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CHAPTER 16

Visuotopic organization of corticocortical connections in the visual system

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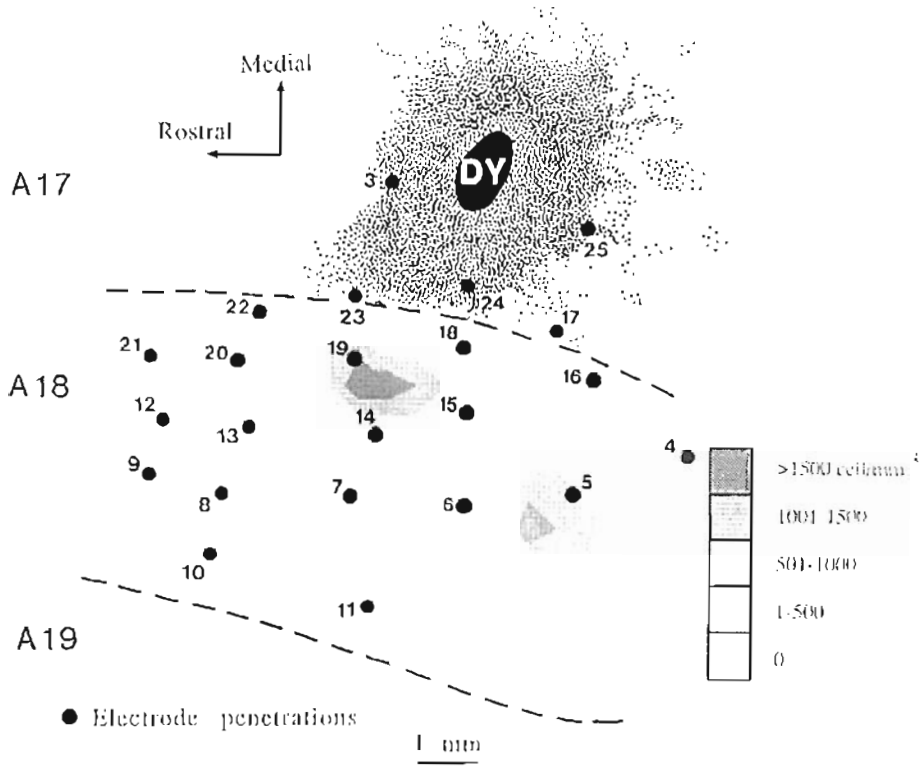
Introduction

Most structures in the visual system contain a representation of the contralateral visual hemifield and are interconnected by a dense network of connections. It is usually thought that these connections are visuotopically organized, i.e., that they link together regions of these visual structures which represent the same zone of the visual world. More specifically, such visuotopically organized connections are supposed to link neurons with overlapping receptive fields (RFs). A particularly clear example of such an organization was demonstrated between the lateral geniculate nucleus (LGN) and the striate cortex by Tanaka (1983) who identified pairs of interconnected LGN and cortical neurons by cross-correlation and showed that the RFs of the afferent LGN neurons were contained within the RF of the recipient cortical neuron. Visuotopic organization is not limited to thalamocortical connections, however, as evidenced by the results of McIlwain's studies of corticotectal connections with electrical stimulation (McIlwain, 1973, 1977) which showed a similar visuotopic organization. McIlwain, summarizing his results, gave a definition of visuotopic connections: "the cells of the striate cortex which project functionally to a collicular neuron also look collectively at the same area of visual space as that collicular cell" (McIlwain, 1973). In this report, we present evidence that some corticocortical connections do not follow this "common view" rule of visuotopic organization and we describe a new concept of organization of corticocortical connections in the visual system.

Visuotopic organization of projections from area 18 to area 17

In the course of our studies of corticocortical connections in the visual system using retrograde tracers, we have always been surprised by the large expanse of cortex containing labeled cells in extrastriate cortical areas after small injections of retrograde tracers are placed in striate cortex. Large extrastriate regions are labeled even when the injections are small enough to mark only narrow collumns of labeled cells in the LGN (Perkel et al., 1986; Salin et al., 1989). This led us to suggest that neurons belonging to extrastriate areas and projecting to a given site in area 17 may, as a population, be encoding a much larger region of visual field than that collectively represented by their target neurons in area 17, thus clearly breaking McIlwain's rule of organization. We have recently addressed this question directly by studying the visuotopic organization of connections between area 18 and area 17 in the cat with electrophysiological mapping. A small injection of a retrograde fluorescent tracer (rhodamine labeled latex microspheres, fast blue or diamidino yellow) was placed in area 17. After an appropriate survival time for the transport of the retrograde label, a fine-grain electrophysiological map was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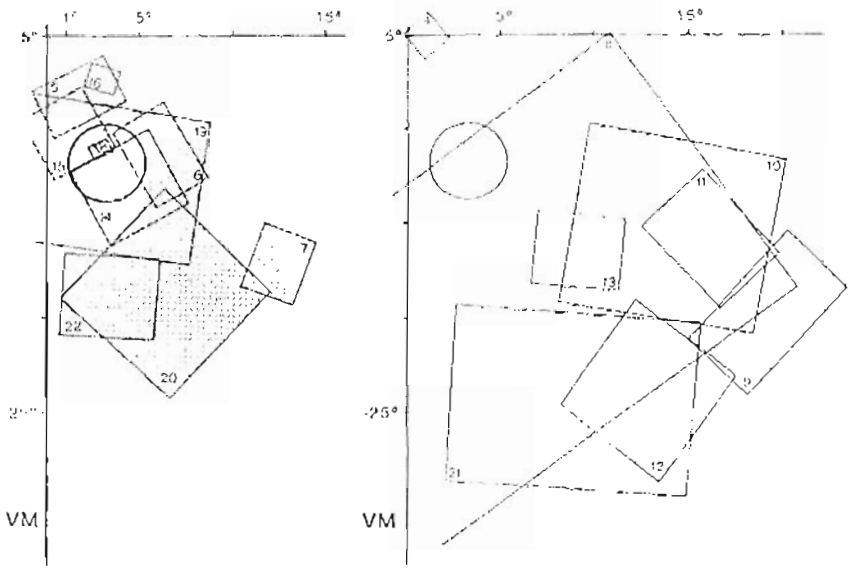
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made of the surface of area 18 in order to identify the extent of visual field encoded in the region containing retrogradely labeled cells. Typical results of such an experiment are presented in Fig. 1. The upper part of the figure illustrates the mechanically flattened surface of the regions of areas 17 and 18 containing the injection site in area 17 and the labeled cells in area 18. The injection site of diamidino yellow (DY) is shown in black in area 17 and the locally labeled cells surrounding it are represented as small dots. Within area 18, the density of labeled cells was estimated by counting neurons in a grid made up of 480 μm side squares placed over the surface of the flattened cortex. In the upper part of Fig. 1, different levels of labeling densities are illustrated by different shades of grey and the points of entry of electrophysiological penetrations are illustrated by the large numbered dots. The positions of these penetrations on the cortical surface were recorded on photographs of the blood vessel pattern and by lesions made by passing current through the microelectrode. Labeled cells were observed with a fluorescence microscope and the labeling density maps and electrophysiological maps were matched using the electrolytic lesions as landmarks.

The lower part of Fig. 1 is divided in two parts; the left part presents the smallest RFs of neurons recorded in penetrations which fell within the region of area 18 containing labeled cells (RFs shaded in grey) and the right part illustrates the smallest RFs of neurons recorded in penetrations located outside the region of labeling (RFs as clear rectangles). The extent of visual field represented by the neurons contained within the uptake zone of the injection site in area 17 was estimated by computing the aggregate RF (Dow et al., 1981) using sizes and positions of RFs recorded in penetrations located in or near the region of high color density surrounding the needle track (see Keizer et al., 1983; Bullier et al., 1984a; Kennedy and Bullier, 1985; Salin et al., 1989, for details on the methods of estimating the extent of the uptake zone of fluorescent dyes). The extent of visual field represented by neurons located in the uptake zone is illustrated by a disk in the lower part of Fig. 1.

The RF pattern of Fig. 1 illustrates the major result obtained in this and numerous other cases: the connections from area 18 to area 17 are not limited to interconnections between visuotopically corresponding regions of these two areas (Salin et al., 1992). Neither the total extents of the RFs, nor even the RF centers of neurons recorded within the zone of labeling in area 18, are contained within the representation of the uptake zone of the tracer in area 17. For example, penetration 5, which was located in a region of relatively high labeling density (501 – 1000 cells/mm^3) in area 18 yielded RFs which were located several degrees away from the aggregate RF of the uptake zone in area 17. As expected, penetrations located close to the highest peak of labeling density gave RFs which tended to overlap with the aggregate RF of the uptake zone (for example penetrations 14, 15 and 19 in Fig. 1), thus demonstrating a partial visuotopic match between strongly interconnected regions in areas 17 and 18. On the other hand, we found numerous cases of penetrations located at the outer border of the labeled zone (for example penetration 7 in Fig. 1) which returned RFs which clearly did not overlap with the representation of the uptake region. Thus, it is likely that some of the connections from area 18 to area 17 are not visuotopically organized: i.e., that

Fig. 1. Electrophysiological mapping of the region of area 18 containing labeled cells after an injection of fluorescent retrograde tracer (diamidino yellow, DY) in area 17. The region of areas 17 and 18 containing the injection site and the labeled cells has been mechanically flattened. The uptake region of the dye is illustrated by the black region labeled DY in area 17. The density of labeled cells is illustrated by shades of grey in area 18 and dots in area 17. Electrode penetrations are represented by large labeled dots. The lower part of the figure illustrates the smallest receptive fields (RFs) encountered within the penetrations in area 18. On the left and in grey are illustrated those RFs recorded in penetrations located within the labeled zone in area 18. On the right are represented as clear rectangles those RFs recorded in penetrations located outside the zone of labeling. The circular region corresponds to the aggregate RF of the uptake region of the dye in area 17 (see text). These results illustrate the presence of non-visuotopic connections from area 18 to area 17.

they link together neurons which have no regions of their RFs in common. This creates a dilemna for organizing cortical areas and transferring information among them.

Visuotopic organization of feedforward and feedback connections

Earlier results from this laboratory (Salin et al., 1989) suggested that none of the sets of cortical afferents terminating in area 17 follow the McIlwain rule of visuotopic organization. In view of the validity of this rule for subcortical and thalamocortical connections, one may wonder whether all corticocortical connections are organized in a similar fashion as afferents to area 17. We examined this question (Salin, 1988) by measuring the topography of the connection from area 17 to area 18, using similar methods as previously reported (Salin et al., 1989). The results showed that it appears to be visuotopically organized, since a column of cells in area 18 representing a zone of visual field 8 – 9° wide is innervated by a region of area 17 which encodes a similar extent of the visual field (Salin, 1988). Similar conclusions have been reached by Ferrer et al. (1988), although the extent of the visual field represented in the convergence region was much smaller in that study than in our results. Sherk and Ombrellaro (1988) also concluded that the projections from area 17 to the visual cortex of the suprasylvian sulcus are visuotopically organized.

Results obtained in the macaque monkey suggest a similar organization for the projections from area V1 to extrastriate areas. In this case, the evidence came from reversible inactivation by cooling of a limited region of area V1 situated on the operculum while recording from areas V3 or V4 (Girard et al., 1991a,b). Cooling inactivated the region of V1 situated below the cooling plate and created a functional scotoma in the visual field of the animal (Girard and Bullier, 1989). When the RFs of neurons in V3 and V4 overlapped with the border of this scotoma, we observed inactivation of the part of the RF located within the scotoma (Girard et al., 1991a,b). The interpretation of this finding is that the connections from V1 to V3 and V4 are visuotopically organized.

It is known that connections from area 17 to extrastriate cortex have different morphological characteristics from the return projections and this difference had led authors to distinguish two types of connections, the feedforward and the feedback connections (Rockland and Pandya, 1979; Maunsell and Van Essen, 1983). Our results in cat and monkey therefore suggest that feedforward connections follow McIlwain's rule of visuotopic organization, like thalamocortical afferents. There may be some relationship between the similar visuotopic organization of feedforward and thalamocortical connections and the fact that they both terminate in layer 4. Another similarity is that inactivation of these connections leads to a silence of the target region (Schiller and Malpeli, 1977; Girard and Bullier, 1989; Girard et al., 1991a). Cortical afferents to area 17, on the other hand, which are mostly of the feedback type, avoid layer 4 and their inactivation does not silence the target area (Dreher and Cottee, 1975; Donaldson and Nash, 1975; Sherk, 1978; Sandell and Schiller, 1982). Thus feedforward and feedback connections do not differ only on morphological characteristics but also appear to be organized along very different functional principles.

Afferents to area 17 share the same convergence window

Feedback connections therefore are morphologically and functionally different from feedforward. Feedforward connections appear to follow McIlwain's rule. It is of interest to determine whether feedback connections also obey a single functional principle. Results on the afferents to area 17 in the cat suggest that this may be so. Despite their widely different topographical organizations, the different sets of cortical afferents converging to a column of cells in area 17 appear to share one functional feature: the RFs of neurons involved in these connections collectively encode the same region of visual field, whether they belong to areas 17, 18 or

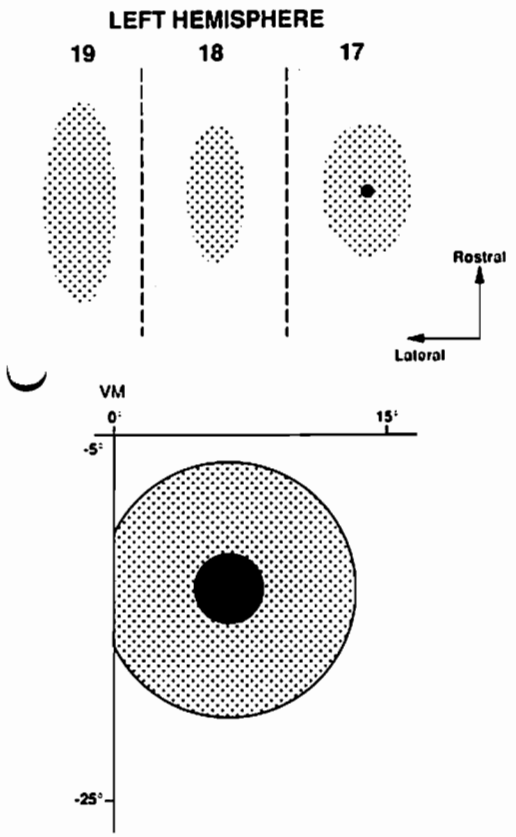

Fig. 2. Schematic representation of the correspondence between cortical regions involved in the connections afferent to area 17 and visual space. The upper part of the figure provides a schematic representation of areas 17, 18 and 19 of the left hemisphere of a cat after flattening. The lower part of the figure illustrates the corresponding regions in visual field (VM, vertical meridian). The large black dot in the upper part of the figure illustrates a column of cells in area 17 and its visual field representation (aggregate RF) is represented by the disk in the lower part of the figure. Neurons in areas 17, 18 and 19 which are afferent to the column in area 17 are represented as small dots in these areas. They all collectively encode a common region of visual field which is called the convergence window.

19. This was demonstrated directly by electrophysiologically mapping the zones in areas 17 and 18 containing labeled cells after an injection was placed in area 17 and with a less direct method for the afferents from area 19. Fig. 2 summarizes these results. The upper part of the figure presents a schematic representation of flattened portions of areas 17, 18 and 19 of the left hemisphere of the cat brain, as seen from above. The lower part of the figure illustrates the lower quadrant of the right visual hemifield which is represented in those regions of areas 17 – 19. Consider a column of cells in a region of area 17 representing visual field situated approximately 10° below the horizontal meridian. This column, which is represented by a large black dot in the upper part of Fig. 2, has a broadly circular aggregate RF measuring approximately 4° in diameter (Salin et al., 1992) which is represented by the black disk in the lower part of the figure. The extent of the cortical surface of area 18 containing cells sending converging projections to this column, the region which we call convergence region (Salin et al., 1989), is illustrated by an elongated cloud of points in area 18 in the upper part of the figure. This convergence region represents a broadly circular region of visual field measuring 11° in diameter (Salin et al., 1992) which is illustrated in the lower part of the figure by the disk-like distribution of dots surrounding the black region of visual field encoded in the column of cells in area 17. By electrophysiological mapping, we found that the region of area 17 surrounding the injection site and containing cells projection to the same column appears to represent the same region of visual field as that represented by the convergence region in area 18. From our earlier results, we also know the rostro-caudal extent of the convergence region in area 19 (Salin et al., 1989). Using published data on the retinotopic organization of area 19 (Tusa et al., 1979; Albus and Beckman, 1980; Duysens et al., 1982), it is then possible to calculate the corresponding extent of visual field encoded in the labeled region in area 19. This gives a region measuring 15 – 20° across in elevation, a fair match for the extent of visual field encoded in the convergence zones of areas 17 and 18. Fig. 2 thus provides a synoptic view of the relationship between the cortical regions containing cells projecting to a column in area 17 and the visual space represented in these regions. Neurons contained in the black dot column in area 17 collectively represent a 4° wide region of visual space and are under the converging influence of a network of neurons in areas 17, 18 and 19 which col-

lectively encode the same large window of visual field measuring 15° across and represented by the stippled region in the lower part of Fig. 2. Let us call this region the convergence window.

Completion of the convergence window by callosal afferents

Callosal connections are known to exhibit similar convergence and divergence as ipsilateral corticocortical connections (Kennedy and Dehay, 1988) and it is therefore interesting to examine whether they also follow the same rule of connectivity. Results in the macaque monkey (Kennedy and Dehay, 1988) and more recently in the cat (Kennedy et al., 1991) demonstrate that, for a given column of cells in area 17, the convergence zones in contralateral visual areas have the same rostro-caudal extents as those in the homologous areas in the ipsilateral hemisphere. When translated in terms of visual field, this means that the population of callosal neurons projecting to a column in area 17 represents a visual field region having the same extent in elevation as that represented by ipsilateral afferent neurons and is therefore likely to be carrying information concerning the same window of visual field as that corresponding to ipsilateral afferents. This is illustrated in Fig. 3 in which we consider the case of a column of cells in area 17 which is located close to the 17 – 18 border in the left hemisphere (black dot within area 17). This column receives converging projections from regions of areas 17, 18 and 19 in the left hemisphere encoding visual field regions which extend only marginally in the left visual hemifield (fine dot region in the lower part of Fig. 3). It also receives projections from a zone of cortex situated at the 17 – 18 border of the right hemisphere representing a small crescent-shaped region in the left visual hemifield (large dot region in the lower part of the figure). Thus, afferents from the 17 – 18 border in the right hemisphere contribute to the completion of the convergence window surrounding the aggregate RF of the column of cells in area 17. In this way, every column of cells in area 17 is under the converging influence of neurons

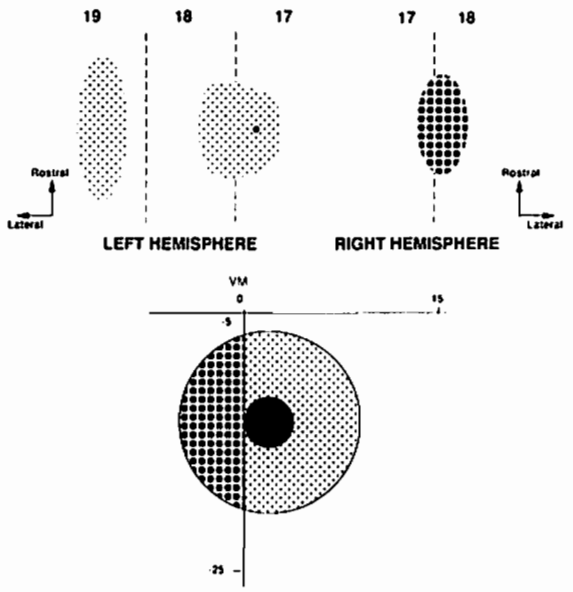

Fig. 3. Participation of callosal connections to the convergence window. The presentation of the figure is similar to that of Fig. 2 except that the column in area 17 is closer to the 17 – 18 border and that afferents from the contralateral (right) hemisphere are represented. Afferents from the ipsilateral hemisphere are illustrated as dots on the cortex and their common convergence window as the dotted region in visual field. Neurons from the right hemisphere which are afferent to the column of cells in area 17 of the left hemisphere are illustrated as large dots and their visual field representation is illustrated by the corresponding crescent-shaped region in the lower part of the figure. This figure illustrates the completion of the convergence window by callosal afferents for neurons with RFs located close to the vertical meridian (VM).

representing a broadly circular window of visual field, whether the column of cells is located in regions of area 17 representing the periphery of the visual field or whether it is located in cortex subserving regions of the visual field situated close to the vertical meridian. Such a completion role of callosal connections is in keeping with one of the functions traditionally assigned to callosal fibers of the visual system, that of providing perceptual continuity across the midline (Whitteridge, 1965). The fact that callosal connections follow the same organization principle as the ipsilateral connections suggests that the network organization of corticocortical connec-

tions includes interhemispheric as well as intrahemispheric connections.

Spatial reciprocity of corticocortical connections

So far, we have only examined the topographic organization of afferents to a column of cells in area 17 and it is not clear how this relates to that of the reciprocal projection from a column in area 17 to area 18. In the course of experiments aimed at characterizing this projection, we found that the spatial organization of corticocortical connections between areas 17 and 18 is reciprocal, i.e., that a column of cells in area 17 innervates the territory of area 18 that contains neurons projecting to it. Similarly, a column of area 18 projects to the region of area 17 which sends projections to it. This spatial reciprocity could provide a structural basis for reverberating loops between the column of cells in area 17 illustrated in Fig. 2 and the convergence regions in the various cortical areas sharing the same convergence window.

Size invariance of the convergence region

Many parameters of the organization of visual structures, such as RF size and magnification factors are known to vary with eccentricity in the visual field and one may wonder whether the convergence region and the convergence window constitute invariants across the visual field or whether their sizes depend on the eccentricity in visual field. To answer this question, we measured the convergence region in cortex subserving lower visual field and in cortex representing central visual field. The results demonstrated that the size of the convergence region for a given cortical area is constant across cortex, corresponding to an oval region measuring 5.3 mm in the rostro-caudal direction and 2.9 mm in mediolateral direction (Salin et al., 1992). This size invariance of the convergence region across cortex suggests that its dimensions are in some way constrained by morphological factors such as extent of axon collateral arborization and dendritic field, factors which do not appear to vary substantially across cortex. In other words, the invariance of the convergence region may be another manifestation of the crystal-like morphological organization of the cortex popularized by the results of Hubel and Wiesel (Hubel, 1982). Given the size invariance of the convergence region and the well-known change in magnification factor with eccentricity, one could predict that the convergence window would be smaller for connections between regions of cortex representing central visual field than for connections between cortical regions encoding the periphery. This is indeed what we found by direct electrophysiological mapping. Instead of a 15° window, as found in peripheral visual field, we observed a convergence window measuring 5 – 7° across in cortex subserving central visual field. Thus, the convergence window appears to be scaled to the RF size and scatter of neurons which are also smaller in cortex representing more central regions of the visual field.

Functional aspects of the network organization of afferents to area 17

What could be the functional counterpart of this convergence window? The results of Mignard and Malpeli (1991) show that some area 18 neurons provide a functionally significant input to cells of the upper layers of area 17. It is clear, however, that neurons of area 18 contained in the convergence region corresponding to a column of cells within area 17 cannot possibly all provide a major excitatory drive, otherwise the RF sizes of the neurons in this column would be determined by the size of the convergence window and would be much larger than they actually are. This lack of a powerful excitatory drive from neurons situated at the periphery of the convergence region is further supported by the results of electrical stimulation of area 18 afferents to area 17, showing that neurons in area 17 can be orthodromically driven from area 18 only when their RFs are in perfect visuotopic correspondence with those of the stimulated neurons in area 18 (Bullier et al., 1988). It is not clear at the moment whether neurons providing non-visuotopic connec-

tions are mostly involved in inhibitory interactions through interneurons or whether they provide subthreshold excitatory drive.

It is likely that at least those neurons of the convergence regions providing non-visuotopic inputs to area 17 neurons are involved in some kind of modulatory influence on the visual responses. It is well established that the RFs of visual cortical neurons possess modulatory regions beyond the so-called classical RF. Visual stimulation of these modulatory regions generate inhibitory and facilitatory effects (Nelson and Frost, 1978, 1985) which are believed to play an important role in cortical processing of visual information (Nelson, 1975; Allman et al., 1985; Orban et al., 1987; Gilbert and Wiesel, 1990). Horizontal connections within a given cortical area are usually assumed to provide the structural basis mediating modulatory interactions beyond the classical RF. However, neurons of area 17 are innervated not only by intrinsic connections but also by neurons situated in several other areas and these interarea connections correspond to the same convergence window as intrinsic connections (Fig. 2). Therefore, it appears likely that modulatory influences coming from regions beyond the classical RF arise from the converging action of the whole network reciprocally coupled to a given column in area 17 and that intrinsic connections only provide one component of these modulatory effects.

Because of the impossibility of identifying non-visuotopic connections with electrical stimulation (Bullier et al., 1988), we have recently used another technique, the temporal cross-correlation (Nelson et al., 1992). This method has been used with success in the retino-geniculo-striate pathway to identify monosynaptically connected pairs of neurons (Cleland et al., 1971; Tanaka, 1983). The signature of such a monosynaptic connection in the cross-correlation histogram (CCH) is a sharply defined peak displaced with respect to the time origin. To our surprise, we practically never isolated such a pattern in a sample of more than two hundred CCHs computed from the firing of neuron pairs with one member of the pair in area 17 and the other in area 18. The majority of the peaks observed in our CCHs were broad (10 – 50 msec) and centered on the origin of time or only slightly displaced with respect to it. The usual interpretation of such a pattern is that the two neurons under study are activated by a common set of neurons (Perkel et al., 1967). Several arguments reviewed elsewhere (Nelson et al., 1992) suggest that such generators of common input belong to the cortex and it is likely that the network organization revealed by our anatomical experiments constitutes the structural basis of these cortical generators. More specifically, we hypothesize that the numerous cortical neurons belonging to the network associated with a given convergence window (Fig. 2) could provide a common input to a pair of neurons in areas 17 and 18 through axonal bifurcation (Bullier and Kennedy, 1987), through recurrent collaterals of axons of pyramidal cells in these two areas, or through polysynaptic chains created by these collaterals. Further support for this hypothesis is provided by the fact that the temporal coupling revealed by the presence of peaks in the CCHs is observed only when the RFs of the coupled neurons are distant by no more than 8°. This value of 8° is remarkably close to the radius of the convergence window at this eccentricity, suggesting that the common input generators may belong to the cortical network collectively representing the convergence window.

Synthesizing the global relationships among perceptual elements remains an unsolved problem in perception since Gestalt theorists brought this question into prominence more than sixty years ago. Today, we see in neuroscience that a column of neurons in area 17 receives convergent input from a network of neurons situated in other cortical areas. Assuming that this convergence is also found at the level of the individual neuron, a neuron of area 17 could therefore be influenced by populations of neurons having different functional characteristics. By switching from one set of such afferents to another for its major source of functional input, a neuron in area 17 could therefore modify considerably its functional characteristics as a spatio-temporal filter.

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