81%	
	L2-3A	GABA or GAD(+) / total neurons = 20%	
	L5-6	GABA or GAD(+) / total neurons = 12%	
monkey	aea 24a,b,c, 25, 32	GABA(+) / total neurons = 23.5-27.3%	Gabbott, Bacon (1996) JCN 364:609
human	temporal lobe, total	GABA(+) / total neurons = 37.73%	del Río & DeFelipe (1996) JCN 369:472
	L2	GABA(+) / total neurons = 44.12%	
	L3	GABA(+) / total neurons = 31.33%	

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こうした無棘性という特徴はあるものの、GABA 作動性介在ニューロンには形態学的にも化学的にも非常に多様なニューロンが認められ、その形態から機能が推測されるようなものもあって、軸索が錐体ニューロンの細胞体を籠状に囲んで抑制するバスケット細胞 basket cell、錐体ニューロンの軸索初節を抑制するシャンデリア細胞 chandelier cell、抑制性軸索を皮質の表層に送るマルティノッティ細胞 Martinotti cell など非常に多彩です (表 2-3)。

表 2-3. 大脳皮質の構成要素：形態学的分類

Spiny cell ... glutamatergic

Pyramidal cell

* Betz cell in layer V of area 4

* Meynert solitary cell in layer V-VI of visual cortex

Spiny stellate cell, granule cell (mostly in layer IV; a few in layer VI)

Star pyramid ~ Grain pyramid of Lorente de Nó

Star cell (only in SmI)

Fusifiform cell (layer VI)

Horizontal cell (layer VIb; probably spiny)

Aspiny/smooth cell ... mostly GABAergic

On the basis of dendritic and somatic morphology

Multipolar cell

Bitufted cell, including chandelier cell and double bouquet cell

Bipolar cell

Neurogliaform/spiderweb cell (\in multipolar; layer IV > II/III) ...Late-spiking

Retzius-Cajal horizontal cell (layer I; developmental)

Horizontal cell (layer VIb)

On the basis of axonal morphology

Basket cell (\in multipolar; axonal basket)

Large basket cell (layer III–V, horizontally spread axons) ...Fast-spiking

Small or short-range basket cell of Szentagothai (layer II)

Nest basket cell

Clutch cell (= Small basket cell in layer IV)

Chandelier cell of Szentagothai / Axoaxonic cell of Somogyi ...Fast-spiking

(\in bitufted, multipolar; mainly in layer II/III; rat, cat, monkey)

Double bouquet cell (cellule fusiforme à double bouquet dendritique of Ramón y Cajal)

(\in bitufted, bipolar ~ multipolar in layer II; vertical axon bundle, mainly descending)

Axon tuft cell of Szentagothai

(small multipolar ~ bitufted cell, layer II, ascending axon to layer I)

Martinotti cell (mainly in layers V–VI; multipolar~bitufted, aspiny~sparsely spiny,

ascending axon to layer I) ... Somatostatin, Calbindin, non-fast-spiking (LTS) cell

Arcade cell (\in multipolar; axon ascending and in turn descending, forming archade)

mainly in layer II–IV

こうした形態学的あるいは化学的分類以外に、電気的特性あるいは発火特性に基づいて少なくとも3種類のニューロンが分類され、一部分は形態学的化学的分類と一致する。ニューロンの細胞内電気記録をとる時、脱分極通電に対する反応をみて、Regular-spiking ニューロン、Intrinsic bursting ニューロン、Fast-spiking ニューロンの3種類に区別されます(図2-2)。このうち、皮質ニューロンに最もたくさん見られる電気的特性はRegular-spikingであり、多くの錐体ニューロンと一部の介在ニューロンがこの発火特性を示します。Intrinsic burstingは皮質第V層の錐体ニューロンの一部に特徴的な発火特性です。Fast-spikingの特性は(1)パルブアルブミン陽性、Kv3.1bカリウムチャネル陽性の介在ニューロングループに限定して見られ、鋭い活動電位が高頻度に持続する発火特性です。これらの電気的性質あるいは発火特性の違いはそれぞれのニューロンが果たしている情報処理の役割における違いを反映するものであり、神経回路を考えるとときには重要な分類特性であると言えます。

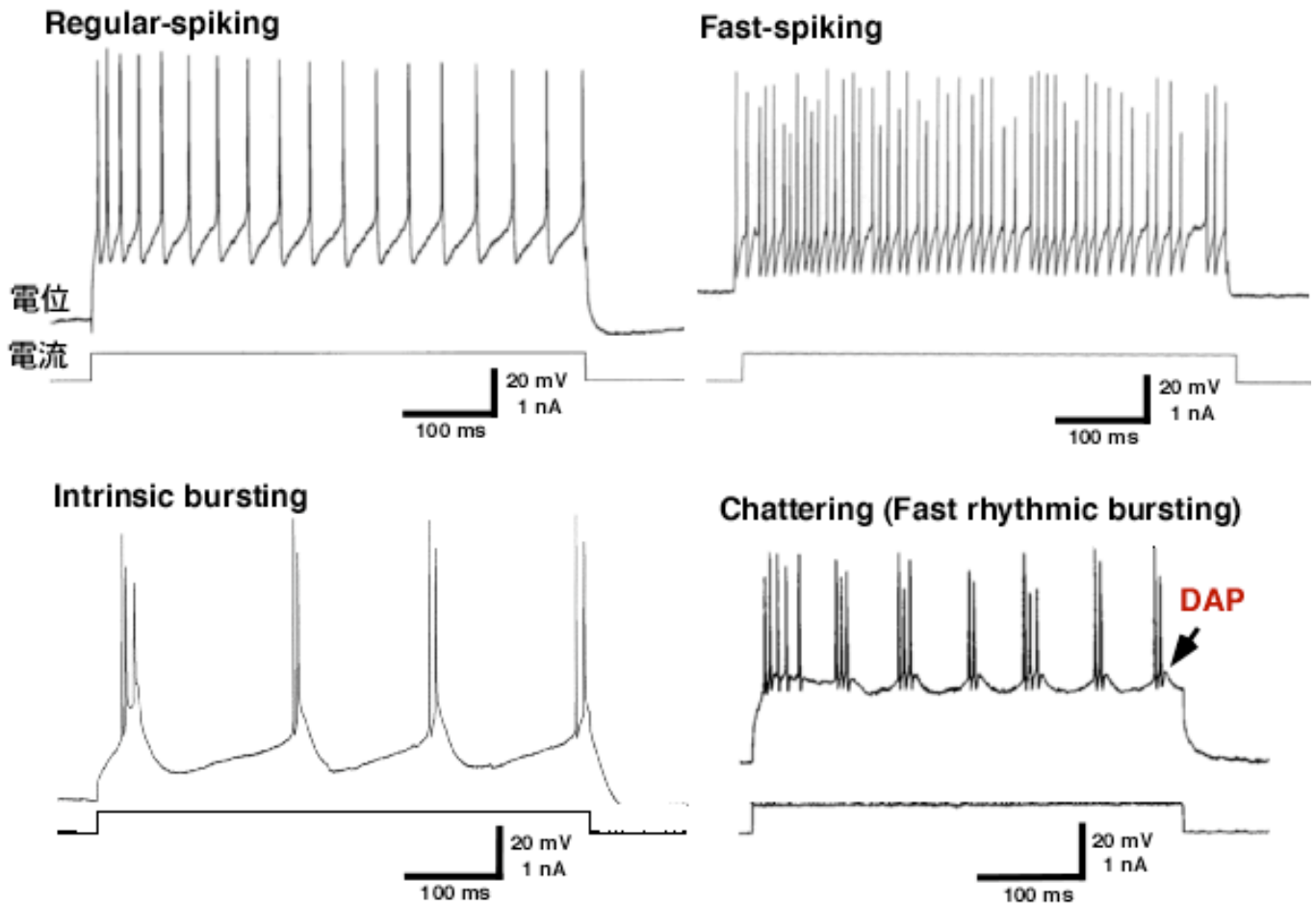


図2-2. 皮質ニューロンの Firing pattern。

Firing pattern of cortical cells

Mountcastle et al JNp 32(69)452; **monkey**, in vivo

*) regular-spiking

Calvin & Sybert JNp 39(78)420; **cat PT neurons**, in vivo intra

Simons JNp 41(78)798; **rat S1**, in vivo

*) fast-spiking

Connors et al JNp 46(82)1302; **guinea pig sensorimotor cortex**, slice

*) Intrinsic burst-generating: multiple decrementing fast spikes riding on a relatively slow depolarizing envelope, evoked at distinct θ , only in 850–1200 μm

McCormick et al JNp 54(85)782; **guinea pig anterior cingulate & sensorimotor areas**,

1) regular spiking: (near θ) single APs, spike frequency is a monotonic function of I

2) bursting: (at a distinct θ) a complex of 3–5 APs riding upon a slow depolarizing envelope, decrementing spike amplitude & rise-rate, terminated by mAHP, not always all-or-none,

3) fast spiking: (near θ) single APs, spike frequency is a monotonic function of I

Montoro et al BR 460(88)168; **visual cortex**;

Agmon & Connors NSL 99(89)137; **mouse S1**, slice

- 1) regular-spiking: adaptation(+), in II–VI
- 2) bursting: repetitive burst (cluster of 2–5 spikes) firing followed by prolonged AHP, in lower V–upper VI

Chagnac-Amitai & Connors JNp 62(89)1149; **rat SmI**, slice

- 1) regular-spiking: adaptation(+), in II–VI
 - a) RS1: DAP(+), adaptation(+)
 - b) RS2: DAP(–), adaptation(+)
 - c) RS3: DAP(+), adaptation(±)
- 2) intrinsically bursting: bursts of ≥ 3 spikes, in IV–V; repetitive bursts in lower V
- 3) fast-spiking: adaptation(–), in II–VI

Silva et al Science 251(90)432; **rat sensorimotor cortex** layer V, slice
 membrane potentials was held btwn –60 & –65 mV,

triggered by 4 ms depolarizing pulse or 100 ms hyperpolarizing pulse

- 1) rhythmic single-spiking: 51% of 81 in V,
- 2) rhythmic bursting: 68% of 65 in V

Chagnac-Amitai et al JCN 296(90)598; **rat S1 & V1**, slice

- 1) 73 intrinsically bursting: burst $\equiv \geq 3$ spikes arising from a slow membrane depolarization
 - a) all-or-none:
 - b) graded: single-spiking at low I, bursts at high I
 - c) repetitive burst-firing
- 2) 28 regular spiking: adaptation(+)

Mason & Larkman JNsci 10(90)1415; **rat V1** layers II/III & V, slice

- 1) burst firing: a large, brief spike followed by a number of broader, decrementing spikes riding on a wave of depolarization; followed by a pronounced AHP; in V
 - a) 2/3 all-or-none, some repetitive
 - b) 1/3 single spikes just supra θ ; burst as I is increased
- 2) repetitive firing:
 - a) initial doublet + repetitive firing: in most III/III
 - b) no initial doublet

Foehring & Wyler NSL 110(90)279; **human**,

Miller et al JCN 297(90)91; **rat somatosensory cortex**, in vivo intra

Agmon & Connors JNsci 12(92)319; **mouse barrel cortex**, slice
 VB stimulation

- 1) regular spiking:
 - a) 36 RS1: initial doublet or triplet of spikes + adaptation(±)
 - b) 5 RS2: adaptation(++)
- 2) 7 intrinsically bursting: mostly repetitive bursts
- 3) 4 fast spiking: adaptation(–)

Van Brederode & Snyder Nsci 50(92)315; **rat sensorimotor area**, slice, VB and VI

- 1) Phasic-tonic: (just above θ) doublets or triplets, followed by single spikes
 (large I) initial doublet or triplet + tonic firing
- 2) Intermediate: (just above θ) single spikes
 (large I) initial doublet or triplet + tonic firing

- 3) Tonic: (just above θ) single spikes
(large I) single spikes

Tseng & Prince JCN 335(93)92; 90 **rat corticospinal neurons**, slice

- 1) 23 adapting: fast (50ms) and slow phase (200 ms) of adaptation; sAHP(+) 15/15; sub θ graded depolarizing response (= hump); only one initial burst of 2–4 spikes; prominent IPSPs by L. I stim; $f > mAHP$?; smaller comata;
- 2) 36 regular spiking without DAP (RS): only fast phase adaptation; $f < mAHP$; sAHP(+) 5/18
- 3) 31 regular spiking with DAP (RS_{DAP}): bursting, large DAP; trains of rhythmic spike bursts (repetitive bursting);

Amitai Nsci 63(94)151; **rat somatosensory cortex**, slice intra

- 1) 28 RS in II/III, 34 RS in V
RS1; fast adaptation alone
RS2; fast adaptation + slow adaptation
- 2) 23 IB in V
RF = rhythmically firing

Kang & Kayano JNp 72(94) 578; **cat motor cortex, layer VI** pyramids, slice intra

- 1) DAP(+) pyramids
- 2) DAP(-) pyramids

2-2) 興奮性ニューロン

(未記載)

錐体細胞と Spiny stellate cell は有棘性樹状突起を持つ興奮性のグルタミン酸作動性のニューロン
*) 錐体ニューロンを投射先で区別する。

2-2-1) L2/3 pyramidal neuron

2-2-2) L4 spiny neuron

2-2-2-1) star pyramid

Lorente de N6 が L1 に到達するものの tuft 形成がほとんどなく発達不良な apical dendrite が存在する L4 spiny neurons を star pyramids と命名しました。

2-2-3) L5 pyramidal neuron

L5 neuron

[Hattox & Nelson 2007 JNp 98:3330-40, mouse S1]

corticothalamic (7.6%), DAP++, adaptation-
corticotrigeminal (7.2%), adaptation-
Va corticostriatal/callosal (26.5%), adaptation++

Donoghue & Kitai JCN 201(81)1; **rat sensory-motor cortex**, corticofugal cells, in vivo intra

Landry et al EBR 57(84)177; **rat PT cells**, in vivo intra

- 1) horizontal collateral
- 2) vertical collateral

Sakai & Woody BR 460(88)1; **cat PT cell**, in vivo intra

Chagnac-Amitai et al JCN 296(90)598; rat neocortex, slice intra

Larkman & Mason, Mason & Larkman JNp 10(90)1407, 1415, **rat visual cortex**, slice intra

Jackie Schiller; **NMDA spike**: EPSP+NMDA current, proximal > distal on L5 Pyr BD,
PPF の原因になる。 pre-bound glutamate, high-pass filter

2 - 2 - 4) **L6a pyramidal neuron** [AD, apical dendrite; BD, basal dendrite]

Ramón y Cajal (1891), Golgi

- 1) medium-size
- 2) triangular, no AD
- 3) fusiform

Lorente de Nó (1949), s/o **mouse**, Golgi

- 1) long spindle, AD to I
- 2) medium spindle, AD to IV(-III)
- 3) short spindle, AD to V

Parnavelas et al BR 261(83)21; **rat area 17**, in vivo intra
2 pyramids of complex type, 1 pyramid of non-oriented type

Peters & Kara JCN 234(1985)218; **rat area 17**, Golgi, EM
pyramids $\geq 95\%$ of total neurons

- 1) 1/4, medium-sized, can have developed BD, resemble smaller layer V pyramids
- 2) 3/4, small, poor BD, resemble layer IV pyramids

Van Brederode & Snyder Nsci 50(92)315, **rat M1 & S1**, slice intra
regular spiking

- 1) 5 long pyramids, superficial part, AD to I-II/III, intermediate firing,
 - 2) 8 short pyramids, deep part, AD to III-IV - V, 1 tonic, 1 phasic-tonic, 6 intermediate firing
- horizontal collaterals in VB-VI, vertical collaterals in superficial layers

Tömböl et al EBR 24(75)107; **cat area 17**, HRP/Golgi
Layer VI pyramids

Lund et al JCN 184(79)599; **cat (monkey) area 17**, Golgi
small to medium

no difference btwn upper & lower VI pyramids

- 1) AD to IV, collaterals in IV
- 2) AD to V, collaterals in V
- 3) (majority) AD to I, collaterals in V, VI and IV

Lin et al BR 172(79)344; **cat area 17**, in vivo intra
≤5 complex, 4 simple, no morphological difference

Gilbert & Wiesel Nature 280(79)120; **cat V1**, in vivo intra
11 layer VI cells, simple in upper VI, complex throughout VI
Fig) 1 pyramid of simple, AD upto III-IV, vertical collaterals to IVab

Gilbert & Wiesel JNsci 3(83)1116; **cat V1**, in vivo intra
8 layer VI spiny cells, 4 clustered collaterals, 3 non-clustered collaterals
Fig) 1 pyramid, simple, collaterals mainly to IV with clusters

Martin & Whitteridge JP353(84)463; **cat V1**, in vivo intra
1 pyramid, S2, mono, X-like
1 pyramid, S1, poly, X-like, collaterals in IVA,B

Noda & Yamamoto 306(84)197; **cat M1**, in vivo intra
not respond to cbl or VL stim
1 pyramid, EP-IPSP by cbr peduncle stim
1 pyramid, EPSP by cbr peduncle stim, AD to I

Mitani et al 235(85)430; **cat A1**, in vivo intra
10 pyramids, 7 anti by MG stim, 1 anti by A2 stim, 3 EPSPs <1.4 ms by MG stim

Katz JNsci 7(1987)1223; **cat area 17**, retrograde & slice intra
1a) >80%, LGd-projecting, medium to large, AD upto III, vertical collateral in IV
1b) 20%, LGd-projecting, small, AD upto IVc, collateral in V-VI
2) claustrum-projecting, AD tall to I, horizontal collateral in (V-)VI

Ghosh et al JCN 269(88)290; **cat area 4 γ** , in vivo intra
no recurrent collaterals
1) 2 'bitufted' cell (modified pyramidal), 1 AD to III, 1 AD to I
2) 2 pyramids, AD to I

Yamamoto & Oka BR 18(93)129; **cat areas 5 & 7**, in vivo intra
20 pyramids, including inverteds (EPSPs; 5 by cbl nu, 8 by VA, 9 by LP stim)

Kang & Kayano JNp 72(94)578; **cat M1**, slice intra
1) 9 DAP(+), 7 short AD to III, collaterals in V-VI
2) 13 DAP(-), 11 long AD to I-II, collaterals in III-V

Lund & Boothe JCN 159(75)305; **monkey area 17**, Golgi
1) upper 1/3 VI pyramids, AD to IIIA-II with branches in VB
2) middle 1/3 VI pyramids, AD to IIIB or IVC α with branches in VA, s/o to LGpc
3) VIb 'pyramids', AD to IVB or IVC α with branches in VA, s/o to LGmc
4) giant Mynert cell, in upper 1/3 VI, AD to IVC α or IVB, not to LG or SC

Lund et al 202(81)19 JCN; **primate V2**, Golgi
1) upper VI pyramids, AD to IIIB, vertical collaterals
2) lower VI 'horizontal' pyramids, AD to IIIB, vertical collateral

Hendry & Jones JNcyt 12(83)277; **monkey areas 3b, 1, 2, 5**, Golgi

AD not beyond IIIA or II; some AD to IIIB or IV

Anderson et al CC 3(93)412; **monkey V1**, in vivo intra
1 pyramid of non-oriented, extensive parasagittal collaterals in 4C β

2-3) 抑制性ニューロン

2-3-1) colocalization table

まず、以下に抑制性ニューロンにおける伝達物質等の共存の状況についての表を掲げます。

表 2-x. 大脳皮質インターニューロンにおける伝達物質等の共存

GABA vs. transmitters

mouse	visual cortex	$GABA \cap ChAT/ChAT=99\%$, $GABA \cap ChAT/GABA=0.7\%$	Gonchar et al (2008) FrontNeuroanat 1:1
rat	cortex	$(GABA \cap ChAT) / ChAT= 50\%$	Kosaka et al., EBR 70:605, 1988
rat	SI cortex	$(ChAT \cap GABA)/CAT= 88\%$	Bayraktar et al. BR 757:209, 1997
rat	cortex	$GABA \supset TH$	Kosaka et al., EBR 66:191, 1987
human	cortex	$(GABA \cap TH) / TH= 50\%$	Trottier et al, NSL 106:76, 1989
rat	cortex	$GABA \supset NOS = NADPHd$	Valtschanoff et al., NSL 157:157, 1993
rat	frontal agranular cortex	$GABA \supset NOS$	Kubota et al., BR 649:159, 1994
rat	mPFC(24b,25,32)	$GABA \supset NADPHd$	Gabbott & Bacon, BR699:321, 1995

GABA vs. CBPs

mouse	visual cortex	$GABA \supset PV (39\%)$ $GABA \supset CR (24\%)$	Gonchar et al (2008) FrontNeuroanat 1:1
rat	cortex	$GABA \supset PV (70\%)$	Celio, Science 231:995, 1986
rat	frontal agranular cortex II/III V-VI VI	$GABA \supset PV, GABA \supset CR$ $GABA \supset strong CB, (GABA \cap CB)/CB=10\%$ $(GABA \cap CB)/CB=96\%$ $GABA \supset strong CB$	Kubota et al., BR 649:159, 1994
rat	neocortex layer I layer II-IV layer V-VI	$CB \cap GABA/CB = 50\%$ $CR \cap GABA \neq \phi, CB \cap GABA = \phi$ $CR \cap GABA/CR = 25\%$ $CR \cap GABA/CR < 25\%$	Rogers, BR587:147, 1992
rat	paleocortex visual	$CR \cap GABA/CR = 25\%$, $CB \cap GABA/CB = 75\%$ $GABA \supset PV (51\%), GABA \cap CR /CR = 94\%$, $GABA \cap CR /GABA = 17\%$	Gonchar and Burkhalter, CC 7:347, 1997
rat	V1 L1-3	$CR \cap GABA/GABA = 17.9\%$, $CR \cap GABA/CR = 94\%$ $CR \cap GABA/CR = 100\%(L1), 90\%(L2/3)$	Gonchar & Burkhalter, CC9:683-96, 1999
VGAT Tg rat	frontal	$PV \cap Venus/Venus=36\%(L2/3), 53\%(L5), 39\%(L6)$ $CR \cap Venus/Venus=36\%(L1), 21\%(L2/3), 11\%(L5), 11\%(L6)$	Uematsu et al 2008 CC 18:315-30
cat	primary auditory cortex	$GABA \supset PV \cup CB (70-75\%)$	Hendry & Jones, BR 543:45, 1991
cat	visual cortex	$GAD \cap CB / CB = 63\%$, $GAD \cap CB / GAD = 20\%$	Demeulemeester et al. JNsci 8:988, 1988
cat	visual cortex	$CB \cap GABA/CB=80\%$, $CB \cap GABA/GABA=18\%$ $GABA \supset PV (37\%)$	Demeulemeester et al, EBR 84:538, 1991
monkey	neocortex	$GABA \supset PV \cup CB (>98\%)$	Hendry et al., EBR 76:467, 1989
monkey	striate cortex	$GABA \supset PV (74\%) \cup CB (12\%)$	van Brederode et al., JCN 298:1, 1990
human	temporal lobe L1	$(GABA \cap CB)/CB=70.58\%$, $(GABA \cap CB)/GABA=33.02\%$ $(GABA \cap CR)/CR=74.2\%$, $(GABA \cap CR)/GABA=46.21\%$ $(GABA \cap CR)/CR=77.88\%$	del Río & DeFelipe (1996) JCN 369:472
rat	hippocampus pyramidal granule, oriens hilus, lucid mol, rad, lac-mol	$GAD \supset PV (40-50\%)$ $GAD \supset PV (20-30\%)$ $GAD \supset PV (15-20\%)$ $GAD \supset PV (1-4\%)$	Kosaka et al., BR 419:119, 1987

rat	piriform cortex L.I piriform cortex L.II piriform cortex L.III	$CB = \phi, PV = \phi$ $GABA \supset PV (11\%) \cup CB (25\%) \supset PV \cap CB (10\%)$ $GABA \supset PV (49\%) \cup CB (80\%) \supset PV \cap CB (47\%)$	Kubota & Jones BR 600:339, 1993
GABA vs. peptides			
mouse	visual cortex	$GABA \cap SS / SS = 98\%, GABA \cap SS / GABA = 23\%$ $GABA \supset VIP (11\%)$ $GABA \supset NPY (8\%)$ $GABA \cap CCK / CCK = 95\%, GABA \cap CCK / GABA = 5\%$	Gonchar et al (2008) FrontNeuroanat 1:1
rat	visual cortex	$GAD \cap SS / SS = 80-85\%$	Lin et al., JCN 244:369, 1986
rat	neocortex (SI, 17)	$GAD \supset SP (18-22\%)$	Penny et al. NSL 65:53, 1986
rat	cortex	$GABA \supset CCK$	Kubota & Kawaguchi, BR 752:175, 1997
rat	frontal agranular cortex	$GABA \supset SS, NPY, VIP$	Kubota et al., BR 649:159, 1994
rat	frontal cortex	$GABA \supset CRF (22\% \text{ in L2/3}, 19\% \text{ in L5}, 22\% \text{ in L6})$	Kubota et al (2011) CC
rat	SI cortex	$GABA \supset VIP$	Bayraktar et al. BR 757:209, 1997
rat	visual	$GABA \cap SS / SS = 90\%, GABA \cap SS / GABA = 17\%$	Gonchar and Burkhalter, CC 7:347, 1997
VGAT Tg rat	frontal	$SS \cap Venus / Venus = 17\% (L2/3), 29\% (L5), 29\% (L6)$ $VIP \cap Venus / Venus = 3\% (L1), 24\% (L2/3), 10\% (L5), 8\% (L6)$ $CCK \cap Venus / Venus = 1\% (L1), 9\% (L2/3), 3\% (L5), 3\% (L6)$	Uematsu et al 2008 CC 18:315-30
rat, cat, monkey	cortex, hippocampus	$GAD \cap SS \neq \phi$	Schmechel et al., NSL 47:227, 1984
mouse	S1 barrel L4 hollow	$GAD \cap PV / GAD = 66\%$	Siucinska & Kossut Nsci 138:716, 2006
cat	cortex	$GAD \supset CCK, SS, NPY$	Hendry et al., PNAS 81:6526, 1984
cat	visual cortex	$GAD \cap SS / SS = 89\%, GAD \cap SS / GAD = 2\%$ $GAD \cap NPY / NPY = 100\%, GAD \cap NPY / GAD = 1\%$ $GAD \cap CCK / CCK = 89\%, GAD \cap CCK / GAD = 11\%$ $GAD \cap CRF = \phi, GAD \cap VIP = \phi$	Demeulemeester et al. JNsci 8:988, 1988
cat	visual cortex hippocampus	$GABA \supset GAD \supset CCK \cup SS$ $GABA \supset GAD \supset CCK \cup SS$	Somogyi et al., J Nsci 4:2590, 1984
monkey	cortex	$(GAD \cap X) / X = 90-95\% (X = CCK, SS, NPY)$	Hendry et al., PNAS 81:6526, 1984
monkey	cerebral cortex	$GABA \supset \text{small tachykinin cell}$ $GABA \cap \text{large tachykinin cell} = \phi$ $NPY \cap SS \supset \text{large tachykinin cell}$	Jones et al., JNsci 8:1206, 1988
rat	hippocampus radiatum pyramidale oriens hippocampus	$GAD \supset CCK (10\%)$ $GAD \supset CCK (15-20\%)$ $GAD \supset CCK (10\%)$ $GAD \supset CCK (6\%)$ $GAD \cap VIP / VIP = 40\%$	Kosaka et al., JCN 239:420, 1985
rat	hippocampus hilus, oriens pyr, lucid, rad CA3 gra, mol, pyr, rad CA1	$GAD \cap SS / SS = 90\%, GAD \cap SS / GAD = 10\%$ $GAD \cap SS / GAD = 30\%$ $GAD \cap SS / GAD = 5-10\%$ $GAD \cap SS / GAD = 2\%$	Kosaka et al., EBR 71:388, 1988
rat	entorhinal cortex	$GABA \cap SS / GABA = 8\%, GABA \cap SS / SS = 18\%$	Wouterlood, Pothuizen 2000 Hipp 10:77-86
GABA vs Receptor			
rat	V1	$GluR1 \cap GABA / GABA = 38\%$ $GluR1 \cap GABA / GluR1 = 28.5\%$ $GluR2-3 \cap GABA / GABA = 10\%$ $GluR2-3 \cap GABA / GluR2-3 = 1.5\%$	Gutiérrez-Ivarluzea et al, NR 8:2495, 1997
rat	neocortex	$GluR1++ \cap GAD / GAD = 30\%$ $GluR1++ \cap GAD / GluR1++ = 90\%$ $GluR1++ \cap GABA / GluR1++ = 95\%$	Kharazia et al, JCN 368:399, 1996
rat	Dentate gyrus Cornu ammonis	$GluRBmRNA \cap GAD67 / GAD67 = 52 \sim 86 (64)\%$ $GluRBmRNA \cap GAD67 / GAD67 = 18 \sim 83 (57)\%$	Racca et al., EJNsci 8:1580, 1996
human	neocortex	$GluR1 \supset GABA$	He et al EBR 112:147, 1996
rat	neocortex	$GABA \supset mGluR1\alpha (20\%)$	Steinhelfer et al 2000 BR 861:37-44
rat	hippocampus	$M2 \cap GABA / M2 = 94\%$	Hojos et al, Nsci 82:355, 1998
rat	neocortex, hippocampus	$mGluR1mRNA (+)$ on $GAD67mRNA$ $mGluR5mRNA (++)$ on $GAD67mRNA$	Kerner et al MolBR 48:259, 1997
rat	neocortex, hippocampus	$5HT3aRmRcGABAir$	Morales et al BR 731:199-202, 1996
BAC Tg mice	S1	$5HT3aRGFP + scRTPCR; GAD65/67+$	Vacurovic et al CC 20:2333-47, 2010

BAC Tg mice S1
monkey F/T/P cortex

5HT3aRGFPCCad67mR
5HT3RirCGABAir

Lee et al JNs 30:16796-808, 2010
Jakab, Goldman-Rakic, JCN417:337-48 2000

between Transmitters

Transmitters vs. CBPs

mouse	visual cortex	$PV \cap ChAT = \phi, CR \cap ChAT = \phi$	Gonchar et al (2008) FrontNeuroanat 1:1
rat	piriform cortex layer II	$CR \cap Asp \neq \phi, CR \cap Glu \neq \phi, (PV \cup CB) \cap (Asp \cup Glu) = \phi$	Frassoni et al., Nsci 83:229, 1998
rat	frontal agranular cortex II/III	$PV \cap NOS = \phi, CR \cap NOS = \phi$	Kubota et al., BR 649:159, 1994
	V-VI	$(NOS \cap only \text{ weakCB}) / NOS = 29\%,$ $(NOS \cap CB) / CB = 8\%, (NOS \cap CB) / NOS = 80\%,$	
rat	frontal cortex all Ls	$NOS \cap CR / CR \approx \phi$ faint $NOS \cap PV / PV = 4\% (L2/3), 11\% (L5), 25\% (L6)$	Kubota et al (2011) CC
rat	cortex	$CAT \cap CR / CAT = 77\%, CAT \cap CR / CR = 45\%$	Taki, 2000
rat	visual	$PV \cap NOS = \phi, CR \cap NOS = \phi$	Gonchar and Burkhalter, CC 7:347, 1997
monkey	neocortex	large $NOS \cap CB = \phi$	Smiley et al 2000 BR 863:205-12

Transmitters vs. Peptides

mouse	visual cortex	$ChAT \cap VIP / ChAT = 100\%, ChAT \cap VIP / VIP = 9\%$ $ChAT \cap SS = \phi, ChAT \cap NPY = \phi, ChAT \cap CCK = \phi$	Gonchar et al (2008) FrontNeuroanat 1:1
rat	cortex	$ChAT \cap VIP / ChAT = 80\%$	Eckenstein, Baugman, Nature 309:153, 1984
rat	cortex	$CAT \cap VIP / CAT = 32\%, CAT \cap VIP / VIP = 19\%$	Chédotal et al, BR 646:181, 1994
rat	cortex	$CAT \cap VIP / CAT = 97\%, CAT \cap VIP / VIP = 47\%$	Taki 2000
rat	SI cortex	$CAT \cap VIP / VIP = 34\%$	Bayraktar et al. BR 757:209, 1997
rat	cortex	$CAT \cap CRF / CAT = 31\%, CAT \cap CRF / CRF = 41\%$	Taki 2000
cat	neocortex	$Glu \cap SP / SP = 7.4\%$ (mostly pyramidal cells)	Conti et al. BR 599:140, 1992
rat	frontal agranular cortex II/III	$SS \cap NPY \supset NOS$	Kubota et al., BR 649:159, 1994
	V-VI	$(NOS \cap SS) / SS = 11\%, (NOS \cap NPY) / NPY = 43\%,$ $(NOS \cap SS) / SS = 26\%, (NOS \cap NPY) / NPY = 52\%,$	
rat	cortex	$CCK \cap NOS = \phi,$	Kubota & Kawaguchi, BR 752:175, 1997
rat	frontal cortex all Ls	$NOS \cap SS \cap SPR / [SS \cap SPR] = 100\%$ $NOS \cap (SS - SPR) \approx \phi$ $NOS \cap VIP / VIP \approx \phi, NOS \cap CCK / CCK \approx \phi$	Kubota et al (2011) CC
rat	visual	$SS \cap NOS / SS = 1.7\%$	Gonchar and Burkhalter, CC 7:347, 1997
rat	frontoparietal	$PPTA \cap ChAT = \phi$ $PPTB \cap ChAT / ChAT = 45.1\%, - / PPTB = 12.9\%$ $PPTA \cap NOS / NOS = 4.2\%, - / PPTA = 3.8\%$ $PPTB \cap NOS = \phi$	Kaneko et al 1998
monkey	neocortex	$SS \cap NPY \supset large \text{ NOS (30\% of SS, 60\% of NPY)}$ small $NOS \cap CB / SNOS = 87\sim 98\%,$ $SNOS \cap CB / CB = 20\%$	Smiley et al 2000 BR 863:205-12

Transmitters vs Receptors

between CBPs

mouse	visual cortex	$PV \cap CR = \phi$	Gonchar et al (2008) FrontNeuroanat 1:1
mouse	frontal, S1, V1 all Ls	$PV \cap CR = \phi$	Xu et al (2010) JCN 518:389-404
rat	neocortex	$CR \cap CB = \phi$	Rogers & Résibois, Nsci 51: 843, 1992
	pyriform cortex	$CR \cap CB = \phi$	
	hippocampus	$CR \cap CB = \phi$	
rat	sensorimotor cortex upper layer	$(PV \cap CB) / PV = 20\%, (PV \cap CB) / CB = 50\%$	Van Brederode, Nsci 44:157, 1991
	deeper layer	$PV \cap CB = \phi$	
	piriform cortex	$PV \approx CB$	
rat	frontal agranular cortex II/III	$(PV \cap CB) / PV = 91\%, (PV \cap strong \text{ CB}) / PV = 11\%$ $(CR \cap CB) / CR = 6\%, PV \cap CR = \phi$	Kubota et al., BR 649:159, 1994
	V-VI	$(PV \cap CB) / PV = 6\%, (PV \cap CB) / CB = 7\%$ $(CR \cap CB) / CR = 17\%, (CR \cap CB) / CB = 4\%$	

rat	visual	$PV \cap CR = \phi$	Gonchar, Burkhalter, CC 7:347, 1997
rat	piriform cortex L.I	$PV \cap CR = \phi, (PV \cap CB) / PV = 5\%, CB \cap CR = \phi,$	Kubota, Jones BR 600:339, 1993
	piriform cortex L.II	$CB = \phi, PV = \phi$	
	piriform cortex L.III	$(PV \cap CB) / PV = 41\%, (PV \cap CB) / CB = 93\%$	
cat	visual cortex	$(PV \cap CB) / PV = 97\%, (PV \cap CB) / CB = 59\%$	Demeulemeester et al., NSL 99:6, 1989
cat	visual cortex	$PV \cap CB = \phi$	Demeulemeester et al, EBR 84:538, 1991
monkey	neocortex	$PV \cap CB < 1\%$	Hendry et al., EBR 76:467, 1989
monkey	prefrontal cortex	$PV \cap CB = \phi, CR \cap CB = \phi, PV \cap CR = \phi$	Condé et al (1994) JCN 341:95
	L1 Cajal-Retzius cell	$CR+ \& CB+$	
human	temporal lobe	$(CR \cap CB) / CB = 6.2\%, (CR \cap CB) / CR = 4.43\%$	del Río & DeFelipe (1996) JCN 369:472
human	temporal cortex	$(CR \cap CB) / CR = 11\%, (CR \cap CB) / CB = 11\%$	delRio, DeFelipe, JChemNeuroanat13:243, 1997
		** much higher coexistence in axons	

CBPs vs Peptides

mouse	frontal, S1, V1	$CR \cap SS / SS = 30\%, CR \cap SS / CR = 33\%$	Xu et al (2006) JCN 499:144
mouse	visaul cortex	$PV \cap SS = \phi, PV \cap VIP = \phi, PV \cap CCK = \phi, PV \cap NPY = \phi,$ $CR \cap SS / SS = 59\%, CR \cap SS / CR = 55\%$ $CR \cap VIP / VIP = 51\%, CR \cap VIP / CR = 35\%$ $CR \cap NPY / NPY = 61\%, CR \cap NPY / CR = 14\%$ $CR \cap CCK / CCK = 48\%, CR \cap CCK / CR = 61\%$	Gonchar et al (2008) FrontNeuroanat 1:1
mouse	frontal all Ls	$CR \cap SS / SS = 26.8\%, CR \cap SS / CR = 41.2\%$ $CR \cap NPY / NPY = 12.4\%, CR \cap NPY / CR = 8.5\%$ $CR \cap VIP / VIP = 30.3\%, CR \cap VIP / CR = 29.9\%$ $PV \cap SS / SS = 0.1\%, PV \cap SS / PV = 0.1\%$ $PV \cap NPY / NPY = 0.5\%, PV \cap NPY / PV = 0.2\%$ $PV \cap VIP = \phi$	Xu et al (2010) JCN 518:389-404
	L1	$CR \cap SS / SS = 57.1\%, CR \cap SS / CR = 17.4\%$ $CR \cap NPY / NPY = 5.9\%, CR \cap NPY / CR = 14.3\%$ $CR \cap VIP = \phi$ $PV \cap SS = \phi, PV \cap NPY = \phi$	
	L2/3	$CR \cap SS / SS = 81.4\%, CR \cap SS / CR = 41.2\%$ $CR \cap NPY / NPY = 10.2\%, CR \cap NPY / CR = 5.1\%$ $CR \cap VIP / VIP = 26.3\%, CR \cap VIP / CR = 28.6\%$ $PV \cap SS = \phi, PV \cap NPY = \phi$	
	L4	$CR \cap SS / SS = 44\%, CR \cap SS / CR = 41\%$ $CR \cap NPY / NPY = 9.5\%, CR \cap NPY / CR = 4.4\%$ $CR \cap VIP / VIP = 53.6\%, CR \cap VIP / CR = 27.2\%$ $PV \cap SS = \phi$ $PV \cap NPY / NPY = 1.7\%, PV \cap NPY / PV = 0.3\%$	
	L5	$CR \cap SS / SS = 11.5\%, CR \cap SS / CR = 51.5\%$ $CR \cap NPY / NPY = 33.3\%, CR \cap NPY / CR = 14.5\%$ $CR \cap VIP / VIP = 42.9\%, CR \cap VIP / CR = 32.5\%$ $PV \cap SS = \phi$ $PV \cap NPY / NPY = 1.5\%, PV \cap NPY / PV = 0.2\%$	
	L6	$CR \cap SS / SS = 5.7\%, CR \cap SS / CR = 33.3\%$ $CR \cap NPY / NPY = 63.9\%, CR \cap NPY / CR = 23.1\%$ $CR \cap VIP / VIP = 27.1\%, CR \cap VIP / CR = 39\%$ $PV \cap SS = \phi, PV \cap NPY = \phi$	
	S1 all Ls	$CR \cap SS / SS = 15.1\%, CR \cap SS / CR = 33\%$ $CR \cap NPY / NPY = 11.8\%, CR \cap NPY / CR = 12.3\%$ $CR \cap VIP / VIP = 26.5\%, CR \cap VIP / CR = 32.4\%$ $PV \cap NPY / NPY = 0.5\%, PV \cap NPY / PV = 0.1\%$ $PV \cap VIP = \phi, PV \cap SS = \phi$	
	L1	$CR \cap SS / SS = 90.9\%, CR \cap SS / CR = 40\%$ $CR \cap NPY = \phi, CR \cap VIP = \phi$ $PV \cap NPY = \phi$	
	L2/3	$CR \cap SS / SS = 57.2\%, CR \cap SS / CR = 37.1\%$ $CR \cap NPY / NPY = 9.9\%, CR \cap NPY / CR = 9.5\%$	

		CR∩VIP/VIP= 21.5%, CR∩VIP/CR= 28%	
		PV∩NPY/NPY=1%, PV∩NPY/PV= 0.8%	
	L4	CR∩SS/SS= 7.1%, CR∩SS/CR= 13.7%	
		CR∩NPY/NPY= 10%, CR∩NPY/CR= 7.8%	
		CR∩VIP/VIP= 35.5%, CR∩VIP/CR= 35.1%	
		PV∩NPY=φ	
	L5	CR∩SS/SS= 8%, CR∩SS/CR= 37.9%	
		CR∩NPY/NPY=14.5%, CR∩NPY/CR= 12.6%	
		CR∩VIP/VIP= 41.3%, CR∩VIP/CR= 38.8%	
		PV∩NPY=φ	
	L6	CR∩SS/SS= 7.1%, CR∩SS/CR= 40%	
		CR∩NPY/NPY= 17.4%, CR∩NPY/CR= 31.2%	
		CR∩VIP/VIP= 28.7%, CR∩VIP/CR= 51%	
		PV∩NPY=φ	
	V1 all Ls	CR∩SS/SS= 27.1%, CR∩SS/CR= 34.3%	
		CR∩NPY/NPY= 21.9%, CR∩NPY/CR= 9.5%	
		CR∩VIP/VIP= 47.4%, CR∩VIP/CR= 39.7%	
		PV∩VIP=φ, PV∩SS=φ, PV∩NPY=φ	
	L1	CR∩SS/SS= 75%, CR∩SS/CR= 18.8%	
		CR∩NPY/NPY= 25%, CR∩NPY/CR= 9.5%	
		CR∩VIP/VIP= 14.3%, CR∩VIP/CR= 18.5%	
	L2/3	CR∩SS/SS= 63.2%, CR∩SS/CR= 26.2%	
		CR∩NPY/NPY= 20.7%, CR∩NPY/CR= 9.4%	
		CR∩VIP/VIP= 43.7%, CR∩VIP/CR= 45.1%	
	L4	CR∩SS/SS= 39.5%, CR∩SS/CR= 39.2%	
		CR∩NPY/NPY= 30.2%, CR∩NPY/CR= 6.6%	
		CR∩VIP/VIP= 59.8%, CR∩VIP/CR= 27.6%	
	L5	CR∩SS/SS= 13.6%, CR∩SS/CR= 54.3%	
		CR∩NPY/NPY=17.5%, CR∩NPY/CR= 9.7%	
		CR∩VIP/VIP= 56.5%, CR∩VIP/CR= 50%	
	L6	CR∩SS/SS= 5.5%, CR∩SS/CR= 18.9%	
		CR∩NPY/NPY= 19.6%, CR∩NPY/CR= 26.2%	
		CR∩VIP/VIP= 59.1%, CR∩VIP/CR= 74.3%	
rat	cortex	PV ∩ CCK = φ, PV ∩ SS ≅ φ (2/934PV)	Kosaka et al., BR 409:403, 1987
rat	neocortex	CR∩SS = φ, CB∩VIP = φ	Rogers, BR587:147, 1992
	layer II-IV	CB∩SS /CB < 66%, CB∩SS /SS = 75%	
		CR∩VIP /CR = 63%, CR∩VIP /VIP = 45%	
	layer V-VI	CB∩SS /CB= 84%, CB∩SS /SS= 84%	
		CR∩VIP /CR = 90%, CR∩VIP /VIP = 95%	
	paleocortex	CR∩SS = φ, CB∩VIP = φ	
		CB∩SS /CB= 49%, CB∩SS /SS= 63%	
		CR∩VIP /CR = 87%, CR∩VIP /VIP = 85%	
rat	frontal agranular cortex	PV∩(VIPUSSUNPY) = φ, CR∩(SSUNPY) = φ	Kubota et al., BR 649:159, 1994
		CB∩VIP = φ	
	I	CR∩VIP = φ	
	II/III	(CR∩VIP) /CR = 71%, (CR∩VIP) /VIP = 57%	
		(CB∩SS) /SS=85%, (strongCB∩SS) /SS=35%	
		(strongCB∩SS) /strongCB=68%	
		(CB∩NPY) /NPY=68%, (strongCB∩NPY) /NPY=37%	
		(strongCB∩NPY) /strongCB=39%	
	V-VI	(CR∩VIP) /CR = 94%, (CR∩VIP) /VIP = 94%	
		(CB∩SS) /SS=92%, (CB∩SS) /CB=68%	
		(CB∩NPY) /NPY=95%, (CB∩NPY) /CB=24%	
rat	cortex	CCK∩PV=φ,	Kubota & Kawaguchi, BR 752:175, 1997
	II/III	(CCK∩CR) /CCK=5%, (CCK∩CR) /CR=2%	
		(CCK∩CB) /CCK<1%	
	V	(CCK∩CR) /CCK=25%, (CCK∩CR) /CR=5%	
		CCK∩CB=φ	
	VI	(CCK∩CR) /CCK=11%, (CCK∩CR) /CR=3%	
		(CCK∩CB) /CCK=8%, (CCK∩CB) /CB<1%	

rat	frontal cortex	PV∩CRF=ϕ CR∩CRF <10% CR∩CRF/CRF=20-30%, -/CR=15% [CR∩CRF∩(no VIP)]= ϕ L2/3 [CR∩CRF∩VIP]/CRF∩VIP]=13% L5 [CR∩CRF∩VIP]/CRF∩VIP]=58% L6 [CR∩CRF∩VIP]/CRF∩VIP]=63% L2/3 [(CR+CRF)∩VIP]/VIP=98% L5 [(CR+CRF)∩VIP]/VIP=92% L6 [(CR+CRF)∩VIP]/VIP=83% NPY∩PV=ϕ, NPY∩CR=ϕ	Kubota et al (2011) CC
rat	visual cortex	PV∩SS = ϕ, CR∩SS = ϕ, CB∩SS /SS = 86% VIP∩CR/VIP =66%, VIP∩CR/CR= 74% CRF∩CR/CRF =8.2%, CRF∩CR/CR= 1.7%	Gonchar and Burkhalter, CC 7:347, 1997 Taki, 2000
rat	frontoparietal	PPTA∩PV/PV = 6.4%, -/PPTA = 68.7% PPTA∩CB/CB = 4.3%, -/PPTA = 27% PPTA∩CR=ϕ, PPTB∩PV=ϕ PPTB∩CB/CB = 3.9%, -/PPTB = 6% PPTB∩CR/CR = 33.3%, -/PPTB = 21.4%	Kaneko et al 1998
rat	neocortex	CsmRNA∩PV/PV = 40% CsmRNA∩CB/CsmR = 47% (L2/3), ~ϕ (L5/6) CsmRNA∩CR=ϕ	de Lecea et al (1997) JNs 17:5868
cat	visual cortex	CB∩SS /CB = 7%, CB∩SS /SS = ? CB∩NPY= ϕ, CB∩VIP =ϕ, CB∩CRF = ϕ	Demeulemeester et al. JNsci 8:988, 1988
cat	visual cortex	PV∩(CCK∩NPY)= ϕ, PV∩SS ≅ ϕ (only a few)	Demeulemeester et al, EBR 84:538, 1991
monkey	medial frontal	(CR∩VIP)/VIP = 80%, (CR∩VIP)/CR = 86%	Gabbott and Bacon BR 744:179, 1997
monkey	neocortex	CB∩tachykinin/CB ≈ CB∩TK/TK < 20%, ≠ ϕ	DeFelipe et al. Nsci 37:655, 1990
rat	dentate hilus	(PV∩SS) / SS= 5.7% , (PV∩SS) / PV= 6.1%	Nitsch et al., BR 528:327, 1990

CBPs vs Receptors

monkey	area 46	NR1∩PV/PV=45%, NR1∩CR/CR=5%, NR1∩CB-non-pyr/CB-non-pyr=24%	Huntley et al, BR749:245, 1997
	area TE1	NR1∩PV/PV=59%, NR1∩CR/CR=6% NR1∩CB-non-pyr/CB-non-pyr=82%	
monkey	M1	NR1∩PV/PV=90%, NR1∩CR/CR=6%, NR1∩PV/PV=88%, NR1∩CR/CR=7% NR1∩PV/PV=83%, NR1∩CR/CR=9%	Huntley et al, JNsci 14:3603, 1994
monkey	Prefrontal	GluR2-3∩PV/PV=32%, GluR5-6-7∩PV/PV=50% GluR2-3∩PV/GluR2-3=2.9% GluR5-6-7∩PV/GluR5-6-7=5.9% GluR2-3∩CB/CB=28%, GluR5-6-7∩CB/CB=31% GluR2-3∩CB/GluR2-3=1.7% GluR5-6-7∩CB/GluR5-6-7=2.4% GluR2-3∩CR/CR<1%, GluR5-6-7∩CR/CR<1% GluR2-3(CR∩CB) / CR = 11% GluR5-6-7∩CR/GluR5-6-7<1%	Huntley et al, JNsci 13:2982, 1993
rat	neocortex, hippocampus	mGluR1mRNA(-) on PVmRNA mGluR5mRNA(++) on PVmRNA	Kerner et al MolBR 48:259, 1997
rat	neocortex	mGluR1α∩CB++ / CB++ = 30% mGluR1α∩CR / CR = 50%, mGluR1α∩PV~ϕ	Steinhelfer et al 2000 BR 861:37-44
rat	neocortex	5HT3RmRNA∩PV=ϕ 5HT3RmRNA∩CB≠ϕ?, 5HT3RmRNA∩CR≠ϕ	Morales & Bloom, JNsci 17:3157, 1997
human	sup temp gyrus	α4nAChR∩PV= 88-89%, α7nAChR∩PV= 88-89%	Krenz et al (2001) J Chem Neuroanat 21: 236
rat	hippocampus	M2∩CR/M2 = 15~36%, M2∩PV/M2 = 3% M2∩PV/M2 = 4%	Hojos et al, Nsci 82:355,1998
mouse	neocortex	CB1∩CBmRNA/CB=24.9-32.8%(L2/3), 13.7%(L5/6) CB1∩PVMRNA/PV=0.5-1%(L2/3), 1.1-1.5%(L5/6) CB1∩CRmRNA/CR=0-1%(L2/3), 0-1.3%(L5/6)	Marsicano & Lutz 1999
BAC Tg mice	S1	5HT3aRGFP∩+scRTPCR; PV-, CR+ in L2/3	Vucurovic et al 2010
BAC Tg mice	S1	5HT3aRGFP∩PVMR=ϕ	Lee et al JNs 30:16796-808, 2010

monkey	F/T/P cortex	5HT3Rir∩smallCBir≠ϕ, 5HT3Rir∩PVir=ϕ 5HT3Rir∩CRir≠ϕ	Jakab, Goldman-Rakic, JCN417:337-48 2000
rat	S1	CB1∩CB/CB1=24%(L2/3),47%(L5/6) CB1∩PV=ϕ, CB1∩CR=ϕ	Bodor et al 2005
between Peptides			
mouse	visaul cortex	CCK∩SS=ϕ, CCK∩VIP=ϕ, NPY∩VIP=ϕ VIP∩SS/SS= 45%, VIP∩SS/VIP=61% NPY∩SS/SS=7%, NPY∩SS/NPY=30% CCK∩NPY/NPY=24%, CCK∩NPY/CCK=43%	Gonchar et al (2008) FrontNeuroanat 1:1
mouse	frontal all Ls	NPY∩SS/SS= 9.3%, NPY∩SS/NPY= 25.4% VIP∩NPY/NPY= 8.4%, VIP∩NPY/VIP= 10.4% VIP∩SS=ϕ	Xu et al (2010) JCN 518:389-404
	L1	NPY∩SS/SS= 5.9%, NPY∩SS/NPY= 16.7% VIP∩NPY/NPY= 3.1%, VIP∩NPY/VIP= 2.5%	
	L2/3	NPY∩SS/SS= 11.5%, NPY∩SS/NPY= 12.9% VIP∩NPY/NPY=14.6%, VIP∩NPY/VIP=12.9%	
	L4	NPY∩SS/SS= 2.8%, NPY∩SS/NPY= 9.7% VIP∩NPY/NPY= 14.5%, VIP∩NPY/VIP= 17.5%	
	L5	NPY∩SS/SS= 6.5%, NPY∩SS/NPY=33.3% VIP∩NPY/NPY= 1.8%, VIP∩NPY/VIP=3.8%	
	L6	NPY∩SS/SS= 17%, NPY∩SS/NPY= 63.9% VIP∩NPY/NPY= 2%, VIP∩NPY/VIP= 4.5%	
	S1 all Ls	NPY∩SS/SS= 6.5%, NPY∩SS/NPY= 19.1% VIP∩NPY/NPY= 7.7%, VIP∩NPY/VIP= 11.8% VIP∩SS=ϕ	
	L1	NPY∩SS=ϕ VIP∩NPY/NPY= 13.6%, VIP∩NPY/VIP= 21.4%	
	L2/3	NPY∩SS/SS= 9.6%, NPY∩SS/NPY= 10.6% VIP∩NPY/NPY=10.5%, VIP∩NPY/VIP=12.2%	
	L4	NPY∩SS/SS= 0.7%, NPY∩SS/NPY= 2.2% VIP∩NPY/NPY= 13.5%, VIP∩NPY/VIP= 15.6%	
	L5	NPY∩SS/SS= 2.1%, NPY∩SS/NPY=12.8% VIP∩NPY/NPY= 4.9%, VIP∩NPY/VIP=9.1%	
	L6	NPY∩SS/SS= 14.1%, NPY∩SS/NPY= 52.5% VIP∩NPY/NPY= 1.1%, VIP∩NPY/VIP= 4%	
	V1 all Ls	NPY∩SS/SS= 5.8%, NPY∩SS/NPY= 21.6% VIP∩NPY/NPY= 8.4%, VIP∩NPY/VIP=6.2% VIP∩SS=ϕ	
	L1	NPY∩SS=ϕ, VIP∩NPY=ϕ	
	L2/3	NPY∩SS/SS= 4%, NPY∩SS/NPY= 12.9% VIP∩NPY/NPY=13.2%, VIP∩NPY/VIP=8.7%	
	L4	NPY∩SS/SS= 2.1%, NPY∩SS/NPY= 14.3% VIP∩NPY/NPY= 7.4%, VIP∩NPY/VIP= 4.7%	
	L5	NPY∩SS/SS= 5.2%, NPY∩SS/NPY=52.4% VIP∩NPY/NPY= 1.9%, VIP∩NPY/VIP=2.8%	
	L6	NPY∩SS/SS= 14.8%, NPY∩SS/NPY= 57.1% VIP∩NPY/NPY= 2.2%, VIP∩NPY/VIP= 2.2%	
rat	visual cortex	VIP∩SS ≠ ϕ, CCK∩SS ≠ ϕ, NPY∩SS ≠ ϕ, CCK∩VIP ≠ ϕ	Papadopoulos et al., BR 420:95, 1987
rat	neocortex	VIP∩CRF= ϕ	Merchenthaler et al AmJAnat165:385, 1982
rat	cortex	VIP∩CRF/VIP =32%, VIP∩CRF/CRF= 88%	Taki
rat	neocortex, hippocampus	SS∩APP ≠ ϕ (many)	Vincent et al. Neurosci. 7:439, 1982
rat	neocortex	SS∩NPY≠ ϕ	Hendry et al., J Nsci 4:2497, 1984
rat	cortex, II/III	(CCK∩VIP) /VIP=24%, (CCK∩VIP) /CCK=63%	Kubota & Kawaguchi, BR 752:175, 1997
	V	(CCK∩VIP) /VIP=12%, (CCK∩VIP) /CCK=51%	
	VI	(CCK∩VIP) /VIP=10%, (CCK∩VIP) /CCK=26%	
	cortex	CCK∩SS=ϕ, CCK∩NPY=ϕ	
rat	frontal agranular cortex II/III	(NPY∩SS)/NPY =71%, (NPY∩SS)/SS =42%	Kubota et al., BR 649:159, 1994

rat	V-VI frontal cortex L2/3 L5/6 L2/3 L5/6 L2/3 L2/3/5 L5/6 L6 L2/3 L5 L6	(NPY \cap SS)/NPY =90%, (NPY \cap SS)/SS =34% CRF \cap SS= ϕ CRF \cap SS/CRF=25-35%, —/SS=20-25% CRF \cap VIP/CRF=90%, —/VIP=% CRF \cap VIP/CRF=60%, —/VIP=% CRF \cap CCK/CRF=40%, CRF \cap CCK/CCK=50% CRF \cap CCK/CRF=20%, —/VIP=20-25% CRF \cap CCK/CCK=30% SS \cap CRF \cap VIP= ϕ , CRF \cap (SS+VIP)/CRF=80% [CCK \cap CRF \cap VIP]/[CCK \cap (CRF+IP)]=89% [CCK \cap CRF \cap VIP]/[CCK \cap (CRF+IP)]=83% [CCK \cap CRF \cap VIP]/[CCK \cap (CRF+IP)]=63% NPY \cap VIP= ϕ	Kubota et al (2011) CC
rat	frontoparietal	PPTA \cap SS/SS = 1.2%, —/PPTA = 10.8% PPTB \cap SS/SS = 1.3%, —/PPTB = 3.7% PPTA \cap NPY/NPY = 1.5%, —/PPTA = 5.4% PPTB \cap NPY/NPY = 0.0%, —/PPTB = 0.0% PPTA \cap VIP/VIP = 0.0%, —/PPTA = 1.8% PPTB \cap VIP/VIP = 47.4%, —/PPTB = 38.8% PPTA \cap CRF= ϕ PPTB \cap CRF/CRF = 58.9%, —/PPTB = 12.7% PPTA \cap CCK= ϕ PPTB \cap CCK/CCK = 83.1%, —/PPTB = 13.3%	Kaneko et al 1998
cat	visual corex	SS \supset NPY, VIP \supset CRF	Demeulemeester et al. JNsci 8:988, 1988
monkey	neocortex	(SS \cap NPY) / NPY = 37% (SS \cap NPY) / SS = 41%	Hendry et al., J Nsci 4:2497, 1984
monkey	cerebral cortex	NPY \cap SS \supset large tachykinin cell(GABA-)	Jones et al., JNsci 8:1206, 1988
human	neocortex	SS \cap APP \neq ϕ (many)	Vincent et al. Nature 298:65, 1982
rat	cortex	CsmR \cap SS/SS=33-42%, CsmR \cap SS/CsmR=23-28% CsmR \cap VIP= ϕ , CsmR \cap CCK= ϕ	de Lecea et al (1997) JNs 17:5868
rat	entorhinal cortex pre- & parasubiculum hippocampus regio superior regio inferior hilus	SS \cap NPY/NPY=71-89%, SS \cap NPY/SS=10-35% SS \cap NPY/NPY=61%, SS \cap NPY/SS=25% SS \cap NPY/NPY=39-66%, SS \cap NPY/SS=56-72% SS \cap NPY/NPY=62-75%, SS \cap NPY/SS=78-94% SS \cap NPY/NPY=52-63%, SS \cap NPY/SS=75-89%	Köhler et al., NSL 78:1, 1987
rat	hippocampus	VIP \cap CCK/VIP= 35%, VIP \cap CCK/CCK=10%	Kosaka et al., JCN 239:420, 1985
rat	neocortex	CsmRNA \cap SS/CsmRNA=33~42% CsmRNA \cap SS/SS=23~28% CsmRNA \cap VIP= ϕ , CsmRNA \cap CCK= ϕ	de Lecea et al JNsci 17:5868, 1997

Peptides vs Receptors

rat	neocortex, hippocampus	mGluR1 α \cap SS \neq ϕ	Baude et al, Neuron 11:771, 1993
rat	neocortex	5HT3RmRNA \cap CCK/CCK=35~66%	Morales & Bloom, JNsci 17:3157, 1997
rat	neocortex	5HT3aR+scRTPCR; VIP+, CCK+	Férezou et al 2002 JNs 22:7389-97
BAC Tg mice	S1	5HT3aRGFP+scRTPCR; VIP+ in L2/3, NPY+ in all L	Vacurovic et al CC 20:2333-47, 2010
BAC Tg mice	S1	5HT3aRGFP \cap SSmR= ϕ	Lee et al JNs 30:16796-808, 2010
rat	neocortex, hippocampus	mGluR1mRNA(++) on SSmRNA mGluR5mRNA(+) on SSmRNA	Kerner et al MolBR 48:259, 1997
rat	hippocampus	M2 \cap SS/M2 = 15%, M2 \cap VIP/M2 =3% M2 \cap CCK/M2 = 3%	Hojos et al, Nsci 82:355,1998
rat	neocortex	mGluR1 α \supset SS++ (75%)	Steinhelfer et al 2000 BR 861:37-44
mouse	neocortex	CB1mRNA \cap CCKmRNA/CCK=77.1-97.4%(L2/3) CB1mRNA \cap CCKmRNA/CCK=86.9-99.6%(L5/6) CB1 \cap CBmRNA/CB=24.9-32.8%(L2/3), 13.7%(L5/6) CB1 \cap PVmRNA/PV=0.5-1%(L2/3), 1.1-1.5%(L5/6) CB1 \cap CRmRNA/CR=0-1%(L2/3), 0-1.3%(L5/6)	Marsicano & Lutz 1999
rat	S1	CB1 \cap CCK/CB1=62%(L2/3), 52%(L5/6) CB1 \cap CCK/CCK = 33%	Bodor et al 2005

		CB1∩CB/CB1=24%(L2/3),47%(L5/6) cf. CCK∩CB/CCK=3% CB1∩VIP/CB1 = 5%, CB1∩VIP/VIP = 3% CB1∩SS=ϕ, CB1∩PV=ϕ, CB1∩CR=ϕ	
rat	frontal cortex L2/3 L2/3 L5/6 L5 L6	SPR∩SS∩NPY/SPR=85% SPR∩SS∩NPY/[SS∩NPY]=22% SPR∩SS∩NPY/SPR=100%, SPR∩SS∩NPY/[SS∩NPY]=34% SPR∩SS∩NPY/[SS∩NPY]=23%	Kubota et al (2011) CC
between Receptors			
rat		GluR1-non-pyr∩GluR2-non-pyr/GluR1-non-pyr=1/(93+1)=1% GluR1-non-pyr∩GluR2-non-pyr/GluR2-non-pyr=1/(6+1)=14%	Kharazia et al, JCN 368:399, 1996
monkey	area 46	NR1∩GluR2-3/GluR2-3=95%, NR1∩GluR5-6-7/GluR5-6-7=100%	Huntley et al, BR749:245, 1997
	area TE1	NR1∩GluR2-3/GluR2-3=95%, NR1∩GluR5-6-7/GluR5-6-7=100%	
monkey	M1, S1, V1	NR1∩GluR2-3∩GluR5-6-7	Huntley et al, JNsci 14:3603, 1994
monkey	Prefrontal	GluR2-3∩GluR5-6-7(70%)	Huntley et al, JNsci 13:2982, 1993
rat	neocortex	GluR1++∩mGluR1α	Steinhelfer et al 2000 BR 861:37-44
monkey	F/T/P cortex	5HT3Rir⊆SPRir	Jakab, Goldman-Rakic, JCN417:337-48 2000
Connexins vs Markers			
mouseP14-20	S1 L4	(Cx36 lacZ∩PVir)/PV = 63%, (Cx36∩PVir)/Cx36 = 78% (Cx36∩SSir)/SSir = 27%, (Cx36∩SSir)/Cx36 = 26%	Deans et al. Neuron 31:477-85, 2001
mouse adult	S1	(Cx36 ir∩PVir)/PVir = 50%	Priest et al SomatoMotorRes18:245-52,2001
mouse adult	cortex	PVir ⊃ Cx36 lacZ	Degen et al, JCN 473:511-25, 2004
mouse adult	hpc	(Cx30.2 lacZ∩PV)/PV = 48% (Cx36 CFP∩PV)/PV = 93% (Cx30.2 lacZ∩Cx36 CFP)/Cx30.2 = 94%	Kreuzberg et al. MCN 37:119-34,2008
	cortex	Cx30.2 lacZ∩Cx36 CFP ≠ ϕ	
	striatum	(Cx30.2∩Cx36)/Cx30.2 = 93%, (Cx30.2∩Cx36)/Cx36 = 82%	
mouse adult	cortex	(Cx36 GFP∩PV)/PV = 99%	Helbig et al. MCN45:47-58, 2010 [BAC Tg]
rat adult	neocortex	(Cx36 mRNA∩NeuN)/NeuN = 4.4(L2/3), 8.7(L4), 11.2(L5), 3.2%(L6) (Cx36∩PV)/PV = 55%	Belluardo et al, BR 865:121-38,2000
	hippocampus	(Cx36∩PV)/PV = 30(oriens),50(CA1pyr),62(CA3pyr),45(hilus),29(DG),81%(Sub)	
α-actinin-2 vs Markers			
rat adult	CA1 SLM	NPY∩α-actinin-2/NPY = 81% bNOS∩α-actinin-2/α-actinin-2 = 46%	Price et al, JNS 25:6775-86, 2005
VGAT Tg rat	frontal	αAc2∩Venus/αAc2 = 100% αAc2 = 67% (L1), 1-10% (L2-6) of Venus cells αAc2∩PV=ϕ, αAc2∩SS=ϕ, αAc2∩CB=ϕ αAc2∩CR/αAc2=14.8%(L1), 3.0%(L2/3),18.8%(L5),16.2%(L6),10.2% αAc2∩VIP/αAc2=1.4%(L1),1.2%(L2/3),0%(L5),0%(L6),0.9% αAc2∩CCK/αAc2=0%(L1),0%(L2/3),0%(L5),2.4%(L6),0.4%	Uematsu et al 2008
rat	frontal cortex	αAc2∩CRF≠ϕ	Kubota et al (2011) CC
	L1	αAc2∩NPY≠ϕ	
	L2/3	αAc2∩NPY/αAc2=95%, -/NPY =32%	
	L5	αAc2∩NPY/αAc2=100%, -/NPY =20%	
	L6	αAc2∩NPY/αAc2=94%, -/NPY =40%	
	all Ls	αAc2∩NPY∩SS≠ϕ	
	L2/3	[NPY∩(αAc2+SS)]/NPY=77%	
	L5	[NPY∩(αAc2+SS)]/NPY=80%	
	L6	[NPY∩(αAc2+SS)]/NPY=85%	
	all Ls	faintNOS∩αAc2/αAc2=26%(L1),34%(L2/3),19%(L5),29%(L6)	

Baude et al, Neuron 11:771, 1993

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2-3-1-1) 次に single-cell RT PCR による解析の結果を解説しましょう。

上記のような immunohistochemistry あるいは in situ hybridization での結果と比べて、single-cell multiplex RT-PCR による結果は結構食い違っていることも多くあります。一つの理由として、single-cell multiplex RT-PCR は感度が高すぎて all or none になりますので、生理的な発現量になっていないものも陽性として捉えてしまう、すなわち functionally false-positive になっている可能性も考えるべきでしょう。また、whole cell の仕事になることから、ラットの年齢が ≤ 22 d-o と若いことも少し気になります。

[Cauli et al 1997; rat frontal; mRNA for PV, CB, CR, SS, NPY, CCK, VIP; GAD, ChAT]

PV+ 30, CB+19/ 34 FS cells

SS+ 29, CB+ 31, PV+ 9/48 RSNP cells;

VIP+ 10, CR+ 10, PV+ 0/ 10 bipolar IS cells

[Porter et al 1998; rat M1 L2/3,5; CR, VIP, ChAT, GAD; GluR1,2,3,4,5,6,7, KA1-2, NR2A,2B,2C,2D] **VIP+37, GAD+ 37, ChAT+CR+ 17, CHAT+CR- 1, ChAT-CR+ 5, ChAT-CR- 14 / 37 IS cells**

[Cauli et al 2000; GAD, CB, PV, CR, NPY, VIP, SS, CCK]
GAD+ 100%, **PV+ 69%, CB+ 56%, NPY+ 50%/ 16 FS cells**
GAD+ 100%, CB+ 75%, SS+ 92%/ 12 RNSP-SS cells
GAD+ 100%, CR+ 53%, CCK+ 81%, VIP+ 91%/ 32 RNSP-VIP cells
GAD+ 94%, CB+ 50%, CR+ 81%, **VIP+ 100%, CCK+ 63%/ 16 IS cells**

[Wang et al 2002; PV, CB, CR, NPY, SS, CCK, VIP]
PV+ 47%, NPY+ 42%, CCK+ 42%/ 19 large basket cells
PV+ 52%/ 29 nest basket cells
PV+ 5%, VIP+ 100%, CCK+ 72%/ 18 small basket cells

[Férézou et al 2002; 5HT3aR, 5HT3bR, GAD, PV, CB, CR, NPY, SOM, VIP, CCK; rat]
5HT3aR-expressing cells; GAD65 95%, GAD67 89%, **VIP 95%, CCK 100%, CB 37%, CR 53%, 3bR 0%**
CCK-expressing cells: 5HT3aR 33%
VIP-expressing cells; 5HT3aR 27%

[Gallopín et al 2006; GAD, CB, CR, NPY, VIP, SS, CCK, CRF, NKB, VGluT1; CCK-A, CCK-B, NK3]
FS cluster 29 cells; (positively related) GAD, NPY48%, CB 33%, SS 38%; FS 76%, RNSP 24%
VIP cluster 28 cells; (positively related) GAD, VIP 96%, CR 68%, CRF, NKB, CCK; RNSP 57%, IS 43%
SS cluster 23 cells; (positively related) GAD, SS 96%, CB 52%, CR 43% ; RNSP 100%

[Hill et al 2007; GAD, VGluT1, CB, CR, NPY, VIP, SS, CCK; CB-1, CB-2]
62 SS cells; GAD100%, SS100%, CB 48%
100 VIP cells; GAD 100%, VIP 100%, CR 55%, CCK 57%

[Toledo-Rodriguez et al 2004; rat P13-16; CB, PV, CR; Kvs, HCNs, SK2, Cavs]
fAHP correlates with; PV, Kv1.6, Kv3.1, Kv3.2, Ca α 1G, Ca β 4
negatively correlates with; CR, Ca α 1I, Kv2.2, HCN4, SK2
mAHP correlates with; SK2, HCN1, PV, Ca α 1B, CR, Kv1.2, Kv β 1
negatively correlates with; Kv3.3, Kv3.1, Kv4.2, Kv3.2
etc

[Toledo-Rodriguez et al 2005; rat P13-16 S1; CB, PV, CR, NPY, VIP, SS, CCK]
large basket; nest basket; small basket; double bouquet; bipolar; neurogliaform; bitufted
Martinotti; chandelier; Cajal-Retzius
key predictor of anatomical class: SS > PV > VIP > NPY

[Vucurovic et al 2010; 5HT3A/GFP BAC Tg mice P14-17; 12 L1 + 41 L2/3 GFP+ cells]
cf. adult; PV(-), SS(-), VIP+ or CR+ in L2/3, NPY+ in all Ls
mostly GAD67 mRNA+; NPY mRNA+ cluster 31; VIP mRNA cluster 22

Cauli B, Audinat E, Lambolez B, Angulo MC, Ropert N, Tsuzuki K, Hestrin S, Rossier J (1997) Molecular and physiological diversity of cortical nonpyramidal cells. *J. Neurosci.* 17:3894-3906. **Irregular-spiking** 初出

Cauli B, Porter JT, Tsuzuki K, Lambolez B, Rossier J, Quenet B, Audinat E (2000) Classification of fusiform neocortical interneurons based on unsupervised clustering. *Proc. Natl. Acad. Sci. USA* 97:6144-6149. [VIP, SS, GAD, CR, CB]

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2-3-2) L1 neurons

L1 (molecular layer) には inhibitory interneurons しか存在していません。

Hestrin & Armstrong [1996] rat (P7-19) V1 cortex

- 1) neurogliaform cells with DAP (~1/3)
- 2) multipolar neurons with axons descending out of L1 and mAHP (~1/3)
- 3) heterogenous

Wozny & Williams [2011] rat (P24-36) S1 cortex

- 1) neurogliaform cells (72/266 = 27%)
- 2) classical-accomodating neurons (137/266 = 52%)
- 3) FS neurons (23/266 = 8.6%)
- 4) burst-spiking (34/266 = 13%)

Hestrin S, Armstrong WE (1996) Morphology and physiology of cortical neurons in layer I. *J Neurosci.* 1996 Sep 1;16(17): 5290-300.

Wozny C, Williams SR (2011) Specificity of Synaptic Connectivity between Layer 1 Inhibitory Interneurons and Layer 2/3 Pyramidal Neurons in the Rat Neocortex. *Cereb Cortex.* 2011 Jan 13. [Epub ahead of print]

2-3-2-1) Cajal-Retzius cell

形状：horizontal bipolar dendrites;

P7-10 rat の L1 に認められた [Hestrin, Armstrong 1996]。

2-3-3) Chemical/molecular classification

大脳皮質の抑制性ニューロンはすべて GABA 作動性でして、表 2-1 にまとめた 3 グループの他に GABAergic である以外に化学的特徴がないもう 1 グループを加えて、4 つの細胞群に分けました。以下、それぞれに詳しいコメントをしましょう。ここでの分類は主として、蛋白質・ペプチドの免疫組織化学あるいは in situ hybridization による分類と考えて下さい。もちろん、形態的・電気生理学的分類も加味して行きます。

表. 皮質ニューロンにおける Calcium-binding protein の発現割合

rat	cortex	GABA ⊃ PV (70%)	Celio, Science 231:995, 1986
rat	frontal agranular cortex	GABA ⊃ PV	Kubota et al., BR 649:159, 1994
rat	visual	GABA ⊃ PV (51%),	Gonchar and Burkhalter, CC 7:347, 1997
cat	primary auditory cortex	GABA ⊃ PV ∪ CB (70-75%)	Hendry & Jones, BR 543:45, 1991
cat	visual cortex	GABA ⊃ PV (37%)	Demeulemeester et al, EBR 84:538, 1991
monkey	neocortex	GABA ⊃ PV ∪ CB (>98%)	Hendry et al., EBR 76:467, 1989
monkey	striate cortex	GABA ⊃ PV (74%)	van Brederode et al., JCN 298:1, 1990
monkey	A1 cortex	PV=12%, CB=7%, CR=20% in total neurons	Glezer et al (1998) JChemNeuroanat 15:203
monkey	V1 cortex	PV=8%, CB=11%, CR=9% in total neurons	
human	temporal lobe total	CB=15.72%, CR=17.5% in total neurons	del Río & DeFelipe (1996) JCN 369:472
	L2	CB=24.73%, CR=21.67% in total neurons	
	L3	CB=6.71%, CR=13.32% in total neurons	
dolphin	A1 cortex	PV=7%, CB=21%, CR=17% in total neurons	Glezer et al (1998) JChemNeuroanat 15:203
dolphin	V1 cortex	PV=5%, CR=13%, CB=18% in total neurons	

del Río M, DeFelipe J (1996) Colocalization of calbindin D-28k, calretinin, and GABA immunoreactivities in neurons of the human temporal cortex. J Comp Neurol 369:472-82.

Glezer II, Hof PR, Morgane PJ (1998) Comparative analysis of **calcium-binding protein**-immunoreactive neuronal populations in the auditory and visual systems of the bottlenose **dolphin** (*Tursiops truncatus*) and the macaque **monkey** (*Macaca fascicularis*). J Chem Neuroanat 15(4):203-37.

2-3-3-1) Group I (parvalbumin, Kv3.1b, fast-spiking)

Kv3.1b カリウムチャンネルと parvalbumin を発現しているニューロン群です。少なくともラットにおいて、Kv3.1b と parvalbumin の発現一致率は parvalbumin+ L5 pyramidal cell [下記*参照]を除いて高いので、この意味で比較的均一なニューロン群であると言えます。電気的には **Fast-spiking cell** と呼ばれる群に一致することになります。その理由は、Kv3.1b は高閾値で action potential の時に主に活性化される delayed rectifier のひとつで、kinetics が速いので、Kv3.2 と共同して action potential の後半を削り取り、action potential 幅を短くするからです。そうして、Na channel の不活化を取り、ニューロンが高頻度に発火できるようにしていますので、Fast-spiking という特性と Kv3.1b 発現という特性は機能的に一致してきます。Fast-spiking cell と parvalbumin 産生細胞の一致については下記のような論文があります。

Cauli B, Audinat E, Lambolez B, Angulo MC, Ropert N, Tsuzuki K, Hestrin S, Rossier J (1997) Molecular and physiological diversity of cortical nonpyramidal cells. J. Neurosci. 17:3894-3906. **PV mRNA+ 30 in 34 FS cells**

Cauli B, Porter JT, Tsuzuki K, Lambolez B, Rossier J, Quenet B, Audinat E (2000) Classification of fusiform neocortical interneurons based on unsupervised clustering. Proc. Natl. Acad. Sci. USA 97:6144-6149. **PV mRNA+ 69% in 16 FS cells**

Kawaguchi, Y. (1995) Physiological subgroups of nonpyramidal cells with specific morphological characteristics in layer II/III of rat frontal cortex. J Neurosci 1995;15(4):2638-55. [**PV+ 12/ 12 FS cells**] **5 basket, 2 chandelier/ 12 PV+ cells**

Kawaguchi Y, Kondo S (2002) **Parvalbumin**, somatostatin and cholecystokinin as chemical markers for specific GABAergic interneuron types in the rat **frontal** cortex. J Neurocytol 31:277-87. [review](#)

Kawaguchi Y, Kubota Y (1993) Correlation of physiological subgroupings of nonpyramidal cells with **parvalbumin** and calbindin D28k-immunoreactive neurons in **layer V** of rat **frontal** cortex. J Neurophysiol 70:387-96. **18 FS-PV+ cells**

Kawaguchi Y, Kubota Y (1997) GABAergic cell subtypes and their synaptic connections in rat frontal cortex. Cereb Cortex 7: 476-86. [**PV, CB, SS, VIP**] [review](#)

Kawaguchi Y, Kubota Y (1998) Neurochemical features and synaptic connections of large physiologically-identified GABAergic cells in the rat frontal cortex. Neurosci 85: 677-701. [**CCK, PV, SS**] **FS 12/ 12 PV+ cells**

Povysheva NV, Zaitsev AV, Toraru DC, Gonzalez-Burgos G, Lewis DA, Krimer LS (2008) **Parvalbumin**-positive **basket** interneurons in **monkey** and **rat prefrontal** cortex. J Neurophysiol 100: 2348-60. **PV+ 11(78%)/ 14 rat L2/3 FS cells; PV+ 14 (67%)/ 21 monkey L2/3 FS cells**

Zaitsev AV, Gonzalez-Burgos G, Povysheva NV, Kroner S, Lewis DA (2005) Localization of calcium-binding proteins in physiologically and morphologically characterized interneurons of monkey dorsolateral prefrontal cortex. *Cereb Cortex* 15: 1178-86. [PV, CR, CB] PV+ 14/36 FS cells; PV- / 43 RSNP cells; 14 FS/ 14 PV+ cells

Zaitsev AV, Gonzalez-Burgos G, Povysheva NV, Kröner S, Lewis DA, Krimer LS (2009) Interneuron diversity in layers 2-3 of monkey prefrontal cortex. *Cereb Cortex* 19: 1597-615. [PV, CR, CB, SS, NPY] 相関 chandelier/linear arbor ~ FS ~ PV

ただし、最近 mouse neocortex L2/3 で PV+ nonFS cells の存在が報告されました [Blatow et al 2003]。multipolar bursting cell と名付けられ、CB にも陽性である (9/9) ことが分かっています。CB∩PV/ PV = 33~35% in L2/3 of frontal & S1 と報告されています。

Blatow M, Rozov A, Katona I, Hormuzdi SG, Meyer AH, Whittington MA, Caputi A, Monyer H (2003) A novel network of multipolar bursting interneurons generates theta frequency oscillations in neocortex. *Neuron* 38: 805-17.

Group I の parvalbumin neuron は GABAergic neuron であることは確定しています。さらに、Group I の一部に、cortistatin [de Lecea et al 1997] あるいは preprotachykinin A (substance P の前駆体) [Kaneko et al 1998] を発現しているニューロン群がサブグループとして存在しているようです。

表. Group I neurons の化学的特性

rat	cortex	GABA ⊃ PV (70%)	Celio, Science 231:995, 1986
rat	frontal agranular cortex	GABA ⊃ PV	Kubota et al., BR 649:159, 1994
rat	visual	GABA ⊃ PV (51%),	Gonchar and Burkhalter, CC 7:347, 1997
cat	primary auditory cortex	GABA ⊃ PV ∪ CB (70-75%)	Hendry & Jones, BR 543:45, 1991
cat	visual cortex	GABA ⊃ PV (37%)	Demeulemeester et al, EBR 84:538, 1991
monkey	neocortex	GABA ⊃ PV ∪ CB (>98%)	Hendry et al., EBR 76:467, 1989
monkey	striate cortex	GABA ⊃ PV (74%)	van Brederode et al., JCN 298:1, 1990
rat	neocortex (SI, 17)	GAD ⊃ SP (18-22%)	Penny et al. NSL 65:53, 1986
monkey	cerebral cortex	GABA ⊃ small tachykinin cell GABA ∩ large tachykinin cell = φ	Jones et al., JNsci 8:1206, 1988
rat		CSmR∩PV/PV = 40%	de Lecea et al (1997) JNs 17:5868
rat	frontoparietal	PPTA∩PV/PV = 6.4%, -/PPTA = 68.7% PPTB∩PV=φ	Kaneko et al 1998

de Lecea L, del Rio JA, Criado JR, Alcántara S, Morales M, Danielson PE, Henriksen SJ, Soriano E, Sutcliffe JG (1997)

Cortistatin is expressed in a distinct subset of cortical interneurons. *J. Neurosci.* 17:5868-5880. CS∩PV/PV = 40%

Kaneko T., Murashima M., Lee T., Mizuno N (1998) Characterization of neocortical non-pyramidal neurons expressing preprotachykinins A and B: A double immunofluorescence study in the rat. *Neuroscience*, vol. 86 (no. 3), pp. 765-781, June 8, 1998.

形態学的には主に **Basket cell** と **Chandelier cell** に分類されます [Karube et al., 2004; Kawaguchi 1995; Kawaguchi & Kubota, 1998; Zaitsev et al., 2005, 2009]。Basket cell はさらに large, small, nest basket cells と分類されます。軸索が basket を形成せず、直線状に走るので linear arbor cell とよぶこともあります [Zaitsev et al 2009, monkey prefrontal L2/3]が、典型的な axon basket を形成しなくとも axosomatic bouton が 15% などの基準で basket cell と呼んだりする研究者もいます [Kawaguchi et al] ので、定義の問題でもあります。ただし最近、この 2 種に加えて、ゆるい基準で考えても basket と言えない (もちろん chandelier とも言えない) **wide arbor cell** が加えられたりしています [Kawaguchi & Kondo 2002]。

Karube F, Kubota Y, Kawaguchi Y (2004) Axon branching and synaptic bouton phenotypes in GABAergic nonpyramidal cell subtypes. *J Neurosci* 24:2853-65. [late-spiking basket 初出]

他には上記文献参照

反対に形態的分類から見ると、**Large basket cell** の 50% が、**Small basket cell** の 5% のみが PV mRNA を発現していたという報告があります [Wang et al 2002]。また、**Nest basket cell** といって主に L2/3 に見いだされて local nest of axons と long extending axons をもつタイプも 50% が PV を産生すると報告されています [Gupta et al 2000; Wang et al 2002]。Non-fast-spiking で parvalbumin- / Kv3.1b- な basket cell については 2 - 3 - 4 - 1) **Basket cell** を参照して下さい。

Wang Y, Gupta A, Toledo-Rodriquez M, Wu CZ, Markram H (2002) Anatomical, physiological, molecular and circuit properties of **nest basket** cells in the developing somatosensory cortex. *Cereb Cortex* 12: 395-410. [13-15 d rat] PV+ 47%/ 19 large basket cells; PV+ 52%/ 29 nest basket cells; PV+ 5%/ 18 small basket cells

*一部の L5/6a 錐体ニューロンに parvalbumin が発現しているという仕事があります。

Jinno, S, Kosaka, T (2004) Parvalbumin is expressed in glutamatergic and GABAergic corticostriatal pathway in **mice**. *J Comp Neurol* 2004;477(2):188-201. **PV+ GAD- L5 corticostriatal neuron**

Johnson, JK, Casagrande, VA (1995) Distribution of calcium-binding proteins within the parallel visual pathways of a **primate** (*Galago crassicaudatus*). *J Comp Neurol* 1995;356(2):238-60. **bush baby V1 L5/6 pyramidal-like**

McMullen, NT, Smelser, CB, de Venecia, RK. A quantitative analysis of parvalbumin neurons in **rabbit auditory neocortex**. *J Comp Neurol* 1994;349(4):493-511. **L6a pyramidal**

Spatz, WB, Illing, RB, Weisenhorn, DM (1994) Distribution of cytochrome oxidase and parvalbumin in the primary visual cortex of the adult and neonate **monkey**, *Callithrix jacchus*. *J Comp Neurol* 1994;339(4):519-34. **marmoset V1 L5 pyramidal-like** (10-20% of PV+ cells)

Stichel, CC, Singer, W, Heizmann, CW, Norman, AW (1987) Immunohistochemical localization of calcium-binding proteins, parvalbumin and calbindin-D 28k, in the adult and developing visual cortex of cats: a light and electron microscopic study. *J Comp Neurol* 1987;262(4):563-77. **cat V1 pyramidal-like**

Tanahira, C, Higo, S, Watanabe, K, Tomioka, R, Ebihara, S, Kaneko, T, Tamamaki, N (2009) Parvalbumin neurons in the forebrain as revealed by parvalbumin-Cre transgenic **mice**. *Neurosci Res* 2009;63(3):213-23. **S1 > M1 > V1 L5 pyramidal**

van Brederode, JF, Helliesen, MK, Hendrickson, AE (1991) Distribution of the calcium-binding proteins parvalbumin and calbindin-D28k in the sensorimotor cortex of the **rat**. *Neuroscience* 1991;44(1):157-71. **S1 L2/3 & L5/6 pyramidal-like** (not in M1)

2 - 3 - 3 - 2) **Group II** (somatostatin & calbindin)

Somatostatin や Calbindin を含有するニューロン群で、Martinotti cell がこの群に属してきます。一部に Neuropeptide Y (NPY), Nitric oxide synthase (NOS), NK1 receptor (substance P receptor) などを含有するサブグループが存在しています。ただし、NPY+ cells は Neurogliaform cell などを含み多様なグループになります [後述]。

最近マウスでは calbindin が Group III にも発現していることが報告され、group II のマーカーとしては優れていないことがわかっています []。

表. **Group II neurons** の化学的特性

rat	cortex	GABA ⊃ NOS = NADPHd	Valtschanoff et al., NSL 157:157, 1993
rat	frontal agranular cortex	GABA ⊃ NOS	Kubota et al., BR 649:159, 1994
rat	mPFC(24b,25,32)	GABA ⊃ NADPHd	Gabbott & Bacon, BR699:321, 1995
rat	visual cortex	GAD ∩ SS / SS = 80-85%	Lin et al., JCN244:369, 1986
rat	frontal agranular cortex	GABA ⊃ SS, NPY	Kubota et al., BR 649:159, 1994
rat	visual	GABA ∩ SS / SS = 90%, GABA ∩ SS / GABA = 17%	Gonchar and Burkhalter, CC 7:347, 1997
rat, cat, monkey	cortex, hippocampus	GAD ∩ SS ≠ φ	Schmechel et al., NSL47:227, 1984
cat	cortex	GAD ⊃ SS, NPY	Hendry et al., PNAS 81:6526, 1984
cat	visual cortex	GAD ∩ SS / SS = 89%, GAD ∩ SS / GAD = 2%	Demeulemeester et al. JNsci 8:988, 1988

		GAD \cap NPY/NPY=100%, GAD \cap NPY/GAD=1%	
cat	visual cortex	GABA \supset GAD \supset SS	Somogyi et al., J Nsci 4:2590, 1984
monkey	cortex	(GAD \cap X) / X = 90-95% (X= SS, NPY)	Hendry et al., PNAS 81:6526, 1984
monkey	cerebral cortex	GABA \cap large tachykinin cell = ϕ	Jones et al., JNsci 8:1206, 1988
rat	frontal agranular cortex II/III V-VI	SS \cap NPY \supset NOS (NOS \cap SS)/SS=11%, (NOS \cap NPY)/NPY=43%, (NOS \cap SS)/SS=26%, (NOS \cap NPY)/NPY=52%, SS \cap NOS/SS = 1.7%	Kubota et al., BR 649:159, 1994
rat	visual		Gonchar and Burkhalter, CC 7:347, 1997
rat	frontal agranular cortex II/III V-VI	(NPY \cap SS)/NPY =71%, (NPY \cap SS)/SS =42% (NPY \cap SS)/NPY =90%, (NPY \cap SS)/SS =34%	Kubota et al., BR 649:159, 1994
cat	visual corex	SS \supset NPY	Demeulemeester et al. JNsci 8:988, 1988
monkey	neocortex	(SS \cap NPY) / NPY = 37% (SS \cap NPY) / SS = 41%	Hendry et al., J Nsci 4:2497, 1984
monkey	cerebral cortex	NPY \cap SS \supset large tachykinin cell(GABA-)	Jones et al., JNsci 8:1206, 1988
human	neocortex	SS \cap APP $\neq \phi$ (many)	Vincent et al. Nature 298:65, 1982
rat	cortex	C \cap SmR \cap SS/SS=33-42%, C \cap SmR \cap SS/C \cap SmR=23-28%	de Lecea et al (1997) JNs 17:5868

Calbindin group

rat	frontal agranular cortex II/III V-VI VI	GABA \supset strong CB , (GABA \cap CB)/CB=10% (GABA \cap CB)/CB=96% GABA \supset strong CB	Kubota et al., BR 649:159, 1994
rat	neocortex layer I paleocortex	CB \cap GABA/CB = 50% CB \cap GABA = ϕ CB \cap GABA/CB = 75%	Rogers, BR587:147, 1992
rat	piriform cortex L.I piriform cortex L.II piriform cortex L.III	CB = ϕ GABA \supset PV (11%) \cup CB (25%) \supset PV \cap CB (10%) GABA \supset PV (49%) \cup CB (80%) \supset PV \cap CB (47%)	Kubota & Jones BR 600:339, 1993
cat	A1	GABA \supset PV \cup CB (70-75%)	Hendry & Jones, BR 543:45, 1991
cat	visual corex	GAD \cap CB / CB = 63%, GAD \cap CB / GAD = 20%	Demeulemeester et al. JNsci 8:988, 1988
cat	visual cortex	CB \cap GABA/CB=80%, CB \cap GABA/GABA=18%	Demeulemeester et al, EBR 84:538, 1991
monkey	neocortex	GABA \supseteq PV \cup CB (>98%)	Hendry et al., EBR 76:467, 1989
monkey	striate cortex	GABA \supset PV (74%) \cup CB (12%)	van Brederode et al., JCN 298:1, 1990
rat	frontal Ag cortex II/III	CB \supset pyramidal cells	Kubota et al., BR 649:159, 1994
rat	SM cortex II/III	CB \supset pyramidal cells	Van Brederode, Nsci 44:157, 1991
rat	frontal agranular cortex II/III V-VI	(NOS \cap only weakCB)/NOS=29%, (NOS \cap CB)/CB=8%, (NOS \cap CB)/NOS=80%, PV \cap CB < 1%	Kubota et al., BR 649:159, 1994
monkey	neocortex		Hendry et al., EBR 76:467, 1989
cat	visual cortex	PV \cap CB = ϕ	Demeulemeester et al., NSL 99:6, 1989
cat	visual cortex	PV \cap CB = ϕ	Demeulemeester et al, EBR 84:538, 1991
rat	sensorimotor cortex upper layer deeper layer piriform cortex	(PV \cap CB) / PV = 20%, (PV \cap CB) / CB = 50% PV \cap CB = ϕ PV \approx CB	Van Brederode, Nsci 44:157, 1991
rat	frontal agranular cortex II/III V-VI	(PV \cap CB)/PV =91%, (PV \cap strong CB)/PV =11% (PV \cap CB) / PV = 6%, (PV \cap CB) / CB = 7% (PV \cap CB) / PV = 5%	Kubota et al., BR 649:159, 1994
rat	visual		Gonchar and Burkhalter, CC 7:347, 1997
rat	piriform cortex L.II piriform cortex L.III	(PV \cap CB) / PV = 41%, (PV \cap CB) / CB = 93% (PV \cap CB) / PV = 97%, (PV \cap CB) / CB = 59%	Kubota & Jones BR 600:339, 1993
rat	neocortex pyriform cortex hippocampus	CR \cap CB = ϕ CR \cap CB = ϕ CR \cap CB = ϕ	Rogers & Résibois, Nsci 51: 843, 1992
rat	frontal agranular cortex II/III V-VI	(CR \cap CB) /CR = 6% (CR \cap CB) /CR = 17%, (CR \cap CB) /CB = 4%	Kubota et al., BR 649:159, 1994
rat	visual	CB \cap CR= ϕ	Gonchar and Burkhalter, CC 7:347, 1997

monkey	area 46	$NR1 \cap CB\text{-non-pyr}/CB\text{-non-pyr}=24\%$	Huntley et al, BR749:245, 1997
	area TE1	$NR1 \cap CB\text{-non-pyr}/CB\text{-non-pyr}=82\%$	
monkey	Prefrontal	$GluR2\text{-}3 \cap CB/CB=28\%$, $GluR5\text{-}6\text{-}7 \cap CB/CB=31\%$ $GluR2\text{-}3 \cap CB/GluR2\text{-}3=1.7\%$ $GluR5\text{-}6\text{-}7 \cap CB/GluR5\text{-}6\text{-}7=2.4\%$	Huntley et al, JNsci 13:2982, 1993
rat	neocortex	$CB \cap VIP = \phi$	Rogers, BR587:147, 1992
	paleocortex	$CB \cap VIP = \phi$	
rat	frontal agranular cortex	$CB \cap VIP = \phi$	Kubota et al., BR 649:159, 1994
cat	visual corex	$CB \cap VIP = \phi$, $CB \cap CRF = \phi$	Demeulemeester et al. JNsci 8:988, 1988
rat	cortex II/III	$(CCK \cap CB)/CCK < 1\%$	Kubota & Kawaguchi, BR 752:175, 1997
	cortex V	$CCK \cap CB = \phi$	
	cortex VI	$(CCK \cap CB)/CCK=8\%$, $(CCK \cap CB)/CB < 1\%$	
rat	neocortex II-IV	$CB \cap SS /CB < 66\%$, $CB \cap SS /SS = 75\%$	Rogers, BR587:147, 1992
	neocortex V-VI	$CB \cap SS /CB = 84\%$, $CB \cap SS /SS = 84\%$	
	paleocortex	$CB \cap SS /CB = 49\%$, $CB \cap SS /SS = 63\%$	
rat	frontal agranular cortex II/III	$(CB \cap SS)/SS=85\%$, $(strongCB \cap SS)/SS=35\%$ $(strongCB \cap SS)/strongCB=68\%$	Kubota et al., BR 649:159, 1994
	V-VI	$(CB \cap SS)/SS=92\%$, $(CB \cap SS)/CB=68\%$	
rat	visual	$CB \cap SS /SS = 86\%$	Gonchar and Burkhalter, CC 7:347, 1997
rat	cortex	$CSmR \cap CB/CSmR = 47\%$ (L2/3), $\sim \phi$ (L5/6)	de Lecea et al (1997) JNs 17:5868
cat	visual corex	$CB \cap SS /CB = 7\%$, $CB \cap SS /SS = ?$	Demeulemeester et al. JNsci 8:988, 1988
rat	frontal agranular cortex II/III	$(CB \cap NPY)/NPY=68\%$, $(strongCB \cap NPY)/NPY=37\%$ $(strongCB \cap NPY)/strongCB=39\%$	Kubota et al., BR 649:159, 1994
	V-VI	$(CB \cap NPY)/NPY=95\%$, $(CB \cap NPY)/CB=24\%$	
cat	visual corex	$CB \cap NPY = \phi$	Demeulemeester et al. JNsci 8:988, 1988
monkey	neocortex	$CB \cap tachykinin/CB \approx CB \cap TK/TK < 20\%$, $\neq \phi$	DeFelipe et al. Nsci 37:655, 1990

SS 発現ニューロンの電氣的・形態的特性は regular-spiking non-pyramidal (RSNP) または burst-spiking non-pyramidal (BSNP) であり、BNSP は long LTS を伴うものです。

rat P18-22	frontal cortex L2/3 L5	RSNP 19, BNSP 1/20 SS+; include Martinotti RSNP 15, BNSP 18/33 SS+; include Martinotti	Kawaguchi, Kubota 1996
rat P18-22	frontal cortex	5 Martinotti, 9 wide-arbor/18 large RSNP SS+	Kawaguchi, Kubota 1998
rat	frontal L2/3 L5	6 Martinotti 5 Martinotti	Karube et al 2004

Goldberg et al (2004) は P13-17 mouse V1/S1 L5 で 13 SS+ cells の内、7 個が rebound burst を伴う LTS cell であり、L5 LTS cells は Martinotti cell であったとしています。Marinelli et al も 56 個の P13-21 rat S1 L5 LTS cell with rebound burst の内、36 個が SS+, 8 個が CCK+ だったと報告しました。

scRT-PCR 法による SS mRNA の検出では、SS は 67/67 Martinotti cells で発現していました [Toledo-Rodriguez et al 2005] が、SS は 4(12%) of 34 FS cells, 28(58%) of 48 RSNP cells, 5(50%) in 10 IS cells に発現していました [Cauli et al 1997]。

- Cauli B, Audinat E, Lambolez B, Angulo MC, Ropert N, Tsuzuki K, Hestrin S, Rossier J (1997) Molecular and physiological diversity of cortical nonpyramidal cells. J Neurosci. 1997 May 15;17(10):3894-906.
- Goldberg JH, Lacefield CO, Yuste R (2004) Global dendritic calcium spikes in mouse layer 5 low threshold spiking interneurons: implications for control of pyramidal cell bursting. J Physiol. 2004 Jul 15;558(Pt 2):465-78.
- Karagiannis A, Gallopin T, Dávid C, Battaglia D, Geoffroy H, Rossier J, Hillman EM, Staiger JF, Cauli B (2009) Classification of NPY-expressing neocortical interneurons. J Neurosci. 2009 Mar 18;29(11):3642-59.
- Karube F, Kubota Y, Kawaguchi Y (2004) Axon branching and synaptic bouton phenotypes in GABAergic nonpyramidal cell subtypes. J Neurosci. 2004 Mar 24;24(12):2853-65.

- Kawaguchi Y, Kubota Y (1996) Physiological and morphological identification of somatostatin- or vasoactive intestinal polypeptide-containing cells among GABAergic cell subtypes in rat frontal cortex. *J Neurosci.* 1996 Apr 15;16(8): 2701-15.
- Kawaguchi Y, Kubota Y (1998) Neurochemical features and synaptic connections of large physiologically-identified GABAergic cells in the rat frontal cortex. *Neuroscience.* 1998 Aug;85(3):677-701. [wide arbor cell 初出]
- Marinelli S, Pacioni S, Bisogno T, Di Marzo V, Prince DA, Huguenard JR, Bacci A (2008) The endocannabinoid 2-arachidonoylglycerol is responsible for the slow self-inhibition in neocortical interneurons. *J Neurosci.* 2008 Dec 10;28(50):13532-41.
- Toledo-Rodriguez M, Goodman P, Illic M, Wu C, Markram H (2005) Neuropeptide and calcium-binding protein gene expression profiles predict neuronal anatomical type in the juvenile rat. *J Physiol.* 2005 Sep 1;567(Pt 2):401-13.

2-3-3-3) Group III

コリン作動性であったり、vasoactive intestinal polypeptide (VIP), calretinin, corticotropin releasing factor (CRF), cholecystokinin (CCK), preprotachykinin B (neurokinin B の前駆体)などを産生したり、vesicular glutamate transporter 3 (VGluT3) [Hioki et al ()], μ -opioid receptor [Taki et al ()] を発現したりする形態的には主として ‘bipolar/bitufted neuron’ に括られるニューロン群です。化学的に多彩なグループでいろいろなサブグループが存在しています。

表. Group III neurons の化学的特性

rat	cortex	(GABA \cap ChAT) / ChAT= 50%	Kosaka et al., EBR 70:605, 1988
rat	SI cortex	(ChAT \cap GABA)/ChAT= 88%	Bayraktar et al. BR 757:209, 1997
rat	neocortex		Rogers, BR587:147, 1992
	layer I	CR \cap GABA = ϕ , CB \cap GABA = ϕ	
	layer II-IV	CR \cap GABA/CR = 25%	
	layer V-VI	CR \cap GABA/CR < 25%	
rat	frontal agranular cortex	GABA \supset CR	Kubota et al., BR 649:159, 1994
rat	visual	GABA \cap CR /CR = 94%, GABA \cap CR /GABA = 17%	Gonchar and Burkhalter, CC 7:347, 1997
rat	frontal agranular cortex	GABA \supset VIP	Kubota et al., BR 649:159, 1994
rat	SI cortex	GABA \supset VIP	Bayraktar et al. BR 757:209, 1997
cat	visual corex	GAD \cap VIP = ϕ	Demeulemeester et al. JNsci 8:988, 1988
rat	cortex	GABA \supset CCK	Kubota & Kawaguchi, BR752:175, 1997
cat	cortex	GAD \supset CCK	Hendry et al., PNAS 81:6526, 1984
cat	visual cortex	GABA \supset GAD \supset CCK	Somogyi et al., J Nsci 4:2590, 1984
cat	visual corex	GAD \cap CCK/CCK = 89%, GAD \cap CCK/GAD=11%	Demeulemeester et al. JNsci 8:988, 1988
monkey	cortex	(GAD \cap CCK) /CCK = 90-95%	Hendry et al., PNAS 81:6526, 1984
cat	visual corex	GAD \cap CRF = ϕ	Demeulemeester et al. JNsci 8:988, 1988
rat	cortex	ChAT \cap VIP/ChAT = 80%, ChAT \cap VIP/VIP= ?	Eckenstein, Baugman, Nature 309:153, 1984
rat	SI cortex	ChAT \cap VIP/VIP= 34%	Bayraktar et al. BR 757:209, 1997
rat	neocortex		Rogers, BR587:147, 1992
	layer II-IV	CR \cap VIP /CR = 63%, CR \cap VIP /VIP = 45%	
	layer V-VI	CR \cap VIP /CR = 90%, CR \cap VIP /VIP = 95%	
rat	frontal agranular cortex		Kubota et al., BR 649:159, 1994
	I	CR \cap VIP = ϕ	
	II/III	(CR \cap VIP) /CR = 71%, (CR \cap VIP) /VIP = 57%	
	V-VI	(CR \cap VIP) /CR = 94%, (CR \cap VIP) /VIP = 94%	
monkey	medial frontal	(CR \cap VIP)/VIP = 80%, (CR \cap VIP)/CR = 86%	Gabbott and Bacon BR 744:179, 1997
rat	cortex		Kubota & Kawaguchi, BR 752:175, 1997
	II/III	(CCK \cap CR)/CCK=5%, (CCK \cap CR)/CR=2%	
	V	(CCK \cap CR)/CCK=25%, (CCK \cap CR)/CR=5%	

rat	VI cortex, II/III V VI	(CCK∩CR)/CCK=11%, (CCK∩CR)/CR=3% (CCK∩VIP)/VIP=24%, (CCK∩VIP)/CCK=63% (CCK∩VIP)/VIP=12%, (CCK∩VIP)/CCK=51% (CCK∩VIP)/VIP=10%, (CCK∩VIP)/CCK=26%	Kubota & Kawaguchi, BR 752:175, 1997
cat	visual cortex	VIP ⊃ CRF	Demeulemeester et al. JNsci 8:988, 1988

bipolar neuron の発火特性は irregular spiking bipolar neuron と言われている、VIP と calretinin を発現していると報告されています [Cauli et al (1998) JNs 17: 3894; Porter et al (1998) EJN 10:3617]。一方で、VIP 陽性ニューロンの発火特性は regular-spiking と irregular spiking の両方があり、両者とも fusiform であって 2:1 程度の分布頻度であることがわかっています [Cauli et al (2000) PNAS 97: 6144]。

Cauli B, Audinat E, Lambolez B, Angulo MC, Ropert N, Tsuzuki K, Hestrin S, Rossier J (1997) Molecular and physiological diversity of cortical nonpyramidal cells. J. Neurosci. 17:3894-3906.

Cauli B, Porter JT, Tsuzuki K, Lambolez B, Rossier J, Quenet B, Audinat E (2000) Classification of fusiform neocortical interneurons based on unsupervised clustering. Proc. Natl. Acad. Sci. USA 97:6144-6149.

Porter JT, Cauli B, Staiger JF, Lambolez B, Rossier J, Audinat E (1998) Properties of bipolar VIPergic interneurons and their excitation by pyramidal neurons in the rat neocortex. Eur. J. Neurosci. 10:3617-3628.

* primate/hominid/human cingulate cortex で、**CR+ pyramidal cell** の存在が報告されています [Hof et al 2001]。また、ヒトの新皮質で CR+ asymmetric synapse が見つかり [del Rio & Defelipe 1997]、サルの新皮質深層でも CR+positive terminal の 43% が asymmetric synapses を作る事が報告されています [Melchitzky et al 2005]。これらのオリジンとして CR+ pyramidal cell を考えたいくなります。

del Rio MR, DeFelipe J (1997) Synaptic connections of calretinin-immunoreactive neurons in the human neocortex. J. Neurosci. 17:5143-5154, reprint(+), ID = 4126

Hof PR, Nimchinsky EA, Perl DP, Erwin JM (2001) An unusual population of pyramidal neurons in the anterior cingulate cortex of hominids contains the calcium-binding protein calretinin. Neurosci Lett. 2001 Jul 20;307(3):139-42.

Melchitzky DS, Eggan SM, Lewis DA (2005) Synaptic targets of calretinin-containing axon terminals in macaque monkey prefrontal cortex. Neuroscience. 2005;130(1):185-95.

2-3-3-4) Group IV (no clear chemical/molecular marker)

化学的にはあまり明確なマーカーが見つからない GABA 作動性ニューロンをここに group IV としました。ですから、waste basket 的なカテゴリーと理解して下さい。

具体例としては、Neurogliaform cell などが含まれることとなります。Late-spiking neurogliaform cell については 2-3-4-4) Neurogliaform cell を参照して下さい。

2-3-3-5) NPY-producing cells

様々な種で、NPY は SS や nNOS を発現するグループを含んでおり [Kubota et al 1994]、少なくとも一部は group II に属するニューロンに発現していると考えられ、1) Martinotti cell の形態を取るものが報告されています [Karagiannis...Cauli 2009]。しかし、同時に 2) Neurogliaform cell の形態

を取るものや、3) fast-spiking PV+ に発現することも報告されており [Karagiannis...Cauli 2009]、calretinin や VIP を発現する[Xu...Callaway 2010] など、group III や group IV などの一部を含むヘテロな集団と考えるべきだということになります。

CBPs and peptides

rat	frontal agranular cortex II/III V-VI	SS \cap NPY \supset NOS (NOS \cap NPY)/NPY=43%, (NOS \cap NPY)/NPY=52%,	Kubota et al., BR 649:159, 1994
monkey	neocortex	SS \cap NPY \supset large NOS (30% of SS, 60% of NPY)	Smiley et al 2000 BR 863:205-12
mouse	visaul cortex	PV \cap NPY= ϕ , CR \cap NPY/NPY=61%, CR \cap NPY/CR=14%	Gonchar et al (2008) FrontNeuroanat 1:1
mouse	frontal all Ls	CR \cap NPY/NPY= 12.4%, CR \cap NPY/CR= 8.5% PV \cap NPY/NPY= 0.5%, PV \cap NPY/PV= 0.2%	Xu et al (2010) JCN 518:389-404
	S1 all Ls	CR \cap NPY/NPY= 11.8%, CR \cap NPY/CR= 12.3% PV \cap NPY/NPY= 0.5%, PV \cap NPY/PV= 0.1%	
	V1 all Ls	CR \cap SS/SS= 27.1%, CR \cap SS/CR= 34.3% CR \cap NPY/NPY= 21.9%, CR \cap NPY/CR= 9.5% PV \cap NPY= ϕ	
rat	frontal agranular cortex II/III V-VI	PV \cap (VIP \cup SS \cup NPY) = ϕ , CR \cap (SS \cup NPY) = ϕ (CB \cap NPY)/NPY=68%,(strongCB \cap NPY)/NPY=37% (strongCB \cap NPY)/strongCB=39% (CB \cap NPY)/NPY=95%, (CB \cap NPY)/CB=24%	Kubota et al., BR 649:159, 1994
cat	visual corex	CB \cap NPY = ϕ	Demeulemeester et al. JNsci 8:988, 1988
cat	visual cortex	PV \cap (CCK \cup NPY) = ϕ	Demeulemeester et al, EBR 84:538, 1991
between Peptides			
mouse	visaul cortex	NPY \cap VIP= ϕ NPY \cap SS/SS=7%, NPY \cap SS/NPY=30% CCK \cap NPY/NPY=24%, CCK \cap NPY/CCK=43%	Gonchar et al (2008) FrontNeuroanat 1:1
mouse	frontal all Ls	NPY \cap SS/SS= 9.3%, NPY \cap SS/NPY= 25.4% VIP \cap NPY/NPY= 8.4%, VIP \cap NPY/VIP= 10.4%	Xu et al (2010) JCN 518:389-404
	S1 all Ls	NPY \cap SS/SS= 6.5%, NPY \cap SS/NPY= 19.1% VIP \cap NPY/NPY= 7.7%, VIP \cap NPY/VIP= 11.8%	
	V1 all Ls	NPY \cap SS/SS= 5.8%, NPY \cap SS/NPY= 21.6% VIP \cap NPY/NPY= 8.4%, VIP \cap NPY/VIP=6.2%	
rat	visual cortex	NPY \cap SS \neq ϕ	Papadopoulos et al., BR 420:95, 1987
rat	neocortex, hippocampus	SS \cap APP \neq ϕ (many)	Vincent et al. Neurosci. 7:439, 1982
rat	neocortex	SS \cap NPY \neq ϕ	Hendry et al., J Nsci 4:2497, 1984
rat	frontal agranular cortex II/III V-VI	(NPY \cap SS)/NPY =71%, (NPY \cap SS)/SS =42% (NPY \cap SS)/NPY =90%, (NPY \cap SS)/SS =34%	Kubota et al., BR 649:159, 1994
cat	visual corex	SS \supset NPY	Demeulemeester et al. JNsci 8:988, 1988
monkey	neocortex	(SS \cap NPY) / NPY = 37%, (SS \cap NPY) / SS = 41%	Hendry et al., J Nsci 4:2497, 1984
monkey	cerebral cortex	NPY \cap SS \supset large tachykinin cell(GABA-)	Jones et al., JNsci 8:1206, 1988
human	neocortex	SS \cap APP \neq ϕ (many)	Vincent et al. Nature 298:65, 1982

Karagiannis A, Gallopin T, Dávid C, Battaglia D, Geoffroy H, Rossier J, Hillman EM, Staiger JF, Cauli B (2009) Classification of NPY-expressing neocortical interneurons. J Neurosci. 2009 Mar 18;29(11):3642-59. [mouse](#)

Xu X, Roby KD, Callaway EM (2010) Immunochemical characterization of inhibitory mouse cortical neurons: three chemically distinct classes of inhibitory cells. J Comp Neurol. 2010 Feb 1;518(3):389-404.

2 - 3 - 4) Morphological classification

理想としては、chemical あるいは molecular な分類と形態学的分類が一致してくると本当によかったのですが、なかなかそういう具合には行きません。ここでは形態の特徴から interneuron を分類してそれぞれについて述べてみましょう。

2-3-4-1) Basket cell

Basket cell は元々、ネコやサル of 皮質ニューロンで軸索が籠 axon basket を形成して他の細胞体を囲むものをそう読んでいました [Ramón y Cajal 1911]。同様のニューロンはラットでは見いだしがたかったのですが、axon basket を形成しないまでもその axon varicosities のかなりの部分 (16-40%) が錐体ニューロンの細胞体と近位樹状突起に inputs するものは存在しますので、これらを basket cell と呼んでいます。元々 **large basket cell** (aspiny multipolar cell; long horizontal axons; mainly in L4) と **small basket cell** (local axon cluster) の区別はありましたが、最近ではこれに第3の、small basket のような密度の高い local nest of axons と長距離を走る axon の両者を持つ **nest basket cell** [Gupta et al 2000; Wang et al 2002] を加えて3種類存在するとも言われています。さらに、下降性の軸索を持ち、VIP/CRF+ な **descending basket cell** というニューロンも報告されています [Karube et al 2004]。

ラットの large basket cell あるいは nest basket cell の約50%は PV mRNA を発現していますが、small basket cell はたった5%しか発現しません [Wang et al 2002]。small basket cell の72%が CCK mRNA を発現しています [Wang et al 2002]。

Basket cell の firing pattern としては、最も多いのが Fast-spiking ですが、他に late-spiking type や non-FS type も多数存在しているようです [Karube et al 2004]。例えば、**descending basket cell** は non-FS type です [Karube et al 2004]。non-FS large basket は CCK を発現していることが多く、non-FS small basket は VIP/CCK/CRF などを発現していることが多いようです [Karube et al 2004]。

2-3-3-1) Group I も参照して下さい。

Gupta A, Wang Y, Markram H (2000) Organizing principles for a diversity of GABAergic interneurons and synapses in the neocortex. *Science* 287: 273-8. [**nest basket cell** 初出]

Karube F, Kubota Y, Kawaguchi Y (2004) Axon branching and synaptic bouton phenotypes in GABAergic nonpyramidal cell subtypes. *J Neurosci* 24:2853-65. [**late-spiking basket** 初出]

Kawaguchi Y, Kubota Y (1996) Physiological and morphological identification of somatostatin- or vasoactive intestinal polypeptide-containing cells among GABAergic cell subtypes in rat frontal cortex. *J Neurosci* 16:2701-15. **L2/3 VIP+ small basket cell** (2/ 31 VIP+ cells)

*Kisvardy ZF, Martin KAC, Whitteridge D, Sonogyi P (1985) Synaptic connections of intracellularly filled **clutch cells**: a type of **small basket cell** in the visual cortex of the cat. *J Comp Neurol* 241:111-37. **clutch cells** 初出

Ramón y Cajal S, *Histologie du Système Nerveux de l'Homme et des Vertébrés*. Tome II. Maloine, Paris, 1911, 997p. **basket cell** 初出

Wang Y, Gupta A, Toledo-Rodriguez M, Wu CZ, Markram H (2002) Anatomical, physiological, molecular and circuit properties of nest basket cells in the developing somatosensory cortex. *Cereb Cortex* 12: 395-410. [13-15 d rat]

2-3-4-2) Chandelier cell または Axoaxonic cell

Chandelier neuron あるいは axoaxonic neuron については、主に L2/3 に存在すると考えられています。しかし、下記の Golgi study の場合、染色がきまぐれですので、頻度を云々することは正しくないでしょう。

De Carlos JA, López-mascaraque L, Ramón y Cajal-Añeras S, Valverde F (1987) **Chandelier cells** in the **auditory cortex** of **monkey** and **man**: a **Golgi** study. *Exp Brain Res* 66:295-302. L3,4>2,5,6 in monkey; L3, upperL4 in man

- Fairén, A, Valverde, F. (1980) A specialized type of neuron in the **visual cortex** of **cat**: a **Golgi** and electron microscope study of **chandelier cells**. *J Comp Neurol* 1980;194(4):761-79. **V1/2 L2/3**
- Jones, EG. (1975) Varieties and distribution of non-pyramidal cells in the **somatic sensory cortex** of the squirrel **monkey**. *J Comp Neurol* 1975;160(2):205-67. **Golgi, S1, type 4 nonpyramidal かの chandelier か?**
- Lund, JS, Henry, GH, MacQueen, CL, Harvey, AR. (1979) Anatomical organization of the primary visual cortex (**area 17**) of the **cat**. A comparison with area 17 of the macaque **monkey**. *J Comp Neurol* 1979;184(4):599-618. **Golgi, L4 chandelier cell**
- Marin-Padilla, M. (1987) The chandelier cell of the **human** visual cortex: a **Golgi** study. *J Comp Neurol* 1987;256(1):61-70. **V1, L3/4 border > other layers**
- Müller-Paschinger, IB, Tömböl, T, Petsche, H. **Chandelier neurons** within the **rabbits'** cerebral cortex. A **Golgi** study. *Anat Embryol (Berl)* 1983;166(1):149-54. **L2/3**
- Peters, A, Proskauer, CC, Ribak, CE. (1982) **Chandelier cells** in **rat** visual cortex. *J Comp Neurol* 1982;206(4):397-416. **V1/2 L2/3**
- Somogyi, P. (1977) A specific '**axo-axonal**' interneuron in the **visual** cortex of the **rat**. *Brain Res* 1977;136(2):345-50. **L2/3**
- Somogyi P, Freund TF, Cowey A (1982) The **axo-axonic** interneuron in the cerebral cortex of the **rat, cat** and **monkey**. *Neurosci* 7:2577-607. **V1/2 L2/3** in rat; **V1 L3,5, M1 L3** in cat; **V2 L3** in monkey
- Szentágothai, J. (1975) The 'module-concept' in cerebral cortex architecture. *Brain Res* 1975;95(2):475-96. **chandelier**
- *Szentágothai, J, Arbib, MA. (1974) Conceptual models of neural organization. *Neurosci Res Prog Bull* 1974;12:307-510. s/o chandelier cell の初出
- Krimer LS, Zaitsev AV, Czanner G, Kröner S, González-Burgos G, Povysheva V, Iyengar S, Barrionuevo G, Lewis DA (2005) Cluster analysis-based physiological classification and morphological properties of inhibitory neurons in **layers 2-3** of **monkey** dorsolateral prefrontal cortex. *J Neurophysiol* 94: 3009-22. **FS chandelier cell in L2/3**

Chandelier neuron かの fast-spiking で、parvalbumin 陽性であることは以下の論文で示されています。ただし、小数、nonFS chandelier cell も報告されています [Kawaguchi 1995, 1/ 4 chandelier cells]。

- Karube F, Kubota Y, Kawaguchi Y (2004) Axon branching and synaptic bouton phenotypes in GABAergic nonpyramidal cell subtypes. *J Neurosci* 24:2853-65. **2 chandeliers in L2/3**
- Kawaguchi, Y. (1995) Physiological subgroups of nonpyramidal cells with specific morphological characteristics in **layer II/ III** of rat frontal cortex. *J Neurosci* 1995;15(4):2638-55. **4 chandelier cells in L2/3; FS 3/ 4 chandelier cells, PV+ 12/ 12 FS cells**
- Kawaguchi Y, Kubota Y (1998) Neurochemical features and synaptic connections of large physiologically-identified GABAergic cells in the rat frontal cortex. *Neurosci* 85: 677-701. **2 chandelier cells in L2/3**
- Zaitsev AV, Gonzalez-Burgos G, Povysheva NV, Kroner S, Lewis DA (2005) Localization of calcium-binding proteins in physiologically and morphologically characterized interneurons of monkey dorsolateral prefrontal cortex. *Cereb Cortex* 15: 1178-86.
- Zaitsev AV, Gonzalez-Burgos G, Povysheva NV, Kröner S, Lewis DA, Krimer LS, Lewis DA (2009) Interneuron diversity in layers 2-3 of monkey prefrontal cortex. *Cereb Cortex* 19: 1597-615.

また、parvalbumin あるいは CRF の免疫活性 (ir) で特徴的な chandelier-like GABAergic **axon cartridge** が認められることを以下の論文が報告しています。この手法でみますと、chandelier cell の頻度分布が推定されます。

parvalbumin cartridge はサルの M1, S1 で L2/3 に、あるいは V1 L2, V2 L2/3, temporal cortex L2-4 > L5/6 に多く認められる (V1 < V2 < TE) こと [DeFelipe & González-Albo 1998; DeFelipe et al., 1989, 1999], サルの V1 には少ないが、occipital association と prefrontal の L2/3 に多いこと [Lewis & Lund 1990]、ヒトの temporal cortex では L2 と L6 にたくさん認められること [Fonseca 1993] 等が報告されています。さらに、CRF+ chandelier cartridge の存在が squirrel monkey prefrontal L4 で報告されています (面白いことに macaque では認められていません) [Lewis & Lund 1990]。

最近、plasma membrane GABA transporter (GAT1) ir が chandelier cartridge の良い指標になってきているようです。human prefrontal cortex (areas 9, 46) あるいは多くの associative areas の L2-6

に GAT-1 chandelier cartridge が分布しています (L3B/5A に若干少ない; S1, V1, V2 に少なく、L2 を除いて M1 にも少ない) [Woo et al 1998; Inda et al 2007]。同じ論文 [Woo et al 1998] の中で統合失調症患者では GAD-1+ cartridge が減少していると報告されているのは興味深いことです。

ラットの medial prefrontal cortex (ant cingulate, infralimbic, prelimbic) L2/3 で、GAD1+ cartridge が多く認められています [Hardwick et al 2005]。ラットでは GAT1+ cartridge が parvalbumin cartridge より目立つようであり、おなじ GABAergic marker でも GAD67+ cartridge は認めがたいようです。このことは GABAergic marker より、その細胞種ごと、部位ごとに微妙な発現量の差があることを示唆します。これが、マウスになりますと complex GAT1+ cartridge (典型的な chandelier cartridge) は V1, V2, S2, S2, Ad, orbital, insular, retrosplenial, motor, frontal, parietal associative areas には少なく、A2v, temporal association の L5/6 に、あるいは dorsal peduncular, infralimbic, prelimbic areas の L2-4 にめだつようです [Inda et al 2009]。ただし彼らは simple GAT1+ cartridge (1-2 rows x 3-5 boutons) は皮質全体に分布していると報告していますが、この 'simple cartridge' については axoaxonic terminal なのかどうか異なる吟味が必要です。

DeFelipe J, Hendry SHC, Jones EG (1989) Visualization of chandelier cell axons by **parvalbumin** immunoreactivity in **monkey** cerebral cortex. *ProNAS* 86: 2093-7.

DeFelipe J, González-Albo MC. (1998) Chandelier cell axons are immunoreactive for **GAT-1** in the **human** neocortex. *Neuroreport*. 1998 Feb 16;9(3):467-70.

DeFelipe, J, González-Albo, MC, Del Río, MR, Elston, GN (1999) Distribution and patterns of connectivity of interneurons containing calbindin, calretinin, and **parvalbumin** in visual areas of the occipital and temporal lobes of the macaque **monkey**. *J Comp Neurol* 1999;412(3):515-26.

Fonseca M, Soriano E, Ferrer I, Martínez A, Tuñón T (1993) Chandelier cell axons identified by **parvalbumin**-immunoreactivity in the normal **human** temporal cortex and in Alzheimer's disease. *Neurosci* 55:1107-16.

Hardwick, C, French, SJ, Southam, E, Totterdell, S. A comparison of possible markers for chandelier cartridges in **rat** medial prefrontal cortex and hippocampus. *Brain Res* 2005;1031(2):238-44. [**GAT-1**]

Inda, MC, DeFelipe, J, Muñoz, A. The distribution of chandelier cell axon terminals that express the GABA plasma membrane transporter **GAT-1** in the **human** neocortex. *Cereb Cortex* 2007;17(9):2060-71.

Inda, MC, DeFelipe, J, Muñoz, A. Morphology and distribution of chandelier cell axon terminals in the **mouse** cerebral cortex and claustramygdaloid complex. *Cereb Cortex* 2009;19(1):41-54. [**GAT-1**]

Lewis, DA, Lund, JS. (1990) Heterogeneity of chandelier neurons in monkey neocortex: **corticotropin-releasing factor**- and **parvalbumin**-immunoreactive populations. *J Comp Neurol* 1990;293(4):599-615.

Williams, SM, Goldman-Rakic, PS, Leranth, C (1992) The synaptology of **parvalbumin**-immunoreactive neurons in the primate prefrontal cortex. *J Comp Neurol* 1992;320(3):353-69. **PV+ cartridge**

Woo, TU, Whitehead, RE, Melchitzky, DS, Lewis, DA. A subclass of prefrontal gamma-aminobutyric acid axon terminals are selectively altered in schizophrenia. *Proc Natl Acad Sci U S A* 1998;95(9):5341-6. [**GAT-1**]

2-3-4-3) Double bouquet cell

Yáñez IB, Muñoz A, Conreras J, Gonzalez J, Rodriguez-Veiga E, DeFelipe J (2005) Double bouquet cell in the human cerebral cortex and a comparison with other mammals. *J Comp Neurol* 486: 344-60.

2-3-4-4) Neurogliaform cell

Neurogliaform cell は小さくて丸い細胞体を持ち、樹状突起が短く、密度の高い軸索を出して錐体細胞の樹状突起に入力するという形態学的特徴を持っています [Ramón y Cajal 1899; Kisvárdy et al 1990; Kawaguchi, Kubota 1997; Tamás et al 2003]。ラットにおいて閾値に近い pulse 電流入力に対して slow ramp depolarization を示す **Late-spiking (LS) neuron** として同定された [Kawaguchi 1995; Tamás et al. 2003; Simons et al. 2005; Povysheva et al. 2007; Uematsu et al 2008] ニューロンとして、最近、 α -actinin-2 という NMDA receptor/actin binding protein が発現している

ことが報告されています [Ratzliff, Soltesz 2001; Price et al. 2005; Uematsu et al 2008, 7+ /8 neurogliaform cells]。しかし、サルの neurogliaform cell では late-spiking には見えずに [Povysheva et al 2007, Zaitzev et al 2008], initial adaptation が強く、calbindin と neuropeptide Y を発現していると報告されました。

ただし、late-spiking の特徴については basket cell でも見受けられることがあるようです [Karube et al 2004, 3(L2/3) in 7(L2/3)+2(L5)=12 LS cells]。

最近、NPY/GFP BAC TG mice で GFP+ cell の一部に Neurogliaform cell の形態を取るものが報告されています [Karagiannis...Cauli 2009]。

LS cell に 5HT3aR が発現していることが報告されています [Lee et al 2010]。

- Karagiannis A, Gallopin T, Dávid C, Battaglia D, Geoffroy H, Rossier J, Hillman EM, Staiger JF, Cauli B (2009) Classification of NPY-expressing neocortical interneurons. *J Neurosci*. 2009 Mar 18;29(11):3642-59. mouse
- Karube F, Kubota Y, Kawaguchi Y (2004) Axon branching and synaptic bouton phenotypes in GABAergic nonpyramidal cell subtypes. *J Neurosci* 24:2853-65.
- Kawaguchi Y (1995) Physiological subgroups of nonpyramidal cells with specific morphological characteristics in layer II/III of rat frontal cortex. *J Neurosci* 15:2638-55. **LS cell 初出**
- Kawaguchi Y, Kubota Y (1997, review?) GABAergic cell subtypes and their synaptic connections in rat frontal cortex. *Cerebral Cortex* 7:476-486.
- Kisvárdy ZF, Gulyas A, Ceroukas D, North JB, Chubb IW, Somogyi P (1990) Synapses, axonal and dendritic patterns of GABA-immunoreactive neurons in human cerebral cortex. *Brain* 113: 793-812. [Golgi & GABA-ir]
- Lee S, Hjerling-Leffler J, Zaghera E, Fishell G, Rudy B (2010) The largest group of superficial neocortical GABAergic interneurons expresses ionotropic serotonin receptors. *J Neurosci*. 2010 Dec 15;30(50):16796-808.
- Povysheva NV, Zaitzev AV, Kroner S, Krimer OA, Rotaru DC, Gonzalez-Burgos G, Lewis DA, Krimer LS (2007) Electrophysiological differences between neurogliaform cells from monkey and rat prefrontal cortex. *J Neurophysiol* 97: 1030-9. [Monkey neurogliaform cells do not seem to have the late-spiking phenotype.]
- Price CJ, Cauli B, Kovacs ER, Kulik A, Lambollez B, Shigemoto R, Capogna M (2005) Neurogliaform neurons form a novel inhibitory network in the hippocampal CA1 area. *J Neurosci*. 2005 Jul 20;25(29):6775-86. [bNOS 7+ of 15 neurogliaform cells in CA1 lacun-mol; NPY&alpha-actinin-2/NPY =81%, bNOS&alpha-actinin-2/alpha-actinin-2 =46% in CA1SLM]
- Ramón y Cajal (1899) Estudios sobre la corteza cerebral humana. *Corteza visual. Revisita Trimestral Micrografica* 4:1-63.
- Ratzliff ADH, Soltesz I (2001) Differential immunoreactivity for alpha-actinin-2, an N-methyl-D-aspartate-receptor/actin binding protein, in hippocampal interneurons. *Neuroscience* 103:337-49.
- Simon A, Oláh S, Molnár G, Szabadics J, Tamás G (2005) Gap-junctional coupling between neurogliaform cells and various interneuron types in the neocortex. *J Neurosci*. 2005 Jul 6;25(27):6278-85.
- Tamás G, Lörincz A, Simon A, Szabadics J (2003) Identified sources and targets of slow inhibition in the neocortex. *Science* 299:1902-1905.
- Uematsu M, Hirai Y, Karube F, Ebihara S, Kato M, Abe K, Obata K, Yoshida S, Hirabayashi M, Yanagawa Y, Kawaguchi Y (2008) Quantitative chemical composition of cortical GABAergic neurons revealed in transgenic venus-expressing rats. *Cerebral Cortex* 18:315-330.
- Zaitzev AV, Povysheva NV, Gonzalez-Burgos G, Rotaru D, Fish KN, Krimer LS, Lewis DA (2008) Interneuron diversity in layers 2-3 of monkey prefrontal cortex. *Cereb Cortex*.

2-3-4-5) **Martinotti cell** (未記載)

- Kawaguchi Y, Kubota Y (1997) GABAergic cell subtypes and their synaptic connections in rat frontal cortex. *Cerebral Cortex* 7:476-486.

2-3-4-6) **Arcade cell** (未記載)

Kawaguchi Y, Kubota Y (1996) Physiological and morphological identification of somatostatin- or vasoactive intestinal polypeptide-containing cells among GABAergic cell subtypes in rat frontal cortex. *J Neurosci* 15:2701-15. **L2/3, 5 VIP+ arcade cell** (5/ 31 VIP+ cells)

2-3-4-7) Wide arbor cell

当初、somatostatin 産生 interneuron のなかで、Martinotti cell とは言えないタイプとして記述されました [Kwaguchi & Kubota 1998]。axon として特に上行性のものが目立つではなく、全ての方向に広く分布しているタイプです。その後、parvalbumin+, fast-spiking neuron においても、記載されました [Kawaguchi & Kondo 2002]。

Kawaguchi Y, Kondo S (2002) Parvalbumin, somatostatin and cholecystokinin as chemical markers for specific GABAergic interneuron types in the rat frontal cortex. *J Neurocytol* 31:277-87.

Kwaguchi Y, Kubota Y (1998) Neurochemical features and synaptic connections of large physiologically-identified GABAergic cells in the rat frontal cortex. *Neurosci* 85: 677-701. [**wide arbor cell** 初出]

2-3-4-8) Clutch cell → cf. basket cell

Kisvady ZF, Martin KAC, Whitteridge D, Sonogyi P (1985) SYnaptic connections of intracellularly filled **clutch cells**: a type of **small basket cell** in the visual cortex of the cat. *J Comp Neurol* 241:111-37.

2-3-4-9) Linear arbor cell

Zaitsev AV, Gonzalez-Burgos G, Povysheva NV, Kröner S, Lewis DA, Krimer LS (2009) Interneuron diversity in layers 2-3 of **monkey prefrontal** cortex. *Cereb Cortex* 19: 1597-615. [**PV, CR, CB, SS, NPY**] **linear arbor cell**

2-3-4-10) Dendrite-targeting cell

Tamás G, Buhl, EH, Somogyi P (1997) Fast IPSP elicited via multiple synaptic release sites by different types of GABAergic neurone in the cat visual cortex. *J Physiol* 500:715-38. 6 basket, **5 Dendrite-targeting cell**, 4 double bouquet

Tamás G, Somogyi P, Buhl EH. Differentially interconnected networks of GABAergic interneurons in the **visual cortex** of the **cat**. *J Neurosci* 1998;18(11):4255-70. **Dendrite-targeting cell**

Thomson AM, West DC, Wang Y, Banniser AP (2002) Synaptic connections and small circuits involving excitatory and inhibitory neurons in layers 2–5 of adult rat and cat neocortex: triple intracellular recordings and biocytin labelling in vitro. *Cereb Cortex* 12:936-53. **Dendrite-targeting cell**, basket cell

2-3-4-11) Ivy cell

海馬の str pyramidale に存在して nNOS/NPY を発現するニューロン。str lacunosum-moleculare に存在する neurogliaform cell に類似。

Fuentealba P, Begum R, Capogna M, Jinno S, Márton LF, Csicsvari J, Thomson A, Somogyi P, Klausberger T (2008) **Ivy cells**: a population of nitric-oxide-producing, slow-spiking GABAergic neurons and their involvement in hippocampal network activity. *Neuron*. 2008 Mar 27;57(6):917-29.

*Szabadics J, Soltesz I (2009) Functional specificity of mossy fiber innervation of GABAergic cells in the hippocampus. *J Neurosci*. 2009 Apr 1;29(13):4239-51.

Tricoire L, Pelkey KA, Daw MI, Sousa VH, Miyoshi G, Jeffries B, Cauli B, Fishell G, McBain CJ (2010) Common origins of hippocampal **Ivy** and nitric oxide synthase expressing neurogliaform cells. *J Neurosci*. 2010 Feb 10;30(6):2165-76.

2-3-5) 発火特性による抑制性ニューロンの分類

cortical inhibitory interneuron の発火特性を示す言葉として

fast spiking (FS)

regular spiking (RS)

low threshold spike (LTS)

late-spiking (LS)
burst-spiking (BS)
irregular spiking (IS)

等があります。以下では個々に説明して行きましょう。また、最近の Petilla terminology [Nat Rev Neurosci 9: 557-568, 2008] では、steady-state と step-onset の 2 軸に基づいた

<i>steady state</i> :	<i>step-onset</i>
fast-spiking:	continuous, delayed, stuttering
non-adapting non-fast spiking:	(initial) burst, continuous
adapting:	(initial) burst, continuous, delayed
irregular spiking:	(initial) burst, continuous
intrinsic burst firing:	(initial) burst, continuous
accelerating:	delayed

という分類を提案しています。

cf. Kawaguchi group の発火特性による non-pyramidal cell の分類は

FS, LTS	rat frontal L5	[Kawaguchi 1993; Kawaguchi, Kubota 1993]
FS, LTS, LS, RS	rat frontal L2/3	[Kawaguchi 1995]
FS, BS, RS(, LS)	rat frontal	[Kawaguchi, Kubota 1996, 1997, 1998]
FS, LS, nonFS = RS+BS+phasic firing,		[Kawaguchi, Kondo 2002]
* LTS (≥ 2 spikes on hump from hyper) は BS に含まれる使っています。		
FS, LS, nonFS	rat frontal	[Karube et al 2004; Kawaguchi et al 2006]
FS, RS, BS, LS	rat frontal	[Uematsu et al 2008]

というように変遷してきており、最近では LTS cell についてはその使用を控えています。

Kawaguchi Y (1993) Groupings of nonpyramidal and pyramidal cells with specific physiological characteristics in **rat frontal cortex**. J Neurophysiol 69:416-31. [LTS 初出; P16-22]

Kawaguchi Y, Kubota Y (1993) Correlation of physiological subgroupings of nonpyramidal cells with parvalbumin and calbindin D28k-immunoreactive neurons in layer V of rat frontal cortex. J Neurophysiol 70:387-96. FS-PV, **LTS-calbindin** [P16-20]

Kawaguchi Y. (1995) Physiological subgroups of nonpyramidal cells with specific morphological characteristics in **layer II/III** of rat **frontal cortex**. J Neurosci 1995;15(4):2638-55. ここまでは LTS を使っている [P18-22]

Kawaguchi Y, Kubota Y (1996) Physiological and morphological identification of somatostatin- or vasoactive intestinal polypeptide-containing cells among GABAergic cell subtypes in rat frontal cortex. J Neurosci. 1996 Apr 15;16(8):2701-15.

Kawaguchi Y, Kubota Y (1997, review?) GABAergic cell subtypes and their synaptic connections in rat frontal cortex. Cereb Cortex. 1997 Sep;7(6):476-86.

Kawaguchi Y, Kubota Y (1998) Neurochemical features and synaptic connections of large physiologically-identified GABAergic cells in the rat frontal cortex. Neurosci 85: 677-701. [CCK, PV, SS] 12 PV+ / 12 FS cells, 5 basket, 2 chandelier / 7 FS cells

Kawaguchi Y, Kondo S (2002, review) Parvalbumin, somatostatin and cholecystokinin as chemical markers for specific GABAergic interneuron types in the rat frontal cortex. J Neurocytol. 2002 Mar-Jun;31(3-5):277-87. Review.

Karube F, Kubota Y, Kawaguchi Y (2004) Axon branching and synaptic bouton phenotypes in GABAergic nonpyramidal cell subtypes. J Neurosci 24:2853-65. [late-spiking basket 初出] 34 basket, 2 chandelier / 36 FS cells

Kawaguchi Y, Karube F, Kubota Y. (2006) Dendritic branch typing and spine expression patterns in cortical nonpyramidal cells. Cereb Cortex. 2006 May;16(5):696-711.

Uematsu M, Hirai Y, Karube F, Ebihara S, Kato M, Abe K, Obata K, Yoshida S, Hirabayashi M, Yanagawa Y, Kawaguchi Y (2008) Quantitative chemical composition of cortical GABAergic neurons revealed in transgenic venus-expressing rats. Cereb Cortex. 2008 Feb;18(2):315-30.

2-3-5-1) Fast-spiking (FS)

その発火特性は. . .

McCormick et al JNp 54(85)782; **guinea pig anterior cingulate & sensorimotor areas**, [FS 初出]

3) fast spiking: (near θ) single APs, spike frequency is a monotonic function of I

FS neuron からみた分子・化学的あるいは形態学的特徴は以下の文献を参照して下さい。

Karube F, Kubota Y, Kawaguchi Y (2004) Axon branching and synaptic bouton phenotypes in GABAergic nonpyramidal cell subtypes. J Neurosci 24:2853-65. [**late-spiking basket** 初出] 34 basket, 2 chandelier / 36 FS cells

Kawaguchi, Y. (1995) Physiological subgroups of nonpyramidal cells with specific morphological characteristics in layer II/III of rat frontal cortex. J Neurosci 1995;15(4):2638-55. [**PV+ 12/ 12 FS cells**] **26 local axon arbors and horizontal axon arbors, 3 chandelier / 29 FS cells**

Kawaguchi Y, Kubota Y (1993) Correlation of physiological subgroupings of nonpyramidal cells with **parvalbumin** and calbindin D28k-immunoreactive neurons in **layer V** of rat **frontal** cortex. J Neurophysiol 70:387-96. **18 FS-PV+ cells**

Kawaguchi Y, Kubota Y (1998) Neurochemical features and synaptic connections of large physiologically-identified GABAergic cells in the rat frontal cortex. Neurosci 85: 677-701. [CCK, **PV**, SS] **12 PV+ / 12 FS cells, 5 basket, 2 chandelier/ 7 FS cells**

Povysheva NV, Zaitsev AV, Toraru DC, Gonzalez-Burgos G, Lewis DA, Krimer LS (2008) **Parvalbumin-positive basket** interneurons in **monkey and rat prefrontal** cortex. J Neurophysiol 100: 2348-60. **PV+ 11(78%)/ 14 rat L2/3 FS cells; PV+ 14 (67%)/ 21 monkey L2/3 FS cells**

Zaitsev AV, Gonzalez-Burgos G, Povysheva NV, Kroner S, Lewis DA (2005) Localization of calcium-binding proteins in physiologically and morphologically characterized interneurons of monkey dorsolateral prefrontal cortex. Cereb Cortex 15: 1178-86. [**PV**, CR, CB] **PV+ 14/36 FS cells; PV- / 43 RSNP cells**

Krimer LS, Zaitsev AV, Czanner G, Kröner S, González-Burgos G, Povysheva V, Iyengar S, Barrionuevo G, Lewis DA (2005) Cluster analysis-based physiological classification and morphological properties of inhibitory neurons in **layers 2-3** of **monkey** dorsolateral prefrontal cortex. J Neurophysiol 94: 3009-22. **FS chandelier cell in L2/3**

Wang Y, Gupta A, Toledo-Rodriguez M, Wu CZ, Markram H (2002) Anatomical, physiological, molecular and circuit properties of **nest basket** cells in the developing **somatosensory** cortex. Cereb Cortex 12: 395-410. [13-15 d rat] 5 large basket & 10 nest basket/ **15 FS cells**

Spike-width of Fast-spiking (FS) cortical neurons

[McCormick et al 1985 J Neurophysiol 54:782-806] Guinea pig neocortex, slice intra, 35-37°C

spike width at base = 0.66 ± 0.19 ms; cf. RS = 1.74 ± 0.41

spike width at 1/2 height = 0.32 ± 0.10 ms; cf. RS = 0.80 ± 0.18

[Baranyi et al 1993 J Neurophysiol 69:0865-79] Cat motor cortex, in vivo intra,

spike width at 1/2 height = 0.25 ± 0.03 ms; cf. RS = $0.41 \sim 0.73$

[Kawaguchi 1987 Brain Res 411:190-5] Rat CA1, slice intra, 32°C

spike width at 1/2 height = 0.30 ± 0.06 ms; cf. non-FS non-pyramidal = 0.61 ± 0.06

[Kawaguchi 1988 Exp Brain Res 72:494-502] Rat CA1, slice intra, 32°C

spike width at 1/2 height = 0.28 ± 0.05 ms; cf. pyramidal = 0.72 ± 0.05

[Kawaguchi 1993 J Neurophysiol 69:416-31] Rat frontal cortex, slice whole cell, 29-30°C

spike width at 1/2 height = 0.57 ± 0.11 ms; cf. LTS = 1.04 ± 0.13

[Kawaguchi & Kubota 1993 J Neurophysiol 70:387-96] Rat frontal cortex layer V, slice whole cell, 29-30°C

spike width at 1/2 height = 0.59 ± 0.09 ms; cf. LTS = 1.24 ± 0.22

[Kawaguchi 1995 J Neurosci 15:2638-55] Rat frontal cortex layer II/III, slice whole cell, 29-30°C

spike width at 1/2 height = 0.43 ± 0.06 ms; cf. LTS = 0.94 ± 0.15 , LS = 0.77 ± 0.19 , RSNP = 0.75 ± 0.13

[Kawaguchi & Kubota 1996 J Neurosci 16:2701-15] Rat frontal cortex, slice whole cell, 29-30°C

spike width at 1/2 height = 0.45 ± 0.06 ms

[Kawaguchi & Kubota 1998 Neurosci 85:677-701] Rat frontal cortex layer II/III, slice whole cell, 29-30°C

spike width at 1/2 height = 0.41 ± 0.06 ms

2-3-5-2) Low threshold spike(ing) (LTS) cell

川口たちが使いだした用語 [Kawaguchi, 1993] ですが、彼ら自身最近は使用しなくなっています。初出では、frontal cortex L5 で 22 cells 報告し、その電気的特性は 1) AP width は FS より広い；2) input impedance が大きくて membrane time constant が長い；3) AHP に 2 components ある；4) spike freq adaptation を示す；5) 過分極から戻った時に LTS を出す (**rebound burst spikes**)、といったものでした。命名ほうからしても最後の LTS の存在が大事でしょう。その最後の論文で、frontal cortex L5 で 10 個の CB(+) LTS cell を報告しました [Kawaguchi Y, Kubota Y, 1993]。その後、Kawaguchi (1995) で、frontal cortex L2/3 で 4 個の LTS を報告しましたが、それ以後余り LTS cell という分類を余り使わなくなります。ただし、Kawaguchi, Kondo (2002) の review では L5 の VIP+/CCK+ or CR+ の BS cell に LTS cell の命名を使用しています。

Connors たち [Gibson et al 1999 ; Beierlein et al 2000, 2003; Deans et al 2001, Amitai et al 2002] は主に S1L4 でこの用語を使い続けていて、regular-spiking RS と区別について以下のように述べています。長い矩形電流注入で連続発火させた時に、mAHP を見ると RS ではその最も深いところが一定であるのに対して、LTS では徐々に上昇することを指標としています [Beierlein et al 2003]。その原因としては発火に伴う Na, K ion の accumulation を推測しています。この定義は Kawaguchi らの定義のうち rebound burst の存在を前提にしておらず、同一のものとは言いがたいようです。

Prince も LTS cell の用語を使っています。Bacci et al (2004) では S1 L5 の 7 個の LTS cells が全て CCK+ であったと報告し、Marinelli et al (2008) でも、S1 L5 の 56 LTS cells 中、36 個で SS+, 8 個で CCK+ であったと報告しました。Yuste 達は、Goldberg JH...Yuste (2004) は V1/S1 L5 の LTS cells が、**rebound burst** を呈して真に LTS cells であるとして、Connors たち [Gibson et al 1999, Beierlein et al 2000, 2003, Deans et al 2001, Amitai et al 2002] の論文で言った S1L4 LTS cells は別のカテゴリーとすべきだとしています。

Bacci A, Huguenard JR, Prince DA (2003) Functional autaptic neurotransmission in fast-spiking interneurons: a novel form of feedback inhibition in the neocortex. *J Neurosci*. 2003 Feb 1;23(3):859-66.

Bacci A, Rudolph U, Huguenard JR, Prince DA (2003) Major differences in inhibitory synaptic transmission onto two neocortical interneuron subclasses. *J Neurosci*. 2003 Oct 22;23(29):9664-74.

Bacci A, Huguenard JR, Prince DA (2004) Long-lasting self-inhibition of neocortical interneurons mediated by endocannabinoids. *Nature*. 2004 Sep 16;431(7006):312-6. 7 CCK+/7 L5 LTS cells

Beierlein M, Gibson JR, Connors BW (2000) A network of electrically coupled interneurons drives synchronized inhibition in neocortex. *Nat Neurosci*. 2000 Sep;3(9):904-10.

Beierlein M, Gibson JR, Connors BW (2003) Two dynamically distinct inhibitory networks in layer 4 of the neocortex. *J Neurophysiol*. 2003 Nov;90(5):2987-3000.

Gibson JR, Beierlein M, Connors BW (1999) Two networks of electrically coupled inhibitory neurons in neocortex. *Nature*. 1999 Nov 4;402(6757):75-9.

Goldberg JH, Lacefield CO, Yuste R (2004) Global dendritic calcium spikes in mouse layer 5 low threshold spiking interneurons: implications for control of pyramidal cell bursting. *J Physiol*. 2004 Jul 15;558(Pt 2):465-78.

Kawaguchi Y (1993) Groupings of nonpyramidal and pyramidal cells with specific physiological characteristics in **rat frontal cortex**. *J Neurophysiol* 69:416-31. [**LTS 初出**; P16-22]

Kawaguchi Y, Kubota Y (1993) Correlation of physiological subgroupings of nonpyramidal cells with parvalbumin and calbindin D28k-immunoreactive neurons in layer V of rat frontal cortex. *J Neurophysiol* 70:387-96. FS-PV, **LTS-calbindin** [P16-20]

- Kawaguchi Y. (1995) Physiological subgroups of nonpyramidal cells with specific morphological characteristics in **layer II/III** of rat **frontal** cortex. *J Neurosci* 1995;15(4):2638-55. ここまでは LTS を使っている [P18-22]
- Kawaguchi Y, Kondo S (2002, review) Parvalbumin, somatostatin and cholecystokinin as chemical markers for specific GABAergic interneuron types in the rat frontal cortex. *J Neurocytol.* 2002 Mar-Jun;31(3-5):277-87. Review.
- Marinelli S, Pacioni S, Bisogno T, Di Marzo V, Prince DA, Huguenard JR, Bacci A (2008) The endocannabinoid 2-arachidonoylglycerol is responsible for the slow self-inhibition in neocortical interneurons. *J Neurosci.* 2008 Dec 10;28(50):13532-41.

2-3-5-3) Late-spiking (LS) cell

2-3-4-4) Neurogliaform cells を参照して下さい。

2-3-5-4) Multipolar bursting (MB)

mouse neocortex L2/3 で、PV(+), CB(9+/9), VIP(-; 0/9), CR 4+/11 な non-FS cell が報告されています。L5 pyramidal の intrinsic bursting (IB) に近い発火特性を持つニューロン群です。L2/3 の FS cell よりはやや樹状突起と軸索が広がる傾向を示します。また、MB cell は相互に高い確率で gap junction を形成していることもわかっています。

Blatow M, Rozov A, Katona I, Hormuzdi SG, Meyer AH, Whittington MA, Caputi A, Monyer H (2003) A novel network of **multipolar bursting** interneurons generates theta frequency oscillations in neocortex. *Neuron.* 38:805-817.

2-3-5-5) burst spiking

2-3-5-6) irregular spiking (IS) interneurons

10 IS in 5 CR+VIP, 1 CR+VIP+SS, 1 CR+VIP+SS+CCK, 1 CB+CR+VIP, 2 CB+CR+VIP+CCK
他に 5 VIP+ RSNP 15 CR+ RSNPがいた。 [Cauli et al 1997 rat SM1 L2/3 L5]

IS in CB1+ upper L2/3 neurons [Galarreta et al 2004 mouse S1]

phasic (rapid adapting RA) or IS in 5 VIP+ L2/3 neurons [Uematsu et al. 2008 rat frontal]

* Petilla terminology [Nature Rev Neurosci 9:557-68, 2008] にも irregular-spiking のカテゴリーが設けられている。

* Kawaguchi 等は IS などを regular-spiking, burst-spiking に分類していることが多い [Kawaguchi 1995 Fig 7B, 8B; Kawaguchi and Kubota 1996 Fig 3B CCK+; Uematsu et al 2008 Fig 6 VIP+]。最近では non-FS とくくっつてもいる [Karube et al 2004 Fig 1C_{2,3}]。

Galarreta M, Erdélyi F, Szabó G, Hestrin S (2004) Electrical coupling among irregular-spiking GABAergic interneurons expressing cannabinoid receptors. *J Neurosci.* 2004 Nov 3;24(44):9770-8.

Kawaguchi Y. (1995) Physiological subgroups of nonpyramidal cells with specific morphological characteristics in **layer II/III** of rat **frontal** cortex. *J Neurosci* 1995;15(4):2638-55. ここまでは LTS を使っている [P18-22]

Kawaguchi Y, Kubota Y (1996) Physiological and morphological identification of somatostatin- or vasoactive intestinal polypeptide-containing cells among GABAergic cell subtypes in rat frontal cortex. *J Neurosci.* 1996 Apr 15;16(8):2701-15.

Karube F, Kubota Y, Kawaguchi Y (2004) Axon branching and synaptic bouton phenotypes in GABAergic nonpyramidal cell subtypes. *J Neurosci* 24:2853-65. [late-spiking basket 初出] 34 basket, 2 chandelier / 36 FS cells

Uematsu M, Hirai Y, Karube F, Ebihara S, Kato M, Abe K, Obata K, Yoshida S, Hirabayashi M, Yanagawa Y, Kawaguchi Y (2008) Quantitative chemical composition of cortical GABAergic neurons revealed in transgenic venus-expressing rats. *Cereb Cortex*. 2008 Feb;18(2):315-30.

2-3-5-7) accelerating spike rates

2-3-5-8) 他の研究者の分類

Zaitsev AV, Gonzalez-Burgos G, Povysheva NV, Kröner S, Lewis DA, Krimer LS, Lewis DA (2009) Interneuron diversity in layers 2-3 of monkey prefrontal cortex. *Cereb Cortex* 19: 1597-615.

monkey dorsolateral prefrontal L2/3

Martinotti cell; dense axonal cluster in L1; CB+ 3/4, SS+ 4/5; **continuous adapting**, vertically oriented cell with baskets (VOBC) ~ descending basket cell (Karube et al 2004);

CR+ 5/8; continuous adapting

double bouquet cell; CR+ 10/12; **continuous adapting**

chandelier cell; fast-spiking; PV+ 3/4; fast-spiking

local arbor pericellular basket cell (LPBC) ~ clutch cell (Kisvardy et al 1985)

~ small basket cell (Kawaguchi & Kubota 1996); CR+ 2/3; **continuous adapting**

neurogliaform cell; CB+ 8/11, NPY+ 4/10; strong initial adaptation (not LS)

curved arbor cell (s/o hetero); **continuous adapting**

linear arbor cell (LAC) ~ large basket cell (Markram et al 2004);

no well-defined pericellular baskets; PV+ 14/24; fast-spiking