Evidence for two complementary patterns of thalamic input to the rat somatosensory cortex

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We provide evidence that the thalamic projections originating from the medial portion of the posterior thalamic complex to the somatosensory cortex of the rat are distributed in a detailed pattern which is complementary to the pattern of projections which originate in the ventral posterior nucleus.

In the two decades since Woolsey and Van der Loos' description of 'barrels' in the somatosensory cortex of the mouse, these discrete cytoarchitectonic units have become the classic example of a one-to-one correspondence between the sensory periphery and its cortical representation. Recent physiological investigations in the rat have shown, however, that the relationship between the mystacial vibrissae and the granule cell aggregates or 'barrels' in the postero-medial barrel subfield (PMBSF) is not as rigid as suggested by either early recording experiments or the anatomical evidence. Indeed, cells within a particular barrel, which by both morphological and functional criteria is related to a particular or principal vibrissa, can also be activated by stimulation of other vibrissae. While there are a number of possible anatomical substrates for this functional convergence, the possible role of thalamic inputs in this process deserves particularly close attention.

The major thalamic projections to the primary somatosensory cortex of the rat has been shown to originate in the ventral posterior nucleus (VP) but the areal distribution of this projection has not been closely specified. In the present study, we have examined the tangential distribution in the rat somatosensory cortex of the projection from the medial division of the posterior thalamic complex (POM), as defined by Jones and Leavitt, and provide evidence that this projection is also distributed in a fashion that is complementary to the projection from VP.

Portions of the posterior thalamic complex have been demonstrated to project to the somatosensory cortex of rodents but the areal distribution of this projection has not been closely specified. In the present study, we have examined the tangential distribution in the rat somatosensory cortex of the projection from the medial division of the posterior thalamic complex (POM), as defined by Jones and Leavitt, and provide evidence that this projection is also distributed in a fashion that is complementary to the projection from VP.

Thirty adult Sprague-Dawley rats were anesthe-
Fig. 1. A: dark-field photomicrograph of a tangential section through the somatosensory cortex of a flattened hemisphere illustrating the distribution of labeled afferents after an injection into POM. SII, second somatosensory area. B: photomicrograph of a coronal section through the thalamus of the same animal which illustrates the site of the injection of WGA-HRP. Bars = 600 \( \mu m \).
tized with a combination of ketamine and xylazine. They received stereotaxically placed injections of wheat germ agglutinin-conjugated horseradish per-

oxidase (WGA–HRP, 5% in water) via a glass micropipette into either VP or POM. The pipette was introduced into the brain through the cerebellum in

Fig. 2. A: bright-field photomicrograph of a tangential section through the somatosensory cortex of a flattened hemisphere in a second case illustrating the distribution of labeled afferents after an injection of WGA–HRP into POM. Note the dark HRP reaction product in ‘dysgranular’ cortex (dys) and in the ‘septa’ (s) between the ‘barrels’ (b). A’: same case as in A, photographed under dark-field illumination. B: bright-field photomicrograph of a tangential section through the somatosensory cortex of a flattened hemisphere illustrating the distribution of labeled afferents after an injection of WGA–HRP into VP. Representations of the trunk (t), hindlimb (h), forelimb (f) and vibrissae belonging to rows e and c (v(e) and v(c), respectively) are indicated for orientation. Note the overall similarity of the patterns of label, how the patterns complement one another and their obvious relationship to the body surface. B’: same case as in B, photographed under dark-field illumination. Bar = 600 μm.
the horizontal plane so as to avoid damage to the cortex. Following a 24 h survival period, the animals were deeply anesthetized and sacrificed by intracardiac perfusion with saline followed by a 1.25% glutaraldehyde and 1% paraformaldehyde buffered fixative solution. The brains were removed, and the cortices were detached and held flattened between glass slides during post-fixation and sucrose infiltration. The thalami were sectioned on a freezing microtome in the coronal plane and the cortices in a plane tangential to the pial surface. Cortical sections were processed for HRP histochemistry according to the protocol of Mesulam, thalamic sections were reacted according to the Adams method and counterstained with neutral red. Sections were mounted on gelatin-coated slides, air dried and coverslipped before viewing.

Following injections of WGA–HRP into the POm anterograde labeling could be detected in the ipsilateral somatosensory cortex in both the 'dysgranular' areas and the 'septa' between the 'barrels'. A typical injection site is illustrated in Fig. 1B and the resultant pattern of label is illustrated in Fig. 1A. POm afferent terminations were also labeled along the posterolateral border of the head representation, in a region which includes at least a portion of the second somatosensory area (SII). There was also label along the posterolateral border of the head representation, between area 17 and the PMBSF, but as this label could be the result of spread of WGA–HRP from the injection site in POm to the lateral posterior nucleus, we will not consider it further. In somatosensory cortex, regions surrounding the head, trunk and limb representations as well as those located between individual whisker representations were labeled following POm injections. Figs. 1A and 2A,A' illustrate the pattern of POm projections to the PMBSF. It can be clearly seen that both the 'dysgranular' areas and the 'septa' are labeled. This can be compared with the contrasting distribution of labeled afferents from VP to this same region which is illustrated in Fig. 2B,B'. Injections into VP result in much denser label than do injections into POm. In the PMBSF, the labeled afferents arising from VP are distributed in dense clusters and the 'dysgranular' areas and 'septa' are relatively free of label. Note that following injections into both nuclei the pattern of label can be related to the body surface and is clearly visible under both dark-field and bright-field illumination. The cases illustrated were chosen to demonstrate the complementarity of the patterns in terms of the vibrissae representation. In other cases of POm injections details as fine as the segmentation within the forepaw representation could be observed. Finally, it should be pointed out that although both patterns appeared most distinct in sections taken from the approximate level of layer IV, the patterns were also discernible in both more superficial and deeper sections.

The present report provides further morphological evidence of the close relationship between the sensory periphery and its central representation first noted by Woolsey and Van der Loos. The complementary distribution of afferent terminations arising from two different thalamic sources (VP and POm) also raises questions about the interplay between these two afferent systems during the course of development. We would assume that the 'negative image' distribution pattern of the POm afferents is a passive reflection of the formation of the terminal distributions of the VP afferents and associated 'barrels' during the course of development. Recently, it has also been reported that the distribution of labeled afferents from VP to this same region which is illustrated in Fig. 1B,B'. This is an ephemeral phenomenon which is not detectable in the mature cortex. Perhaps during development, radial glia play such a role in bringing about the segregation of afferents characteristic of the adult. It should also be pointed out that the distributions of corticocortical projections and of the POm afferent terminations are coextensive in the rat somatosensory cortex. This suggests that similar developmental mechanisms play a role in shaping the distribution of these different afferent systems.

The projection of POm (and of cortico-cortical projections, for that matter) to both the 'dysgranular' areas of somatosensory cortex and the 'septa' of the PMBSF raises another question. Are the 'septa' best regarded as a separate cortical area, part of the 'dysgranular' cortex or part of primary somatosensory cortex? The fact that POm projects to both the 'dysgranular' areas and the 'septa' sheds no light on this question as POm clearly also projects to other cortical areas including the second somatosensory area and agranular motor cortex. In our opinion, the 'septa' are best regarded as a specialized portion of primary somatosensory cortex and not as a part of...
the ‘dysgranular’ somatosensory cortex or as a separate cortical area. It should be noted that in the strict sense the term ‘septa’ as employed by Woolsey and Van der Loos\(^3\) applies to only the fourth cortical layer although the pattern which we report here, as well as the callosal projection pattern, extends through all the cortical layers. The limited functional evidence available also suggests to us that the response properties of neurons in the ‘septa’ more closely resemble those of primary somatosensory cortex\(^4,29\) than those of the ‘dysgranular’ somatosensory cortex\(^7,31\).

Ironically, this further evidence for the close relationship between the periphery and a central structure may also provide the basis for understanding functional convergence and divergence in the rat primary somatosensory cortex. In a recent study, Armstrong-James and Fox\(^4\) noted the precise location within a ‘barrel’ of the neurons from which they recorded. They report that short latency responses to non-principal vibrissae are more frequently found in neurons which are located on the edges of ‘barrels’ rather than in those located in the center of ‘barrels’. In terms of divergence, they note that, as the response acceptability threshold is lowered, the domain within which a single vibrissa can activate cortical neurons expands, and further, that this expansion is largely found in ‘septa’. The projection from POm to the PMBSF provides a possible anatomical substrate for these observations. POm receives its input from a number of diverse somatosensory sources\(^22,21,27\). Functionally, the response properties of the neurons of this nucleus have not been well characterized but the neurons of POm do have much larger receptive fields than those of VP. Many of the neurons in POm can be activated by stimulation of multiple vibrissae while most neurons in VP can only be activated by a single vibrissa\(^5\). Thus, the available evidence would suggest that each of these two spatially separate thalamic pathways are processing different aspects of somatosensory information. How these separate pathways interact in the course of normal cortical functioning remains to be determined.

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