Principles of Organization of the Dorsal Lateral Geniculate Nucleus

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The classic paper discussed in this essay:

Kaas JH, Guillery RW, Allman JM (1972): Some principles of organization in the dorsal lateral geniculate nucleus. *Brain Behav Evol* 6:253–299.

Our paper on the lateral geniculate nucleus (LGN) was a result of one of us (Kaas) being invited to give a talk on the LGN in the Symposium on Basic Thalamic Structure and Function at the Downstate Medical Center in Brooklyn in 1971. I was an unexpected contributor to this symposium of experts on the thalamus as I was a new assistant professor who had published nothing on the LGN. However, my former PhD advisor, I.T. Diamond, had been invited, and he insisted to the organizers that I was working on the LGN (somewhat true) and was an expert (a gross exaggeration). After several attempts by Diamond, the organizers relented under his pressure, and I was invited. All talks were scheduled to be papers in a special issue of the newly formed journal, *Brain, Behavior and Evolution*, under the editorship of Walter Riss. After listening to the other talks, I felt that some were too focused on the author's recent results and not enough on basic issues of thalamic organization and function. On the plane back from the symposium, I rethought the purpose of the planned review and concluded that it should cover what new investigators to the field, as I was, should know. The basic issues at that time included understanding the variable lamination patterns of the LGN across species, the overall retinotopy of the nucleus, and

the nature of the lines of isorepresentation across LGN layers.

At the time of our paper, I had transitioned from a postdoctoral fellow to a new Assistant Professor in the Laboratory of Neurophysiology, headed by Clinton Woolsey, at the University of Wisconsin. The laboratory was a great place to be, with Woolsey and Jerzy Rose, both members of the National Academy of Sciences, and other outstanding faculty, including Wally Welker, who influenced me greatly. Other postdoctoral fellows included Mike Merzenich and Mary Carlson; both became collaborators with me on a number of subsequent papers. The Anatomy Department was just down the hall with Ray Guillery, Maxwell Cowan, and Pete Ralston as faculty, Ken Sanderson as a postdoc, and Margaret Wong Riley as one of the graduate students. Semir Zeki was also there for about 1 year as visiting faculty. In addition, John Allman had joined with me in my small laboratory space, to complete studies on the visual cortex of owl monkeys for his PhD in anthropology from the University of Chicago in 1970. John and I continued these studies in the Laboratory of Neurophysiology until I left for Vanderbilt at the end of 1972.

The timing of the invited review on the LGN was fortuitous because I had just finished a study of geniculocortical relations

in squirrels with Bill Hall and Irving Diamond at Duke University [Kaas et al., 1972], and was working with Ray Guillery and John Allman on separate lines of research that involved the LGN. John Allman and I were collaborating on studies of visual cortex organization in owl monkeys [Allman and Kaas, 1971] which we extended to include microelectrode mapping of the LGN in owl monkeys and macaques. At the same time, I was collaborating with Ray Guillery, a real expert on the LGN [Guillery, 1971], on his studies of the abnormal visual system of Siamese cats [Guillery, 1969]. These studies included obtaining microelectrode maps of the retinotopic organization of the LGN in normal and Siamese cats that were already known to have abnormal retinogeniculate projections [Guillery and Kaas, 1971]. In normal cats, we noticed that a clear discontinuity in layer A of the LGN corresponded to a discontinuity in the input from the nasal hemiretina of the contralateral eye that resulted from the position of the optic disk of the retina, a clear marker of a retinotopic location some 7.5° from the zero vertical meridian in the contralateral visual hemifield. Going to the extensive Wisconsin Brain Collection, we soon found that this marker identified a specific retinotopic position in LGN layers innervated by the contralateral

eye in a wide range of mammalian species [Kaas et al., 1973]. Thus, Ray, John, and I collaborated on the review and were able to document our main points with illustrations from our ongoing and completed research, including some unpublished results and new material from the brain collection.

In brief, our review compared features of LGN organization in cats, squirrels, and owl monkeys. Geniculate layers were defined by Nissl stain architecture, and contralateral and ipsilateral patterns of retinal inputs that were revealed by degenerated fibers stained with the Nauta or Fink-Heimer methods (remember those?) or by transneuronal cell shrinkage (degeneration) after the loss of projections from one eye. Lines of isorepresentation across the LGN layers were clearly revealed by columns of retrograde neuronal loss and degeneration after small lesions in the primary visual cortex. Overall patterns of retinotopy as well as laminar patterns of ocular activation were revealed by the microelectrode mapping methods that were coming into common use. Our comparative approach allowed us to conclude that the 'lines of projection' (isorepresentation) are 'roughly perpendicular to the geniculate

layers for all therian mammals'. We also proposed that the basic laminar pattern of the LGN for anthropoid primates included two M layers of magnocellular neurons (one for the ipsilateral eye and one for the contralateral eye) and two P layers of smaller parvocellular neurons (again, one for the ipsilateral eye and one for each eye) together with small 'intercolated' layers of very small neurons. We recognized that in some primates, portions of the two parvocellular layers representing more central vision split and interdigitate to give the appearance of six geniculate layers (or more), but we felt it was functionally important to distinguish these partial layers, we called leaflets, from full geniculate layers. This conception of the laminar pattern of the LGN was more fully developed in a subsequent study of laminar patterns of retinal inputs across a range of primate species, where a framework of large-celled M layers, smaller-celled P layers and small-celled K (konio-cellular) layers, and interlaminar zones was extended across primate taxa [Kaas et al., 1978]. This conceptual framework and terminology has been widely retained. A more recent description of LGN lamination more extensively covers the leaflet pat-

terns in Old World monkeys, apes, and humans [de Sousa et al., 2013].

Subsequent to our 1972 review, there have been a number of interesting and somewhat unexpected discoveries. These included the finding that the A and A1 layers of the LGN of some carnivores had doubled to form dorsal and ventral pairs for segregated populations of neurons with either 'on center' or 'off center' neurons [Sanderson, 1974], which were later also found in tree shrews [Conway and Schiller, 1983]. Also, we now know that the K layers of the LGN in primates relay color information from the blue-sensitive retinal ganglion cells to the visual cortex [Roy et al., 2009], and that K geniculate neurons project to the extrastriate cortex, including the MT (middle temporal visual area) [Stepniewska et al., 1999], as well as to supragranular layers of the primary visual cortex. Most importantly, we now know that the functional properties of P, M, and K geniculate neurons are very much like those of the X, Y, and W neurons of cats and other mammals [Sherman et al., 1976], suggesting an ancient origin for these three classes of retinal ganglion cells and geniculate neuron targets in early mammals.

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