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# Distribution of calbindin, parvalbumin and calretinin in the lateral geniculate nucleus and superior colliculus in *Cebus apella* monkeys

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**Abstract**

We studied the distribution of the calcium-binding proteins calbindin, parvalbumin and calretinin, in the superior colliculus and in the lateral geniculate nucleus of *Cebus apella*, a diurnal New World monkey. In the superior colliculus, these calcium-binding proteins show different distribution patterns throughout the layers. After reaction for calretinin one observes a heavy staining of the neuropil with few labeled cells in superficial layers, a greater number of large and medium-sized cells in the stratum griseum intermediale, and small neurons in deep layers. The reaction for calbindin revealed a strong staining of neuropil with a large number of small and well stained cells, mainly in the upper half of the stratum griseum superficiale. Intermediate layers were more weakly stained and depicted few neurons. There were few immunopositive cells and little neuropil staining in deep layers. The reaction for parvalbumin showed small and medium-sized neurons in the superficial layers, a predominance of large stellate cells in the stratum griseum intermediale, and medium-sized cells in the deep layers. In the lateral geniculate nucleus of *Cebus*, parvalbumin is found in the cells of both the P and M pathways, whereas calbindin is mainly found in the interlaminar and S layers, which are part of the third visual pathway. Calretinin was only found in cells located in layer S. This pattern is similar to that observed in *Macaca*, showing that these calcium-binding proteins reveal different components of the parallel visual pathways both in New and Old World monkeys. 

*Keywords:* Calcium-binding proteins; Visual system; Visual subcortical nuclei; Primates

## 1. Introduction

The use of immunohistochemical methods in the study of subcortical structures gives additional data allowing interspecies comparison of functional properties in structurally homologous regions. Calbindin (Cb), parvalbumin (Pv) and calretinin (Cr) are calcium-binding proteins (CaBPs) which have been found in various regions of the central nervous system. They are selectively distributed in many subcortical nuclei as well as in various cortical areas, where they seem to be related with distinct neural pathways and functions (Jones and Hendry, 1989; Celio, 1990; Hof and Nimchinsky, 1992).

In the lateral geniculate nucleus (LGN) of primates, Pv is found in relay cells of both the P and M pathways, whereas Cb is found mainly in the S layers and in the interlaminar zones, which belong to the third visual pathway (Jones and Hendry, 1989; Tigges and Tigges, 1991; Mize et al., 1992; Casagrande, 1994; Johnson and Casagrande, 1995; Goodchild and Martin, 1998). Calretinin-immunoreactive (Cr-IR) cells are concentrated in the S layers (Yan et al., 1996).

Complementary tiers of calbindin-immunoreactive (Cb-IR) and parvalbumin-immunoreactive (Pv-IR) cells have also been observed in the superior colliculus (SC) of the rat (Cork et al., 1998) and cat (Mize et al., 1991, 1992). This complementary pattern, however, has not

*Abbreviations:* CaBPs, calcium-binding proteins; Cb, calbindin; Cr, calretinin; ILZ, interlaminar zone; IR, immunoreactive; LGN, lateral geniculate nucleus; M, magnocellular laminae; P, parvocellular laminae; PAG, periaquedutal gray; PBS, phosphate-buffered saline; $PI_L$, pulvinar inferior lateral; $PI_M$, pulvinar inferior medial; Pv, parvalbumin; S, superficial laminae; SC, superior colliculus; SGI, stratum griseum intermediale; SGP, stratum griseum profundum; SGS, stratum griseum superficiale; SO, stratum opticum; SZ, stratum zonale.

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been observed in human, where Pv and Cb-IR neurons were found widely scattered throughout the SC (Leuba and Saini, 1996, 1997). In rhesus monkeys Mize and Luo (1992) have found Cb-IR cells in three tiers of the SC. However, until now, there is no detailed description of the distribution pattern of parvalbumin and calretinin in the SC of monkeys.

The present study aims to report on the distribution of three CaBPs, calbindin, parvalbumin and calretinin, in the superior colliculus and lateral geniculate nucleus, in a single primate species, *Cebus apella*. This cappucin monkey is a medium-sized New World monkey comparable in many aspects to the smallest Old World monkey, *Macaca fascicularis*, popularly known as the Java monkey. Based on brain size, sulcal pattern and diurnal habits the New World monkey *Cebus* is more comparable to the Old World monkey *Macaca* than to the well studied New World monkey *Aotus trivirgatus* (owl monkey). *Aotus* has nocturnal habits and a smaller and less convoluted brain than *Macaca* and *Cebus* (Allman and Kaas, 1971; Gattass and Gross, 1981; Gattass et al., 1981, 1987, 1988 Rosa et al., 1988; Fiorani et al., 1989). Thus, based on similarities between *Cebus* and *Macaca* this study, on the distribution of three CaBPs in the superior colliculus and lateral geniculate nucleus of *Cebus*, will allow a direct comparison of the organization of these subcortical structures in New and Old World monkeys.

## 2. Materials and methods

Eight adult *Cebus apella* monkeys of both sexes were used in this study. All experimental protocols were conducted following the NIH guidelines for animal research and were approved by the committee for animal care and use of the Instituto de Biofísica Carlos Chagas Filho, UFRJ. The animals were deeply anesthetized with sodium pentobarbitone (30 mg/kg) and perfused intracardially with normal saline followed by 2% paraformaldehyde in phosphate-buffered saline (PBS); 2% paraformaldehyde in PBS + 2.5% glycerol; PBS + 5% glycerol; and PBS + 10% glycerol. Serial 40 μm thick coronal sections were obtained using a cryostat. Adjacent series were stained for cell bodies with cresyl violet and for immunocytochemistry for calbindin, parvalbumin and calretinin.

For immunocytochemical reactions, free-floating sections were incubated overnight with anti-calbindin D-28k (1:2500), mouse monoclonal 300 IgG1, or anti-parvalbumin 235 (1:3000), mouse monoclonal IgG1, or anti-calretinin (1:2000) rabbit polyclonal 7696 (Swant-Swiss Antibodies, Bellinzona) in a solution containing 0.05% of bovine albumin and 0.3% Triton X-100 in 0.001 M phosphate buffer saline (PBS), pH 7.4. The sections were rinsed three times in PBS and then incubated for an additional hour in biotinylated anti-mouse (for Cb and Pv) or anti-rabbit (for Cr) secondary antibody (1:200) in PBS with 5% normal horse or goat serum at room temperature. They were rinsed again in PBS and then processed by the avidin–biotin method with ABC kits (Vector Laboratories) for 1 h and 0.05% 3,3′-diaminobenzidine (DAB; Sigma) in PBS with 0.001% $H_2O_2$ for 5 min. The sections were rinsed in PBS and mounted onto gelatinized glass slides, dehydrated through graded alcohols, air dried, and coverslipped with DPX. No labeling was observed in control sections where primary antibodies were omitted.

The distribution of immunoreactive neurons was examined under brightfield microscopy and photographed with a digital camera. Laminar borders in the superior colliculus and in the lateral geniculate nucleus were determined by comparing immunostained sections with adjacent sections stained with cresyl violet.

## 3. Results

### 3.1. Superior colliculus

The immunocytochemistry reactions for calretinin, calbindin and parvalbumin in the SC of the *Cebus* monkey showed that these three CaBPs differ in their distribution pattern throughout the layers of this nucleus (Figs. 1 and 2). They are not however segregated in complementary tiers. Fig. 1-A shows a coronal section through the SC of *Cebus* stained by the Nissl method where the approximate limits of the layers are indicated. After reaction for calretinin (Fig. 1B) we observed a heavily stained neuropil and a small number of Cr-IR cells in the superficial layers, especially at the border between the SZ and SGS. These neurons were small in size (10–20 μm) and with variable forms (Fig. 3A and B). We found mainly horizontal, pyriform and multipolar neurons in this region. In the SGI we found numerous large (30–40 μm) and medium-sized (20–30 μm) stellate cells (Fig. 4A, left). In the deep layers, we observed small Cr-IR neurons scattered among the fibers that cross these layers (Fig. 4A, right).

The reaction for calbindin (Fig. 1C) revealed a strong staining of the neuropil in superficial layers, with a large number of small, well-stained cells, mainly in the upper half of the SGS. These neurons were mainly stellate, bipolar and pyriform in shape (Fig. 3C and D). The intermediate layers were weakly stained and showed few, sparsely distributed small Cb-IR neurons (Fig. 4B, left). There was a small concentration of Cb-IR cells and neuropil intermingled with the fibers in the deep layers. These neurons varied in size and were mainly vertical bipolar and stellate-like cells (Fig. 4B, right).

The reaction for parvalbumin revealed the presence of Pv-IR cells of various sizes and shapes, distributed throughout the nucleus (Fig. 1D). In the superficial layers we observed mainly small and medium-sized round or stellate neurons (Fig. 3E and F), while in the SGI there was a predominance of large multipolar cells (Fig. 4C, left). Medium-sized cells were also observed in deep layers, mainly in the proximity of the periaqueductal gray (Fig. 4C, right). A strong staining of the neuropil was observed both in the upper SGS and in SGI.

### 3.2. Lateral geniculate nucleus

In the LGN, the reactions for CaBPs showed a laminar distribution similar to that observed in *Macaca* (Jones and Hendry, 1989). After reaction for calretinin we observed immunopositive neuropil and a few weakly stained Cr-IR cells which were restricted to layer S, with a small invasion into the first magnocellular layer (Fig. 5A). These Cr-IR neurons were mainly medium-sized bipolar and multipolar cells (Fig. 5B).

Calbindin was mainly found in cells and in the neuropil within the interlaminar zones and S layers (Fig. 6A and B and Fig. 7A). In the former, it was more conspicuous in the lamina between the magno- and parvocelular layers, which was most evident at posterior levels (Fig. 6A). In the intercalated layers Cb-IR cells were bipolar in shape with conspicuous long dendrites which extend within the layer (Fig. 8A). Most Cb positive neurons in S layer were multipolar in shape and were found embedded in a net of richly labeled fibers (Fig. 8B). In the magno- and parvocellular layers we observed few pale Cb-IR cells, scattered throughout the layers.

In contrast to calbindin, parvalbumin positive cells and neuropil were observed both in magno- and parvocellular layers, with the magnocellular layers, however, depicting a heavier stain (Fig. 6C and D and Fig. 7B). Rare cells were observed in the interlaminar layers. Pv positive cells were mainly round in shape with rarely visible dendrites (Fig. 8C and D).

## 4. Discussion

The pattern of Calbindin labeling in the superior colliculus of *Cebus*, observed in this study, is similar to that described in *Rhesus* monkey (Mize and Luo, 1992), with a dense tier within the SGS and another band in the SGP. The intermediary tier, which is quite prominent in the cat (Mize et al., 1991), is less obvious in both *Cebus* and *Rhesus*.

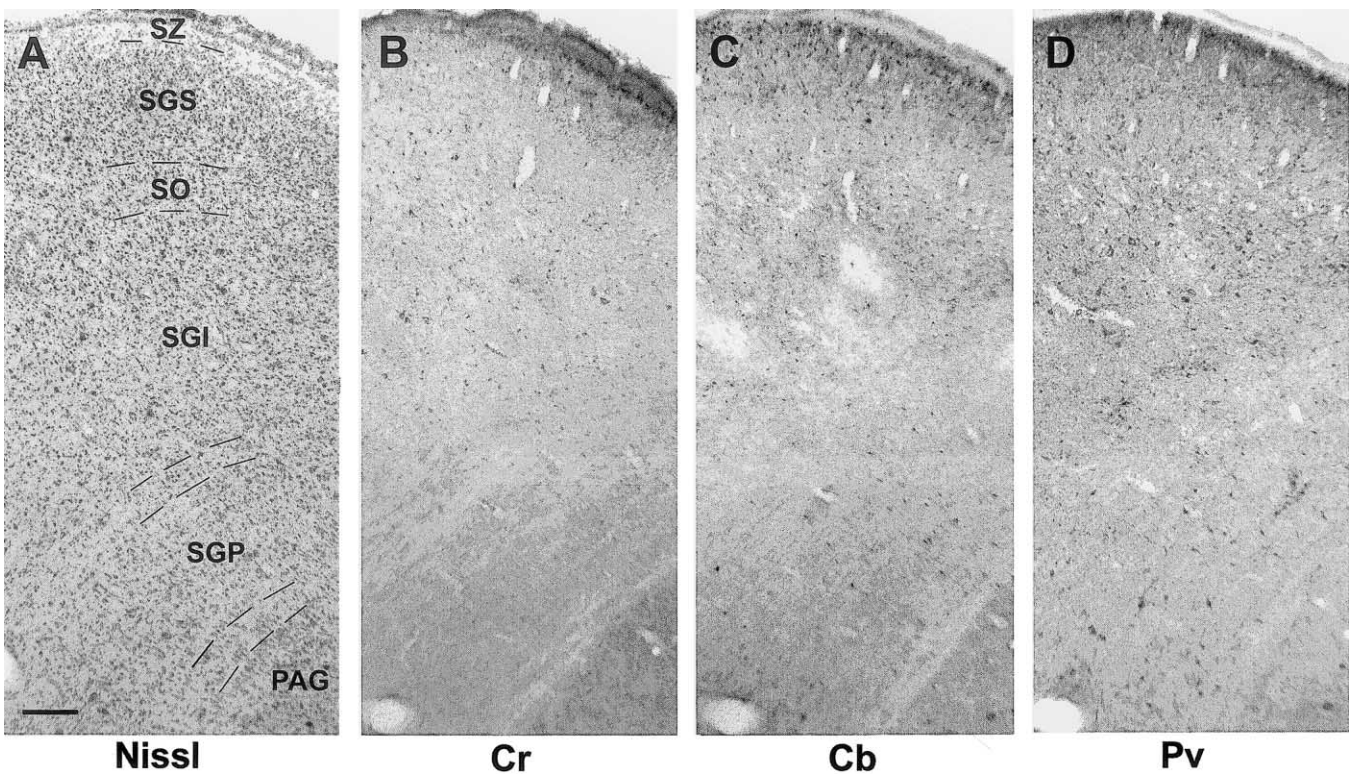


Fig. 1. Photomicrographs of coronal sections of the *Cebus* SC stained by the Nissl method (A), and for calretinin (B), calbindin (C) and parvalbumin (D). PAG, periaquedutal gray; SGI, stratum griseum intermediale; SGP, stratum griseum profundum; SGS, stratum griseum superficiale; SO, stratum opticum; SZ, stratum zonale. Scale bar = 250 μm.

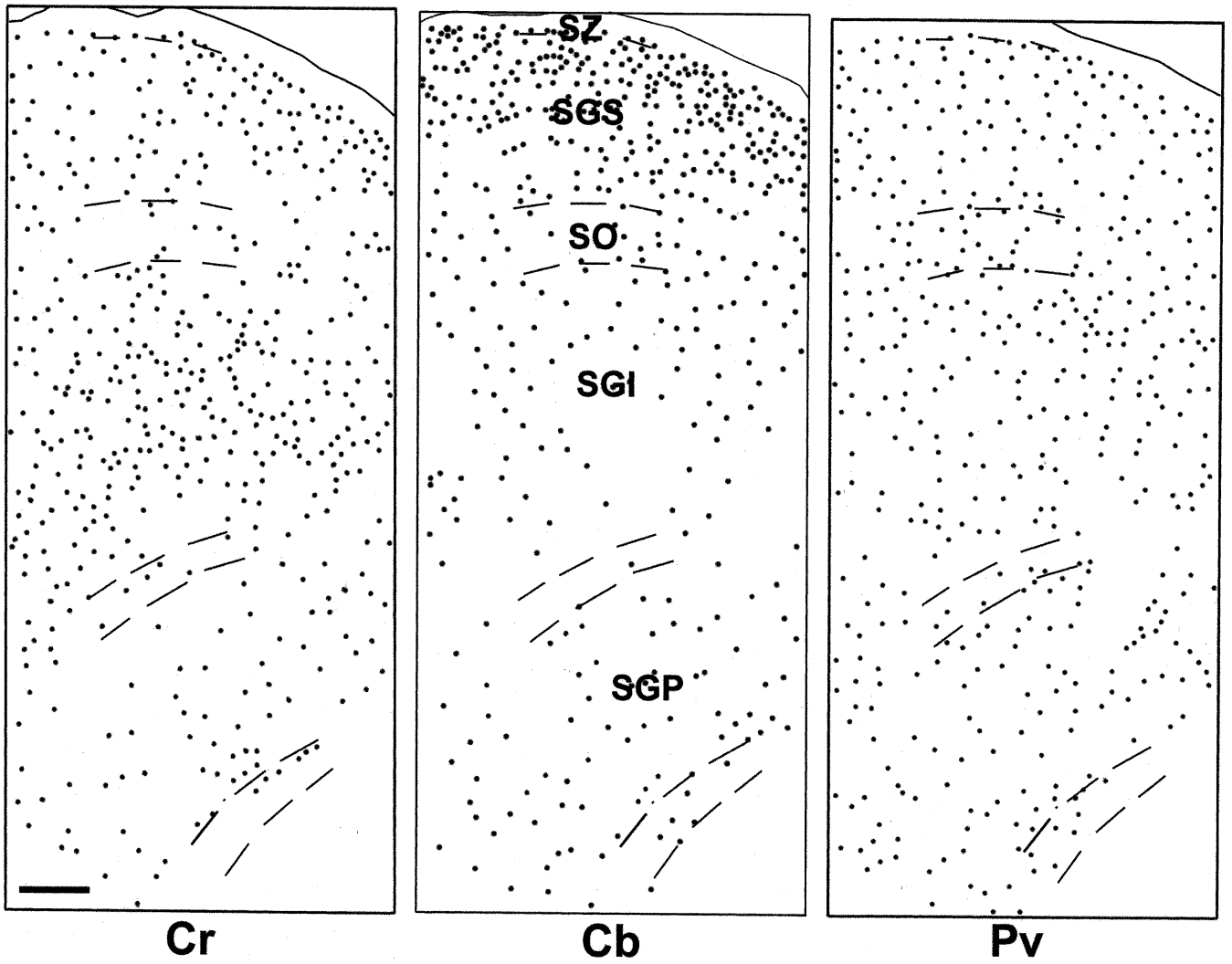


Fig. 2. Schematic drawings of coronal sections illustrated in Fig. 1 depicting the distribution pattern of cells immunoreacted for calretinin, calbindin and parvalbumin in the superior colliculus. For abbreviations see Fig. 1. Scale bar = 250 μm.

In the cat, Pv-IR neurons were found concentrated in a tier within the deep superficial gray and upper optic layers, showing a pattern that is complementary to that of calbindin (Mize et al., 1992). This complementary pattern in the superficial layers of the SC, however, is not observed in humans (Leuba and Saini, 1996) or in *Cebus* (this study). In humans, Cb-IR neurons are found widely scattered throughout the nucleus. In *Cebus*, Cb-IR neurons are mainly found in the upper SGS, while Pv-IR neurons are found scattered throughout the nucleus. In SGI the reaction for parvalbumin showed numerous large multipolar neurons which were not observed after calbindin reaction.

The calretinin immunostaining pattern in the SC of *Cebus* is similar to that found in humans (Leuba and Saini, 1996). In both species Cr-IR neurons are found scattered throughout the nucleus with a high density of Cr-IR puncta in the upper half of SGS, and many large neurons in SGI.

In the LGN of *Cebus*, Pv-IR neurons and processes were found in all six main laminae and few cells in the interlaminar and S layers, regions where calbindin immunoreactivity is dense. This complementary pattern of distribution of Pv-IR and Cb-IR neurons in the LGN of *Cebus* is similar to that described in other primates such as the bush baby, *Galago* (Diamond et al., 1993; Johnson and Casagrande, 1995), the marmoset, Callithrix, (Goodchild and Martin, 1998) and *Macaca* (Jones and Hendry, 1989; Tigges and Tigges, 1991; Yan et al., 1996; Glezer et al., 1998). In human, however, a differential distribution of these calcium-binding proteins was not found (Leuba and Saini, 1996).

Calretinin labeling was found mainly in S layer in LGN of *Cebus*. This labeling is comparable to that found in *Macaca* (Yan et al., 1996) and *Saimiri* (Fortin et al., 1996). In humans, however, Cr-IR neurons were observed in all M and P laminae with a stronger staining in the M laminae, which show a heavier stain

than that observed in other primates (Leuba and Saini, 1996; Cicchetti et al., 1998; Fortin et al., 1998).

The precise functions of the calcium-binding proteins are still unknown. The fact that different subpopulations of cells contain distinct CaBPs may reflect functional differences. In the cerebral cortex of monkeys calbindin and parvalbumin-IR neurons have been described as distinct sub-populations of GABAergic interneurons (Hendry et al., 1989). Physiological studies in frontal cortex of rats showed that Pv-IR neurons are GABAergic, fast-spiking cells that fire repetitively with almost no adaptation, whereas Cb-IR neurons are GABAergic cells that produce low-threshold spikes from hyperpolarized potentials and show spike-frequency adaptation (Kawaguchi and Kubota, 1993). In the LGN of cats, the vast majority of Pv-IR neurons also showed GABA-immunoreactivity (Stichel et al., 1988). However, in the monkey thalamus, most parvalbumin and calbindin-IR cells do not contain GABA, and both cells appear to be relay neurons (Jones and Hendry, 1989). In superior colliculus of cat most Cb-IR cells are interneurons, but only a few Cb-IR neurons contain GABA (4%) and a significant fraction of cells in the superficial tier project to the LGN (2.4%). Pv-IR neurons are mostly projection neurons and, based on laminar position, are likely to project to the lateral posterior nucleus (Mize et al., 1991, 1992).

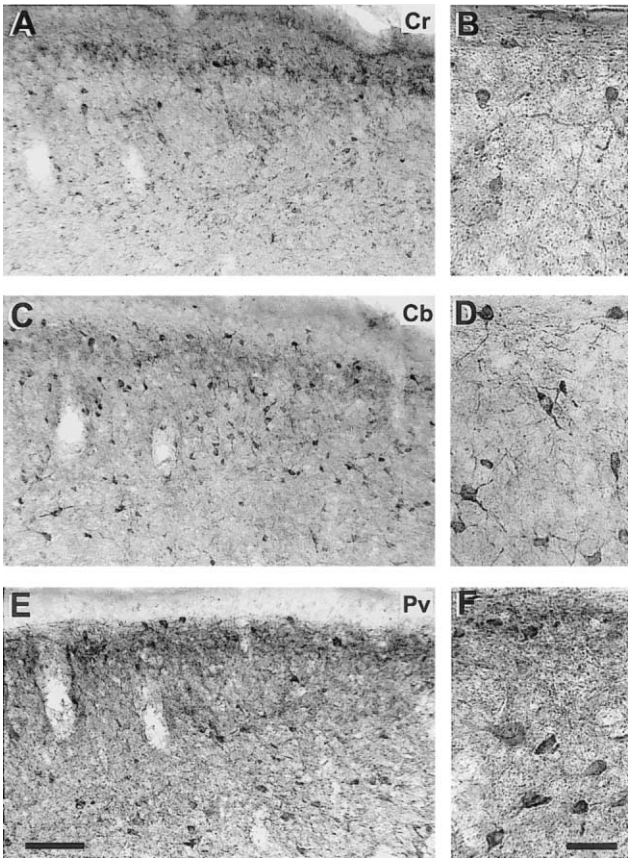


Fig. 3. Photomicrographs of SZ and upper SGS of the superior colliculus stained for calretinin (A, B), calbindin (C, D) and parvalbumin (E, F) illustrating the distribution and morphology of labeled cells. Scale bar in A, C and E = 100 μm; B, D and F = 50 μm.

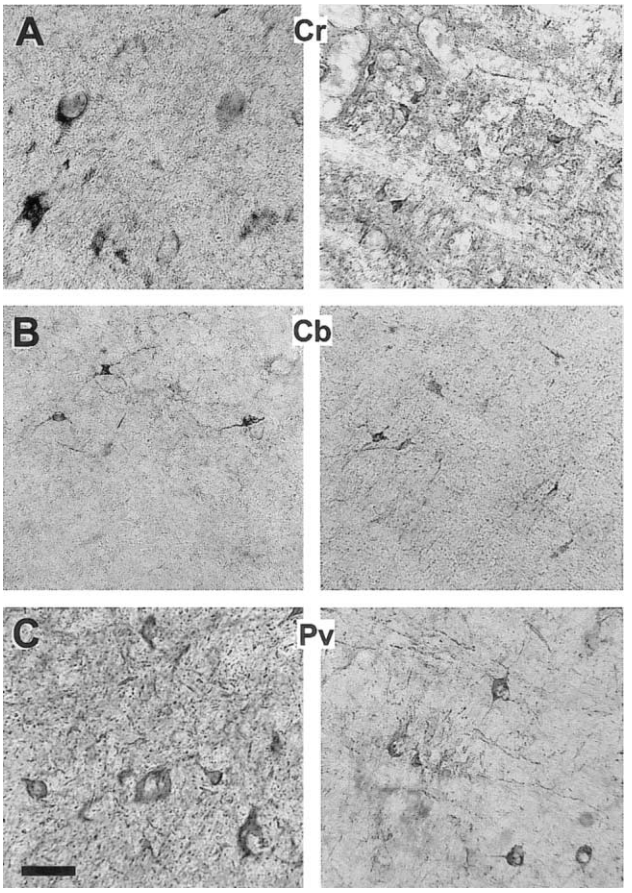


Fig. 4. Photomicrographs of intermediate (left) and deep (right) layers of the superior colliculus stained for calretinin (A), calbindin (B) and parvalbumin (C) showing cell types. Large multipolar cells in the SGI are labeled only by calretinin and parvalbumin. Scale bar = 50 μm.

In primates the visual information is segregated in parallel pathways that originate from different populations of cells in the retina (Ungerleider and Mishkin, 1982; Livingstone and Hubel, 1988; Gattass et al., 1990). The parvocellular and magnocellular pathways are parallel pathways which process color and form and motion, respectively. They originate in P and M retinal ganglion cells and project to layer IV of area V1 via P and M cells of the LGN, which are both parvalbumin positive neurons. A third parallel pathway, which projects to superficial layers I and III of striate cortex, originates in the interlaminar and S layers of the LGN which are, in turn, rich in calbindin. These koniocellular layers receive projections from a population of retinal ganglion cells with small somata and fine caliber axons (Itoh et al., 1982) and also from small fibers originating in the superficial layers of the superior colliculus.

Bishop (1959) suggested that, in all mammals, the small-fiber sensory tracts are phylogenetically older

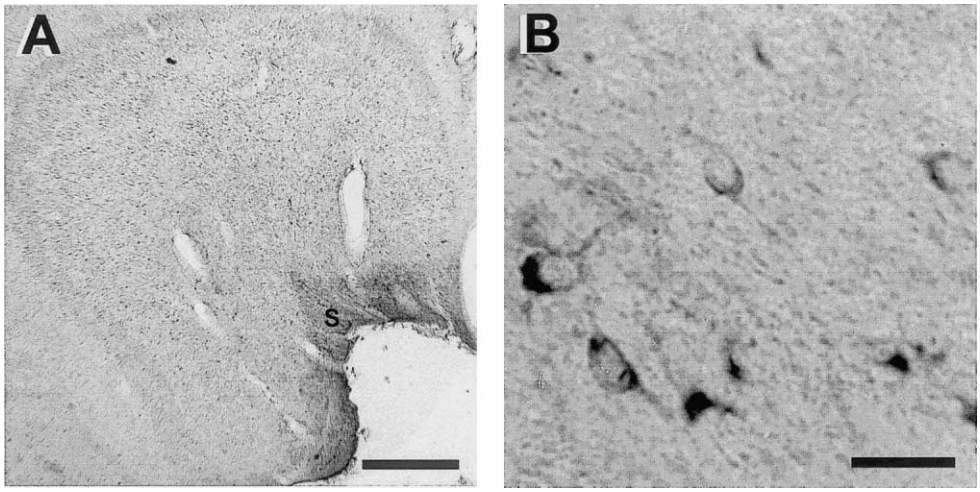


Fig. 5. (A) Photomicrograph of a coronal section through the lateral geniculate nucleus stained for calretinin showing labeled cells and neuropil mainly in the S layer. (B) Higher magnification of the S layer showing weakly stained Cr-IR cells. Scale bars: A = 1 mm; B = 30 μm.

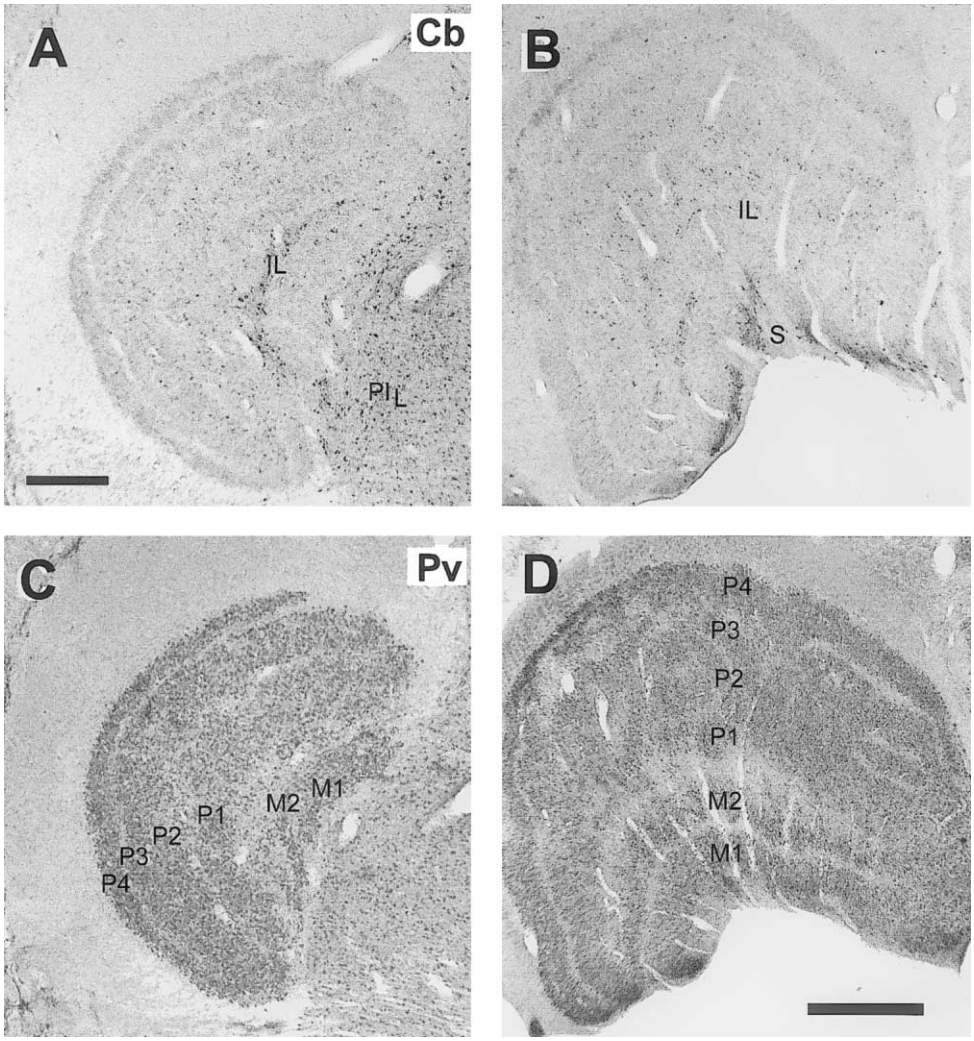


Fig. 6. Photomicrographs of coronal sections of two levels, caudal (A, C) and rostral (B, D), of the lateral geniculate nucleus stained for calbindin (A, B) and parvalbumin (C, D). Calbindin is found mainly in the interlaminar (IL) and superficial (S) layers, whereas parvalbumin labeled cells in both parvocellular (P) and magnocellular (M) layers. $PI_L$, pulvinar inferior lateral. Scale bar in A, C = 500 μm; B, D = 1 mm.

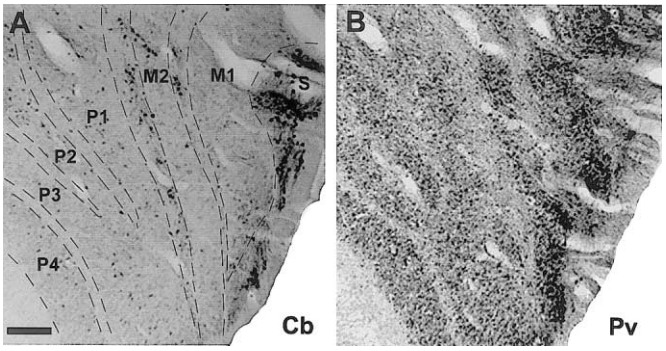


Fig. 7. Photomicrographs at rostral levels of lateral geniculate nucleus showing at a high magnification the layers with Cb-IR cells (A) and Pv-IR cells (B). Scale bar = 200 μm.

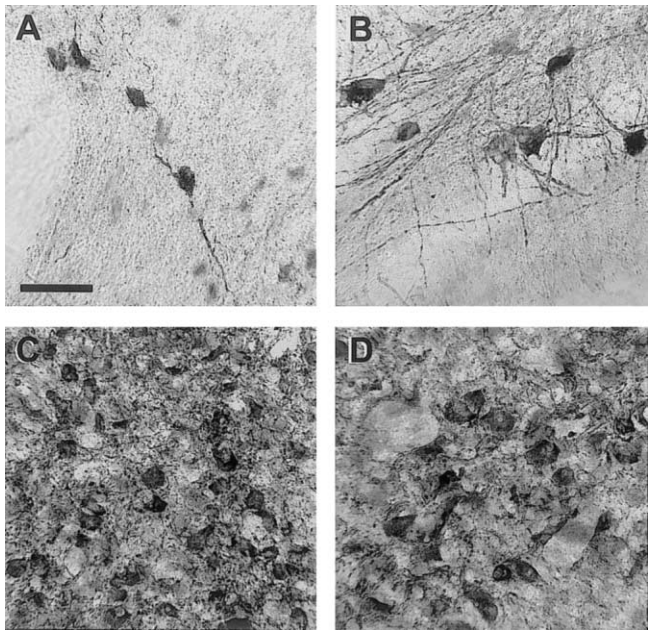


Fig. 8. High power photomicrographs of the lateral geniculate nucleus showing cells labeled for calbindin in the interlaminar (A) and S layers (B) and for parvalbumin in the parvocellular (C) and magnocellular layers (D). Scale bar = 30 μm.

while the large-fiber sensory pathways project to the cortex through the newer areas of the thalamus. Diamond et al. (1993) contributed to Bishop's principle by showing that the small cells in the LGN in the prosimian galago and in the tree shrew (*Tupaia belangeri*), which receive projections from small fibers originating in the SC and relay information to the superficial layers of striate cortex via a small-fiber path, are calbindin positive. In *Cebus*, the reaction for Cb labeled mainly the interlaminar zone located between the magno- and parvocellular inner layers, similarly to what has been observed in another New World monkey, *Callithrix jacchus* (Goodchild and Martin, 1998). This labeling is also similar to that observed in koniocellular layers 4 and 5 of the prosimian *Galago* which are also rich in Cb (Diamond et al., 1993).

In the SC of the cat Cb-IR cells in the upper SGS receive projections from small retinal fibers that probably originate from W cells, while Pv-IR neurons in the deep SGS and upper SO receive retinal and cortical terminals which are probably related to the Y pathway (Mize, 1999). In *Cebus* monkey, however, we did not observe this segregation of Cb and Pv-IR cells in different tiers of SGS. This lack of segregation can be due to the fact that, in monkeys, collicular projections from primary visual cortex, that are from cells apparently dominated by Y-like retinal ganglion cells influences, overlap with the retinal terminations in the SGS (for review, Kaas and Huerta, 1988). In the pulvinar nucleus of monkeys, a chemoarchitectonic subdivision of the inferior pulvinar, $PI_M$, that project to the temporal medial area MT, related to motion perception, is also rich in parvalbumin and poor in calbindin (Cusick et al., 1993; Soares et al., 2001), reinforcing the relationship of the motion pathway with parvalbumin.

In the LGN of marmoset Martin et al. (1997) found that cells that respond to stimuli specific for short wavelength sensitive cones (SWS, blue) were located predominantly in the interlaminar zones. Furthermore, it has been shown that these small relay cells project to the cytochrome oxidase rich blobs in layer III of area V1, regions that process color information (Lachica and Casagrande, 1992). These findings could implicate in a relationship between color function and Cb-IR neurons in the koniocellular pathway. However, nocturnal primates, such as owl monkeys and the prosimian *Galago*, which show a strong reaction for calbindin in the koniocellular layers, have little or no chromatic vision. In *Galago*, cells in these layers exhibit average acuity and contrast sensitivity values that fall within the average values of P and M cells, and could contribute to spatial vision function (Norton et al., 1988).

The immunohistochemical subdivisions of the SC and LGN provide additional data for the comparison of functional data in the visual system in different animals. In addition, immunohistochemical markers may be useful tools in the correlation of specific anatomical compartments of these subcortical structures with the different pathways of visual information processing.

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## References


Allman, J.M., Kaas, J.H., 1971. Representation of the visual field in striate and adjoining cortex of the owl monkey (*Aotus trivirgatus*). Brain Res. 35, 89–106.

Bishop, G.H., 1959. The relation between nerve fiber size and sensory modality: phylogenetic implications of the afferent innervation of cortex. J. Nerv. Ment. Dis. 128, 89–114.

Casagrande, V.A., 1994. A third parallel visual pathway to primate area V1. TINS 17, 305–310.

Celio, M.R., 1990. Calbindin D-28k and parvalbumin in the rat nervous system. Neuroscience 35, 375–475.

Cicchetti, F., Lacroix, S., Beach, T.G., Parent, A., 1998. Calretinin gene expression in the human thalamus. Mol. Brain Res. 54, 1–12.

Cork, R.J., Baber, S.Z., Mize, R.R., 1998. Calbindin D28k- and parvalbumin-immunoreactive neurons form complementary sublaminae in the rat superior colliculus. J. Comp. Neurol. 394, 205–217.

Cusick, C.G., Scripter, J.L., Darensbourg, J.G., Weber, J.T., 1993. Chemoarchitectonic subdivisions of the visual pulvinar in monkeys and their connectional relations with the middle temporal and rostral dorsolateral visual areas, MT and DLr. J. Comp. Neurol. 336, 1–30.

Diamond, I.T., Fitzpatrick, D., Schmechel, D., 1993. Calcium binding proteins distinguish large and small cells of the ventral posterior and lateral geniculate nuclei of the prosimian galago and the tree shrew (*Tupaia belangeri*). Proc. Natl. Acad. Sci. USA 90, 1425–1429.

Fiorani, J.R.M., Gattass, R., Rosa, M.G.P., Sousa, A.P.B., 1989. Visual area MT in the *Cebus* monkey: location, visuotopic organization, and variability. J. Comp. Neurol. 287, 98–118.

Fortin, M., Asselin, M.C., Parent, A., 1996. Calretinin immunoreactivity in the thalamus of the squirrel monkey. J. Chem. Neuroanat. 10, 101–117.

Fortin, M., Asselin, M.C., Parent, A., 1998. Calretinin-immunoreactive neurons in the human thalamus. Neuroscience 84, 537–548.

Gattass, R., Gross, C.G., 1981. Visual topography of the striate projection zone in the posterior superior temporal sulcus (MT) of the macaque. J. Neurophysiol. 46, 621–638.

Gattass, R., Gross, C.G., Sandell, J.H., 1981. Visual topography of V2 in the macaque. J. Comp. Neurol. 201, 519–539.

Gattass, R., Sousa, A.P.B., Rosa, M.G.P., 1987. Visual topography of V1 in the *Cebus* monkey. J. Comp. Neurol. 259, 529–548.

Gattass, R., Sousa, A.P.B., Gross, C.G., 1988. Visuotopic organization and extent of V3 and V4 of the macaque. J. Neurosci. 8, 1831–1845.

Gattass, R., Rosa, M.G.P., Sousa, A.P.B., Pinon, M.C.G., Fiorani, M. Jr, Neuenschwander, S., 1990. Cortical streams of visual information processing in primates. Braz. J. Med. Biol. Res. 23, 375–393.

Glezer, I.I., Patrick, R.H., Morgane, P.J., 1998. Comparative analysis of calcium-binding protein-immunoreactive neuronal populations in the auditory and visual system of the bottlenose dolphin (*Tursiops truncatus*) and the macaque monkey (*Macaca fascicularis*). J. Chem. Neuroanat. 15, 203–237.

Goodchild, A.K., Martin, P.R., 1998. The distribution of calcium-binding proteins in the lateral geniculate nucleus and visual cortex of a New World monkey, the marmoset, *Callithrix jacchus*. Visual Neurosci. 15, 625–642.

Hendry, S.H., Jones, E.G., Emson, P.C., Lawson, D.E., Heizmann, C.W., Streit, P., 1989. Two classes of cortical GABA neurons defined by differential calcium binding protein immunoreactivities. Exp. Brain Res. 76, 467–472.

Hof, P.R., Nimchinsky, E.A., 1992. Regional distribution of neurofilament and calcium-binding proteins in the cingulate cortex of the macaque monkey. Cereb. Cortex 2, 456–467.

Itoh, K., Conley, M., Diamond, I.T., 1982. Retinal ganglion cell projections to individual layers of the lateral geniculate body in *Galago crassicaudatus*. J. Comp. Neurol. 205, 282–290.

Johnson, J.K., Casagrande, V.A., 1995. Distribution of calcium-binding proteins within the parallel visual pathways of a primate (*Galago crassicaudatus*). J.Comp. Neurol. 356, 238–260.

Jones, E.G., Hendry, S.H.C., 1989. Differential calcium binding protein immunoreactivity distinguishes classes of relay neurons in monkey thalamic nuclei. Eur. J. Neurosci. 1, 222–246.

Kaas, J.H., Huerta, M.F., 1988. The subcortical visual system of primates. Comp. Prim. Biol. 4, 327–391.

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, 387–396.

Lachica, E.A., Casagrande, V.A., 1992. Direct W-like geniculate projections to the cytochrome oxidase (CO) blobs in primate visual cortex: axon morphology. J. Comp. Neurol. 319, 141–158.

Leuba, G., Saini, K., 1996. Calcium-binding proteins immunoreactivity in the human subcortical and cortical visual structures. Vis. Neurosci. 13, 997–1009.

Leuba, G., Saini, K., 1997. Colocalization of parvalbumin, calretinin and calbindin D-28k in human cortical and subcortical visual structures. J. Chem. Neuroanat. 13, 41–52.

Livingstone, M., Hubel, D., 1988. Segregation of form, color, movement, and depth: anatomy, physiology, and perception. Science 240, 740–749.

Martin, P.R., White, A.J.R., Goodchild, A.K., Wilder, H.D., Sefton, A.E., 1997. Evidence that blue-on cells are part of the third geniculo-cortical pathway in primates. Eur. J. Neurosci. 9, 1536–1541.

Mize, R.R., 1999. Calbindin 28kD and parvalbumin immunoreactive neurons receive different patterns of synaptic input in the cat superior colliculus. Brain Res. 843, 25–35.

Mize, R.R., Luo, Q., 1992. Visual deprivation fails to reduce calbindin 28kD or GABA immunoreactivity in the Rhesus monkey superior colliculus. Vis. Neurosci. 9, 157–168.

Mize, R.R., Jeon, C.J., Butler, G.D., Luo, Q., Emson, P.C., 1991. The calcium binding protein calbindin-D28k reveals subpopulations of projection and interneurons in the cat superior colliculus. J.Comp. Neurol. 307, 417–436.

Mize, R.R., Luo, Q., Butler, G., Jeon, C.J., Nabors, B., 1992. The calcium binding proteins parvalbumin and calbindin-D28k form complementary patters in the cat superior colliculus. J.Comp. Neurol. 320, 243–256.

Norton, T.T., Casagrande, V.A., Irvin, G.E., Sesma, M.A., Petry, H.M., 1988. Contrast sensitivity function of W-, X- and Y-like relay cells in lateral geniculate nucleus of bush baby (*Galago crassicaudatus*). J. Neurophysiol. 59, 1639–1656.

Rosa, M.G.P., Sousa, A.P.B.and, Gattass, R., 1988. Representation of the visual field in the second visual area in the *Cebus* monkey. J. Comp. Neurol. 275, 326–345.

Soares, J.G.M., Gattass, R., Souza, A.P.B., Rosa, M.G.P., Fiorani, M. Jr, Brandão, B.L., 2001. Connectional and neurochemical subdivisions of the pulvinar in *Cebus* monkeys. Visual Neurosci. 18, 1–17.

Stichel, C.C, Singer, W., Heizmann, C.W., 1988. Light and electron microscopic immunocytochemical localization of parvalbumin in the dorsal lateral geniculate nucleus of the cat: evidence for coexistence with GABA. J.Comp. Neurol. 268, 29–37.

Tigges, M., Tigges, J., 1991. Parvalbumin immunoreactivity of the lateral geniculate nucleus in adult rhesus monkeys after monocular eye enucleation. Visual Neurosci. 6, 375–382.

Ungerleider, L.G., Mishkin, M., 1982. Two cortical visual systems. In: Ingle, D.J., Goodale, M.A., Mansfield, R.J. (Eds.), Analysis of Visual Behavior. MIT Press, Cambridge, MA, pp. 549–586.

Yan, Y.H., Winarto, A., Mansjoer, I., Hendrickson, A., 1996. Parvalbumin, calbindin, and calretinin mark distinct pathways during development of monkey dorsal lateral geniculate nucleus. J. Neurobiol. 31, 189–209.