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Anatomical Guides to the Functional Organization of the Visual Cortex

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Abstract. The emerging picture of the organization of the visual cortex is one of segregated pathways and specialized areas and subareas dealing with different submodalities of vision. The preeminent tool in obtaining this picture has been anatomical. It seems likely that the strategy of submodality segregation is used by the cerebral cortex in building all perceptual categories, not just the visual.

INTRODUCTION

"Anatomy first, then physiology. But if physiology first, then not without anatomy." Thus wrote Gudden, the German anatomist, and his remark seems as valid today as it was over one hundred years ago because the major achievements in understanding cortical physiology have derived their force from anatomical studies and demonstrations. Indeed, new and unforeseen anatomical findings have led to a revision of physiologically based hypotheses and, often implicitly, laid the foundations of new and searching physiological experiments. Thus, one can say that the "patchy" picture of the cerebral cortex that modern anatomical techniques gives us is the manifestation of a functional strategy that the cerebral cortex uses to build up visual perceptual categories—namely that of submodality segregation—and that, given the dominance of vision in the life of higher primates and the extent of cortex devoted to it, it seems likely that a similar strategy is used for other sensory modalities as well.

Perhaps the single most powerful motivating force in cerebral studies—and the visual cortex well illustrates the point—has been the attempt to chart histologically distinct parts of the cerebral cortex and to assign specific functions to each. The first localization of function was discovered by Broca who showed that one faculty, that of producing articulate language, depends upon the integrity of the third frontal convolution of the left temporal lobe. The subsequent discovery of the excitable motor cortex by Fritsch and Hitzig, the demonstration that this cortex is coextensive with a cytoarchitectonically unique region of cortex, and the further discovery that within the motor cortex there is, in both monkey and man, a seemingly orderly representation of movements or muscles, eventually ushered in what Sholl (1956) has called an era of "feverish map making." Each and every cytoarchitectonic difference was used, often uncritically, to subdivide the cortex into ever smaller regions, often without assigning functions to them, and culminating in the elaborate subdivisions of the Vogts which some thought were "fantastic" (Sholl 1956). It also ushered in the concept of the homunculus. If anything, single cell physiology in the visual cortex and the parallel anatomical studies there have taught us that far from being fantastic, such subdivisions may in fact have been modest, even though based on incorrect criteria. In the visual cortex, the tendency today is to subdivide.

FUNCTIONAL SEGREGATION IN THE STRIATE CORTEX

Perhaps the most elaborate subdivision, both anatomically and physiologically, has been achieved in the striate cortex, V1, a cytoarchitectonically uniform cortical area. The first evidence for functional parcellation within it was derived strictly from single cell physiology by Hubel and Wiesel (1977), who showed that cells with common properties are grouped together radially in the form of columns. This was not dissimilar to the discovery by Mountcastle (1957) of functional columns in the somatosensory cortex and, true to Gudden's dictum, had a precursor in the description by both Lorente de No and von Economo of vertically organized columns of cells, though neither of the latter could make sense of this anatomical finding. Paralleling the demonstration of functional orientation columns was the demonstration of ocular dominance columns: a demonstration powerfully reinforced by anatomical evidence (Hubel and Wiesel 1977) which showed that each eye has a genetically predestined territory in striate cortex reserved for it, but that the allegiance is not absolute in that, during the critical period, the connections are labile and cortical territory belonging to one eye may be overtaken by the other. This demonstration derived immense force from the fact that it could be anatomically substantiated. It has also raised questions about whether, in this respect, the striate cortex or perhaps even the visual cortex in general, is different from cortex belonging to other systems. As early as 1917 Leyton and Sherrington had emphasized that "as regards minutiae ... the motor cortex is a labile organ." In more recent studies, where the same somatosensory cortex was repeatedly explored in physiological recordings, Merzenich and his colleagues (Merzenich et al.

1983) have found that there too is a lability prolonged into adult life, a lability that allows one finger to expand its territory into that of another, deafferented, finger. In this respect, the adult somatosensory cortex is not unlike the immature striate cortex. It would not be surprising if the factor that operates to make for lability of retino-cortical connections in the immature striate cortex is not dissimilar to the factor that allows for lability in somatosensory cortex, though curtailed in time. Equally, it is likely that the factor that defines the cortical territory belonging to an eye is not dissimilar to the factor operating to define the cortical territory accessible to a body segment, beyond which incursion is disallowed, though curtailed in space. Thus, a problem raised by studies of visual physiology, together with the supporting anatomy, is one common to all cortical areas—namely what factors operate to define the cortical space belonging to any given body segment, even in adult life.

SUBMODALITY SEGREGATION WITHIN STRIATE CORTEX

Early physiological evidence (Hubel and Wiesel 1977) suggested that, paralleling its uniform cytoarchitecture, the striate cortex is a functionally uniform area, with all cells outside layer IVC being orientation selective and one orientation succeeding another in a remarkable order in the tangential direction. At the same time, the pattern of output from monkey striate cortex showed that V1 sends parallel and independent outputs to the visual areas of the prestriate cortex, which themselves are not equivalent in functional properties (Zeki 1975). This anatomical demonstration, together with the physiological evidence, constituted the first evidence that V1 must act as a segregator, parcelling out different kinds of visual information to different visual areas for further processing (Zeki 1975). It follows that there must be a degree of submodality segregation within V1 not hinted at by its apparent cytoarchitectonic or functional uniformity derived from single cell physiology. The first demonstration of functional segregation within V1 came, not from physiological studies, but from anatomical ones in which V5, the specialized motion area receiving a direct input from V1 (Zeki 1974), was found to receive its input only from the (directionally selective) cells in layer IVb and upper layer 6 (Lund et al. 1975). More recent studies (Shipp and Zeki 1985) show that not every cell in these two layers projects to area V5. Instead, cells projecting to it are clustered and separated from each other by cells projecting elsewhere. Thus, the motion signalling system in V1 is segregated, both radially and tangentially. Another example of the tangential segregation is found with respect to orientation and wavelength selective cells in layers 2 and 3 (Livingstone and Hubel 1984). Here again, it was an anatomical demonstration that modified our picture of the organization of V1 and revealed a "patchiness" related to submodality segregation not hinted at by earlier physiological findings. Whereas the anatomical demonstration of ocular dominance columns corresponded well with physiological results, the anatomical demonstration of orientation columns (using the 2-deoxyglucose label (Horton and Hubel 1981)) gave a less clear-cut result. The reason for this becomes apparent when the striate cortex is stained for the enzyme cytochrome oxidase. Unlike the uniform picture obtained from cytoarchitectonic stains or physiological recordings, the striate cortex is then found to be characterized by repetitively occurring regions of higher cytochrome oxidase content, especially prominent in layers 2 and 3, so that in a tangential section through these layers, stained for cytochrome oxidase, the "blobs" of high cytochrome oxidase content give a polka-dot pattern—a patchiness which is an expression of submodality segregation within V1. Direct physiological recordings from the blobs and the more lightly stained regions in between (the interblob zones) show that, unlike what was previously supposed, orientation (but not wavelength) selective cells are concentrated in the interblob zones and not uniformly distributed throughout the striate cortex. In contrast, the wavelength (but not orientation) selective cells are concentrated within the blobs, where the overwhelming majority of cells are not orientation selective (Livingstone and Hubel 1984). This functional submodality segregation, even at the level of a primary cortical receiving area, naturally reflects the strategy used by the nervous system to construct perceptual categories and is not unique to the visual system, although apparently its expression is best developed there. Thus, in the somatosensory cortex cells registering light touch are separated from those registering ordinary sensibility (Mountcastle 1984). It seems likely that a similar strategy of submodality segregation is used by other sensory systems and cortical areas. At any rate, in the visual system submodality segregation and its anatomical expression is not restricted to V1.

FUNCTIONAL SEGREGATION IN V2

V2 is an area of uniform cytoarchitecture surrounding V1, receiving a direct and topographically organized input from it and having a characteristic field representation within it (Zeki 1978). Early physiological recordings showed that V2 contains a variety of functional cell types, including wavelength, orientation, and direction selective cells (Baizer et al. 1977; Zeki 1978). Here again, the advent of an anatomical technique, that of cytochrome oxidase histochemistry, has led to more detailed physiological studies which reveal a remarkable degree of submodality segregation within V2—another example of "anatomy first, then physiology." When V2 is stained for the enzyme cytochrome oxidase it is found to be characterized by a set of thick and thin stripes, separated from each other by interstripe zones of lower cytochrome oxidase density (Tootell et al. 1983). Direct physiological recordings from these stripes reveals that wavelength selective cells are found only in thin stripes, which contain very few orientation selective cells; direction selective cells are found only in thick stripes; and orientation (but not wavelength) selective cells are found in both thick stripes and interstripes (Hubel and Livingstone 1985; De Yoe and Van Essen 1985; Shipp and Zeki 1985). Parallel mapping studies show that the three sets of stripes map the retina independently; the three maps coexist within the overall topographic map of V2 (Zeki and Shipp, in preparation). Thus, what seemed only five years ago to be a uniform cortical area turns out to be a patchy collection of submodality-specific regions, coexisting within a topographic design but allowing their existence to be revealed by suitable anatomical staining—a degree of subdivision beyond the dreams of even the most ardent localizationalists.

FUNCTIONAL SPECIALIZATION AND MULTIPLE VISUAL AREAS

Paradoxically, the first evidence for submodality segregation and the consequent functional specialization did not come from the most intensively studied of all the visual areas, V1, but from functional studies of the visual areas of the prestriate cortex, which themselves were preceded by anatomical studies. Surrounding the striate cortex, the uniform cytoarchitecture of the prestriate cortex and its thalmic connections had long led many to suppose that it is a single cortical area or, at most, two areas. But the pattern of anatomical inputs to it from V1 (Zeki 1975), and the pattern of callosal connections within it (Zeki 1970), helped identify a number of areas in it. The pattern of callosal connections was especially useful not only in differentiating the areas but also in identifying at least one of their borders with an adjacent area (Zeki 1975, 1977, 1978; Van Essen and Zeki 1978). The reason for this was quite simple and represents one way of using anatomical evidence to derive functional boundaries and differences in the nature of topographic representation between areas. Thus, if the prestriate cortex is made up of several distinct areas, each of which constitutes a more or less complete representation of the visual field, then that representation should include the vertical meridian. Since the representation of vertical meridians in the two hemispheres are callosally connected, it follows that there should be several different patches of callosally connected prestriate cortex, each separate callosal patch belonging to a separate visual area. It also follows that the pattern of each callosal patch should give a hint as to the nature of field representation in that area, e.g., whether it is a very precise or a relatively crude one (in topographic terms). Single cell physiology has given ample confirmation of these suppositions. In particular, where the topographic map is relatively tight, as in V1 and V2, the callosally connected zone at the vertical meridian is itself restricted to a narrow band.

In contrast, where the representation is less precise in topographic terms, as in V5 or the V4 complex, the callosal bands are more widely distributed (Zeki 1977; Van Essen and Zeki 1978). Hence, single cell physiology confirms the suspicions derived from anatomical studies and reveals that there are substantial variations in the nature of retinal representation in different visual areas. These variations carry with them powerful hints of the functional emphases in different areas and indeed raise the more general question of whether one can continue to think of these representations in retinal terms. Just the same kind of picture, and one reflecting variations in the representation of other sensory modalities, is evident from an examination of other systems, such as the somatosensory or motor system (see, for example, Gould et al. 1986).

FUNCTIONAL SPECIALIZATION

The supposition from early physiological recordings in visual cortex was that each area would repeat the same analysis as the antecedent area but at a more complex level (Hubel and Wiesel 1965, 1969). In contrast, physiological studies in the visual areas of the macaque monkey prestriate cortex emphasized another strategy: that of submodality segregation and separate processing of information relating to form, color, and motion, without denying a hierarchical element in the pathway dealing with any given submodality (Zeki 1975, 1978). Perhaps the single most impressive evidence in favor of this view of functional specialization was found in studies of the motion area (V5), in which the majority of cells are directionally selective and none is color or wavelength selective (Zeki 1974). Here the negative evidence (lack of selectivity for color) had almost the same status as the positive evidence (presence of directional selectivity) in determining the specialization of this area in particular and the cortical separation of color and motion in general. In a similar way, the fact that both V3 and V3A have few, if any, wavelength selective cells but substantial numbers of orientation selective cells, some registering disparities (Zeki 1978; Baizer 1982; Burkhalter et al. 1986; Poggio, personal communication), would seem to suggest that these two areas are more concerned with form and depth than with color. In contrast, there are heavy concentrations of wavelength and color-coded cells within the V4 complex and few directionally selective cells within it (Zeki 1978). One therefore is led to the view that there is a functional specialization within the prestriate visual cortex (Zeki 1975, 1978), with different groups of areas emphasizing different functions and not as previous views had supposed, analyzing the same information at ever-increasing levels of complexity, although an important hierarchical element exists within each separate functional pathway. Apart from physiological evidence, powerful support for such a notion has recently come from both anatomical and clinical evidence. The anatomical evidence has shown, in its patchiness, a remarkable submodality specificity. As an example, V2 was known from earlier studies to project to V3, V4, and V5 (Zeki 1971). More recent studies using retrograde labels, and correlating these with cytochrome oxidase histochemistry, have shown that V5 receives its input from the thick stripes of V2, the very ones containing the direction selective cells, whereas V4 receives its input from the thin stripes and the interstripes of V2 (Shipp and Zeki 1985; De Yoe and van Essen 1985). Similarly, V1 was known to project to V2, but more recent studies reveal the order within the patchy nature of these projections; the blobs containing the wavelength selective cells projecting to the thin stripes and the interblobs to the interstripes (Livingstone & Hubel 1984). Thus, it would seem that there are separate pathways and areas dealing with form, color, and motion. Clinical evidence has also supported the theory of functional specialization. Damasio et al. (1980) and others have described patients whose disability, following cerebral lesions sparing V1, is restricted to an achromatopsia without involving other submodalities. Zihl et al. (1983) have described a patient with bilateral cerebral involvement of the superior temporal sulcus region in whom the disability was specifically one of motion perception. It seems probable that such a functional specialization is not unique to the visual cortex, for remarkably similar results have been described in the sensory system of an animal well removed from the monkey, the auditory cortex of the moustached bat (Suga 1984). Specialization may even be detected in the organization of the primate motor cortex (Gould et al. 1986).

Recently, a variant of our view on functional specialization in the visual cortex has been presented by Desimone et al. (1985). While agreeing that motion, form, and color are registered separately, and that motion is processed in areas separate from those dealing with form and color, this view supposes that the latter two are inextricably linked and processed in the same area, the V4 complex, though separately and in parallel. It is an an interesting variant for which one can find evidence both for and against. The evidence for lies in the fact that V4 complex contains both wavelength and orientation selective cells (Zeki 1975, 1978; Desimone et al. 1985) and that it receives its input from both the thin stripes and the interstripes of V2 (Shipp and Zeki 1985; De Yoe and van Essen 1985). Support also comes from the recent behavioral experiments of Heywood and Cowey (personal communication) which show that after extensive lesions of the V4 complex (which also invade the infero-temporal cortex), color discrimination as well as form discrimination is impaired. Finally, the V4 complex is known to project to infero-temporal cortex where lesions cause a pronounced visual defect in both form and color discrimination. The evidence against lies in the physiological and anatomical experiments described above which show that wavelength and orientation selective cells are maintained separately at the level of V1 and V2; that areas such as V3 and V3A, which have plenty of orientation selective cells, have few if any wavelength selective cells, which implies that information on form reaching these two areas must be different and used differently than the information on form reaching V4; that there are well documented human cases showing a selective loss of color vision after damage to prestriate cortex; and that cells in V4, even when orientation but not wavelength selective, often have extensive surrounds which are sometimes wavelength selective (Zeki 1980 and unpublished results; Desimone et al. 1985). In addition, there is the difficulty that every form is assigned a color, be that color black or grey or white: and every color, being confined in a certain space, has a form. On balance, the case that V4 can register form *independently* of color has yet to be made.

FUNCTIONAL SPECIALIZATION, SUBMODALITY SEGREGATION AND THE DISTRIBUTIVE ROLE OF THE CORTEX

The apparent cytoarchitectonic uniformity of large parts of the cerebral cortex has encouraged, perhaps implicitly, a search for some uniform operation that the cerebral cortex may perform repeatedly (see Phillips et al. 1984). One such role is no doubt its distributive function. The evidence for this is both anatomical and physiological, but it is once again a case of "anatomy first, then physiology." At one level, the distributive role may be seen and directly related to submodality segregation in the kind of output that V1 and V2, two visual areas with a heterogeneous population of cells, have—each one projecting to different visual areas and, as physiological evidence has shown, to areas serving different functions. At another level, this distributive role is seen in the patchy nature of connections between some areas: a feature first seen in visual cortex and now known to be a more general feature of cortical connectivity. This would seem to be the anatomical reflection of the fact that, in distributing information, the cortex maintains information related to different submodalities segregated. The most compelling evidence for this comes from studies of visual cortex, but the lessons derived from it may be applicable elsewhere. Thus the connections established between V1 and V2, two areas with a heterogeneous population, or between V2 and V5, the latter a specialized visual area, are patchy in nature (Livingstone and Hubel 1984; De Yoe and van Essen 1985; Shipp and Zeki 1985). However, there is often a pronounced patchiness in the connection subserving a single specialized pathway, hinting at the possibility of sub-submodality differentiation and segregation. Thus, the output from V1 to V5 is patchy in nature (Zeki 1976) and the projections from V6 to the frontal eye fields (Zeki, in preparation) are also patchy, as if different kinds of motion-related information are being maintained segregated or are being segregated out in V1 and V6 and transmitted in a segregated fashion. At a grosser level, the segregatory function of an area such as V5 is strongly hinted at, or even shown (by analogy with V1), by the observation that V5 not only projects to V5A but also to V6 and to the frontal eye fields, all of them motion-related areas, as well as to other areas. It seems likely that V5 sends different kinds of motion-related information to these areas. Of course V5 also has connections with V3 and V4, two functionally different areas; it is possible that it informs these areas of the results of its operations, the same information being used in different ways in the two different areas. The very same kind of argument can be applied to other cortical areas which send out parallel and independent outputs to further areas.

Thus, one uniform operation obviously performed by each cortical area is distributive. Another possible uniform function, repetitively performed, is selective, operating both during development and in adult life. This view (Edelman and Finkel 1984) sees in the rich variability of the dendritic and axonal patterns within the cortex the basis for a selective procedure whereby many different nonisomorphic anatomical variants are functionally equivalent. This view could also provide a basis for understanding a possibly fundamental and repetitive cortical operation involving the correlation of various mapped functions.

In summary, there are certain simple strategies which the visual cortex uses to construct the visual scene, and these are well reflected in its general anatomical organization—the divergent connections from an area attesting to a distributive role and the patchiness of interconnections attesting to submodality segregation. Given the similarity in overall connectional strategy in the cerebral cortex, it seems likely that a similar kind of strategy is used by other cortical systems. This naturally leaves out of account the fundamental question of how information, thus fractionated, is reintegrated—a process that involves a rich reentrant system, which we discuss elsewhere (Zeki 1987, in preparation) and for which we envisage a fundamentally similar kind of operation throughout the cortex. It also leaves out of account the neural bases of the perceptual constancies, well exemplified by color vision, because it seems likely that the implementation of these depends upon variable internal circuitries.

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