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The Rough Seas of Cortical Cartography

Semir Zeki

s.zeki@ucl.ac.uk

University College London, London, UK

Correspondence:

Efforts to parcellate the cortex into areas based on fine-scale anatomical signatures (e.g. cytoarchitectonics) date back to the early years of the last century. In the ensuing decades, rapidly growing knowledge about cortical connections encouraged neurobiologists to search for connectivity-based principles underlying the organization of the cerebral cortex. Using such an approach, the 1991 paper by Felleman and Van Essen presented a connectivity-based hierarchical principle dictating the relationship between cortical areas. This helped invigorate debates on the principles underlying cortical organization, including searches for alternative, or complementary, principles.

Keywords: cortical organization; cortical hierarchies; cortical connections

Cortical anatomy has dominated attempts to give an all-embracing account of how the cerebral cortex is organized. Myeloarchitectonics, cytoarchitectonics, myelogenesis, and multi-modal magnetic resonance imaging (MRI) are some of the approaches that have been used to try and characterize cortical architecture. These techniques have, between them, divided the cerebral cortex into variable numbers of areas, some approaching as many as 200. An implicit assumption behind these analyses has often been that anatomically distinct subdivisions of the cortex are also functionally distinct. With this as a basis, cortical cartographers did not have to pay much attention to the question of what functions could be assigned to their subdivisions. Although none of the resulting schemas has given a satisfactory, all-embracing account of the anatomical principle underlying cortical organization, something of value has remained from each of them. From an historical perspective, one could argue that these schemas, although using different means, represent a search for an elusive principle that governs the organization of the cerebral cortex, which none was able to fully establish. But But However, the debates that these schemas generated touched on important questions regarding the organization of the cerebral cortex, which remain as relevant today as when first raised.

Broadly speaking, two general goals motivate the anatomy-based attempts to characterize cortical organization. The first is to divide the cortex into a set of anatomically defined areas. In that regard, the most frequently cited map so far has been Korbinian Brodmann's, which divided the cerebral cortex into approximately about 50 areas. A second aim, once a list of areas is

defined, has been to assemble these into larger structures, or networks, based on the anatomical projection patterns among the areas.

The primary and the most commonly referred-to example of a study driven by this second goal is the 1991 paper by Felleman and Van Essen [1] (hereinafter the F&VE paper). Its influence is reflected by the sheer number of its citations, the fairly-wide adoption of some of its central theses, particularly that of hierarchical organization, and the regular use of its summary diagram in public lectures to illustrate the complexities of the brain. At its core, the paper is a meta-analysis of the laminar organization of connections between 32 cortical areas, mostly ones involved in some way or another in visual functions. The authors used the results of cortical connectivity studies to give a new definition of hierarchy in the cerebral, and especially the visual, cortex. Their proposed schema gives each visual area a determined position, derived from this pattern of connections, within an overall ~~“single hierarchy”~~“single hierarchy”.

The theory embraced by the paper is based largely on the organization of the visual cortex, and adopts a principle first enunciated by Rockland and Pandya [2], to the effect that forward connections (i.e., those leading away from the primary visual cortex, area V1) could be distinguished from backward connections on the basis of the laminar organization of their terminations. Specifically, the forward connections emanate from the superficial layers and terminate predominantly in layer 4 of the recipient area, whereas the reciprocal, reverse, connections originate in both superficial and deep layers and terminate outside layer 4. This apparent regularity was subject to certain variations and ambiguities, but such departures from the general principle of a ~~“strict hierarchy”~~“strict hierarchy” did not affect materially the overall schema, or so it was assumed.

Altogether, the authors documented 305 identified pathways in the anatomical literature, with many of these pathways (242) representing reciprocal connections between areas (121 pairs of connections). These numbers reflect, in part, the rapidly growing bank of data on primate cortical anatomy ~~in~~during the 1970s and 1980s. To effectively process this information, the authors took an approach that may seem mundane nowadays but was relatively prescient at the time. First, they generated a computerized database of the connections of the brain areas being examined. Second, given the complexity of the resulting visualizations, they actualized the schema on a graphics-drawing-program that allowed users to inspect the diagram in a flexible manner, for instance by switching on or off each of the areas and its corresponding connections.

The F&VE paper was especially successful in projecting a particular view of the cerebral cortex in general, and of the visual cortex in particular, namely that cortical areas can be allocated a given, unique, position in an overall ~~“single hierarchy”~~“single hierarchy”, based on the identification of forward, backward, and lateral patterns of anatomical connections that they establish with each other. In the visual cortex, the lowest area was taken to be V1 (which receives

visual signals from the retina through the lateral geniculate nucleus (LGN) and feeds the further visual areas in the prestriate cortex surrounding it, and beyond. This, in turn, led to the general belief that there are “tiers” of areas, broadly assignable to the “low”, “middle” or “high” ‘low’, ‘middle’, or ‘high’ level categories, a view especially, and uncritically, espoused by those working on the visual brain’s form system (see [3] for a review of the form system of the visual brain (reviewed in [3])). A general supposition, which seemed to support the emphasized hierarchical strategy, was that the functional properties of cells become more complex in successive areas within a hierarchy, for which the most impressive evidence at the time (outside V1) was the increase in the receptive field size of cells in successive areas.

As has become clear since, and as discussed below, the attempt to channel all cortical connections into a single hierarchical schema faces various significant difficulties. The central and most widely adopted conclusion of the F&VE paper, that regarding hierarchies, was disavowed by Hegdé and Felleman in a review published 16 years later [4], where they wrote, “visual processing neither is hierarchical nor parallels the anatomical hierarchy” and, “and, that while the sustaining strength of the notion of hierarchical processing may be that it is rather simple, its fatal flaw is that it is overly simplistic” [4]. The contrast between this perspective and the one of the F&VE paper, encapsulates, in a way, the novel questions about cortical organization that have arisen during the time between the publication of these two papers.

Below are some of the difficulties around the ‘single-hierarchy’ view of visual processing. The first difficulty relates to the starting point of the proposed hierarchy, namely V1. Positioning V1 at the entry point of the cortical visual hierarchy echoes the age-old supposition that V1 is “the sole -entering place of the visual radiation into the organ of psyche” [8]. In fact, it had been established relatively early on that the LGN [5,6,7] and the thalamic pulvinar nucleus [78] project directly to the specialized visual areas of prestriate cortex, thus bypassing V1. These pathways call into question the very foundation of a visual cortical visual hierarchy — namely V1’s role, namely the role of V1 in it; but not many took much notice of that then (and not many do so now). The existence of the anatomical subcortical-prestriate pathways relates to another important observation, which only became known since after the publication of the F&VE paper, namely the arrival times of signals in the visual brain. Specifically, visual signals arrive in the prestriate areas with the same, or even shorter, latencies than they arrive in V1, depending upon stimulus and task (3) [3]. Moreover, the direct thalamic input into prestriate visual areas such as V5 (MT) is potent enough to sustain a conscious, if crude, experience of directional visual motion (9) [9]. Another difficulty with the ‘single-hierarchical hierarchical’ model relates to the prediction from the hierarchical scheme that “higher” ‘higher’ areas have more complex functions than “lower” ‘lower’ ones. This

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