

## PROJECTIONS OF THE PULVINAR-LATERAL POSTERIOR COMPLEX TO VISUAL CORTICAL AREAS IN THE CAT

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**Abstract**—The projections of the pulvinar-lateral posterior complex of the cat were studied using the autoradiographic tracing method and related to 15 previously defined cortical areas. The results indicate that each of three separate zones within the pulvinar-lateral posterior complex has a different pattern of projection. The most lateral zone, the pulvinar, sends fibers to at least seven cortical areas, most of which are known to have input from other visual areas within the brain: the splenial visual area, the cingulate gyrus, and areas 5, 7, 19, 20a and 21a. A zone located just medial to the pulvinar, the lateral division of the lateral posterior complex, projects to at least eight visual areas in the cortex: areas 17, 18, 19, 20a, 21a, 21b, the posteromedial lateral suprasylvian area and the ventral lateral suprasylvian area. The most medial zone, the intermediate division of the lateral posterior complex, projects to at least four cortical areas: 20a, the posterior suprasylvian area, the posterolateral lateral suprasylvian area and the dorsal lateral suprasylvian area. Of the 15 cortical areas that receive fibers from the pulvinar-lateral posterior complex, only three (areas 19, 20a and 21a) receive projections from more than one of these thalamic zones, and only one of the cortical areas (20a) receives fibers from all three zones.

Thus, the data support the division of the pulvinar lateral posterior complex into three zones on the basis of their unique and largely non-overlapping projections to the visual cortex.

ANY ATTEMPT to understand the organization of the visual cortex and its related thalamic centers must begin with some notion of how these regions are functionally subdivided. In the past few years a great deal has been learned about the functional subdivisions of the cat's visual cortex; however, our knowledge of how the extrageniculate visual thalamus is organized is less complete.

Classically, the thalamus has been divided into nuclei, or zones, on the basis of cytoarchitecture (RIOCH, 1929; NIIMI & KUWAHARA, 1973). While there are clear cytoarchitectural differences among groups of cells in the extrageniculate visual thalamus of the cat, cytoarchitecture alone provides little information about how the structural differences are related to functional differences.

Another approach used in subdividing the visual thalamus has been to determine the patterns of connections. GRAYBIEL (1972a,b) first showed that three regions of the pulvinar-lateral posterior (pulvinar-LP) complex can be delineated on the basis of their inputs from the visual cortex, the superior colliculus, or the pretectum. More recently UPDYKE (1977) has studied the pattern of inputs to these thalamic zones from areas 17, 18 and 19 of cat visual cortex and proposed a new terminology based upon his findings. The most

lateral region, the pulvinar, is equivalent to the pulvinar described by RIOCH (1929) and the region known as the lateral pulvinar by NIIMI & KUWAHARA (1973). It is known to receive fibers from cortical area 19 (KAWAMURA, SPRAGUE & NIIMI 1974; UPDYKE, 1977) as well as the pretectum (BERMAN, 1977; GRAYBIEL, 1972a; BERSON & GRAYBIEL, 1978). Recently, lateral parts of this subdivision have been shown to receive direct retinal (BERMAN & JONES, 1977; KAWAMURA, FUKUSHIMA & HATTORI, 1979) and cerebellar (ITOH & MIZUNO, 1979) inputs. Located more medially is a zone Updyke calls LPI, or the lateral part of the lateral posterior nucleus. LPI includes the posterior nucleus of RIOCH (1929) and the inferior pulvinar of NIIMI & KUWAHARA (1973), and receives input from cortical areas 17, 18 and 19 (KAWAMURA *et al.*, 1974; UPDYKE, 1977). Medial to LPI is the zone Updyke refers to as LPi, or the interjacent part of the lateral posterior nucleus. LPi includes the major portion of the lateral posterior nucleus of RIOCH (1929), much of the medial pulvinar of NIIMI & KUWAHARA (1973) and is probably equivalent to the zone BERSON & GRAYBIEL (1978) call LPM. LPi receives input from the superior colliculus (GRAYBIEL, 1972a; GRAHAM, 1977; BERSON & GRAYBIEL, 1978). The inputs to the most medial of Updyke's zones, LPM, are still unknown and are presumably not visual. After recording from the pulvinar-lateral posterior complex, MASON (1978) agreed that its retinotopy supports the subdivisions proposed by GRAYBIEL (1972a) and UPDYKE (1977).

Recently, histological methods have provided further evidence that the pulvinar-LP complex is organized into three zones. BERSON & GRAYBIEL (BER-

*Abbreviations:* ALLS, AMLS, DLS, PLLS, PMLS, VLS, anterolateral-, anteromedial-, dorsal lateral-, posterolateral-, posteromedial- lateral suprasylvian area; HRP, horseradish peroxidase; LP, lateral posterior; LPI, intermediate division of lateral posterior nucleus; LPL, lateral part of lateral posterior nucleus; LPM, medial division of lateral posterior nucleus; PS, posterior suprasylvian area; SVA, splenial visual area.

SON & GRAYBIEL, 1978; also, GRAYBIEL & BERSON, 1980) showed that the medial zone which receives input from the superior colliculus and the lateral zone (pulvinar) which has pretectal input are defined by high acetylcholinesterase activity, and that the zone in between which receives input from striate cortex has very low acetylcholinesterase activity. HUGHES (1980) used a hematoxylin stain to show that the same three zones which he defines on the basis of anatomical connections can be identified myeloarchitecturally. Thus, there are reasons to consider pulvinar, LPI and LPi as functionally distinct subdivisions of the thalamus, although there may be further subdivisions within these regions. Given tentative acceptance of these subdivisions of the thalamus, we asked how these subdivisions relate to the several representations of the visual field within the cortex.

Detailed retinotopic maps are now available for area 17 (TUSA, PALMER & ROSENQUIST, 1978), areas 18 and 19 (TUSA, ROSENQUIST & PALMER, 1979), the region within the lateral suprasylvian sulcus (PALMER, ROSENQUIST & TUSA, 1978) and the region which HEATH & JONES (1971) call areas 20 and 21 (TUSA & PALMER, 1980). Each of the thirteen separate representations of the visual field described in these papers is presumed to correspond to a functional subdivision of visual cortex.

In the light of these recent cortical mapping data, we undertook a study of the cortical distribution of the pulvinar-LP projections, and related the findings to the recently established cortical subdivisions. The results support the subdivision of the posterior thalamus into three zones, and indicate that each zone projects to a number of cortical areas.

## EXPERIMENTAL PROCEDURES

Projections from the pulvinar-lateral posterior complex to cortical areas of the cat were studied using autoradiographic procedures after injections of [ $^3\text{H}$ ]leucine. The pulvinar-lateral posterior complex was injected bilaterally in 13 cats and each hemisphere was treated as a separate case. Ten of the 26 cases had injection sites suitably located within the complex. In each of the injections 0.2–0.3  $\mu\text{l}$  of [ $^3\text{H}$ ]leucine (specific activity = 52.5–67.6 Ci/mMole) dissolved in isotonic saline to a concentration of 20  $\mu\text{Ci}/\mu\text{l}$  was injected over a 20 min period. Injections were made under aseptic conditions in cats anesthetized with pentobarbital sodium.

After survival times of 10–17 days, the cats were reanesthetized and perfused through the heart with 0.9% saline followed by 10% formal-saline. The brains were removed from the skulls, photographed in the dorsolateral plane and stored in formal-saline for a few days. They were then dehydrated and embedded in paraffin, and 10  $\mu$  sections were cut in the coronal plane. Every tenth section was processed for autoradiography and later stained with thionin, and an adjacent Nissl series of sections was also prepared. Detailed drawings were made of brain sections, noting the locations of concentrations of silver grains.

The locations of the injection sites within different subdivisions of the pulvinar-lateral posterior complex were de-

termined in the following manner: thionin-stained sections through the injection site were projected, and the cytoarchitecturally-distinct regions, such as the dorsal lateral geniculate nucleus, the ventral lateral geniculate nucleus, the medial interlaminar nucleus, the lateral dorsal nucleus, the reticular nucleus of the thalamus, the lateral habenula and the medial habenula were drawn. These drawings were then compared with two different series of coronal sections. First, we used a complete series of Nissl and myelin-stained material through the posterior thalamus (Woelcke stain: 50  $\mu\text{m}$  celloidin sections) in which it was sometimes possible to see cyto- and myeloarchitectural differences that defined the zones (see Fig. 1). Specifically, the pulvinar has mostly medium-sized, darkly-staining cells, and is heavily pierced by fibers. LPI is more difficult to distinguish: the cells in LPI are similar in size and staining characteristics to those in the pulvinar, and there are fewer fibers running the width of the zone. LPI is more heavily and evenly stained by the Woelcke stain, but is devoid of the fiber bundles which are characteristic of pulvinar and LPI. We projected independently the Nissl and myelin-stained slides, and drew boundaries between the three zones, and often found a striking correspondence. However, even the excellent histology of these Nissl and myelin series did not always permit a clear delineation of the zones, and we supplemented these series of coronal sections with a published series of coronal drawings through the same region (UPDYKE, 1977), which shows the locations of pulvinar, LPI and LPi in relation to AP level and cytoarchitectural landmarks. Aided by both of these series, we estimated the boundaries of pulvinar, LPI and LPi in our Nissl-stained sections. Finally, we projected the adjacent autoradiographic sections onto the drawings and shaded in the injection site throughout its full extent.

The locations of thalamic projections in cortex indicated by clusters of silver grains were determined for each case and were related to the cortical subdivisions described below. Area 17 was identified architectonically in our Nissl-stained material. Where the boundaries of area 17 were difficult to see, we used the physiological mapping data of TUSA *et al.* (1978) to help us delimit the area. The borders between most of the other visual areas in cat cortex were difficult to see in our Nissl material, and for these areas we relied heavily on the data from mapping experiments done in our laboratory (TUSA *et al.*, 1979; PALMER *et al.*, 1978; TUSA & PALMER, 1980; TUSA, PALMER & ROSENQUIST, 1981). The brains which TUSA *et al.* (1981) used for electrophysiological experiments and the brains we used for anatomical experiments were cut in the same plane, and section-by-section comparisons were possible. In practice, this method of assigning silver grains to a particular visual area based upon mapping data posed few problems, since the label nearly always respected the predicted borders of the cortical areas (see Discussion). The locations of areas 17, 18 and 19 are shown in Fig. 2 and described in detail in the published mapping studies (TUSA *et al.*, 1978, 1979). The other 10 visual areas which were mapped in our laboratory (TUSA *et al.*, 1981) and five additional cortical areas are described below.

*Lateral suprasylvian visual areas.* Of the six lateral suprasylvian areas recently mapped in detail (PALMER *et al.*, 1978), five are discussed in the present paper as sites of terminal label. Two of these are on either bank of the middle suprasylvian sulcus: the posteromedial lateral suprasylvian area (PMLS), and the posterolateral lateral suprasylvian area (PLLS). Just anterior to PMLS and

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