CLASSICAL PERSPECTIVES

Thirty years of a very special visual area, Area V5

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In the late 1960s, I began to work on a large and ill-defined cortical zone surrounding the primary visual cortex (V1) and known indifferently as the 'visual association cortex'. It seemed to me at the time that the work of Hubel and Wiesel had extracted as much juice out of V1 as was then possible, even though many were still working on it. The 'association' cortex, by contrast, had attracted little attention. My view then was, and remains, that if you want to work in an over-crowded area, be sure to have not only a brilliant experiment in mind, but also one that works.

By 1969, I had already shown that, among the anatomical outputs from V1 in the macaque, is one consisting of large myelinated fibres terminating in an isolated, well-defined, zone of the posterior bank of the superior temporal sulcus, which I subsequently called V5. At that time, the most influential view of how the visual brain functions was that of Hubel and Wiesel. They had supposed that it analyses the world in piece-meal and hierarchical fashion, with cells at successive stages of the visual pathways having ever larger receptive fields and re-analysing the same features at progressively more complex levels. The convergent anatomical output to V5 from the topographically organized V1 was consistent with this view because it led to the emergence of larger receptive fields, one of the requirements of the hierarchical doctrine. But the properties of cells in V5 suggested otherwise. Right from the start, it became evident that these cells were not re-analysing all the information at a higher level of complexity, in spite of their relatively large receptive fields. Instead, they were specialized to process a particular attribute of the visual world, namely visual motion. For all were responsive to motion and the overwhelming majority were directionally selective. Most were indifferent to orientation, giving their optimal response to an appropriately moving spot. All cells were also indifferent to the colour of the moving stimulus and, though many studies have since tried, none has been able to show colour selectivity in V5 (Zeki, 1974). This is not to say that V5 cells are incapable of responding to moving colour stimuli, even if equiluminant, but only that they always respond in a 'colour-blind' fashion.

The last point is crucial. Since the macaque has very good colour vision, it seemed inevitable that colour must be processed elsewhere than in V5, which is specialized for motion. The study of V5 thus provided the foundation stone for the theory of functional specialization (Zeki, 1978) and showed that Hubel and Wiesel's doctrine of exclusive hierarchies was only partially correct, for single subsystems only. Evidently, different attributes are processed in parallel, in different parts of the brain. Since its description, several studies have demonstrated the segregated and seemingly specialized anatomical inputs to V5 and other visual areas, thus providing further, anatomical, bases for functional specialization.

V5 is not unique to macaques but is characteristic of all primates. Allman & Kaas (1971) mapped topographically an area they named MT in the owl monkey, but without characterizing it functionally. Some 10 years later (Zeki, 1980; Baker *et al.* 1981) this area was also shown to have a preponderance of directionally selective cells, though ones that are somewhat more exigent in their requirements than their macaque counterparts. It is therefore an irony that, had I studied the owl monkey instead of the macaque, given as well the owl monkey's impoverished colour vision, I might have just adhered to the hierarchical doctrine of Hubel and Wiesel.

In fact, most subsequent studies have concentrated on macaque and human V5. Of the former, the most impressive have been those of Newsome *et al.* (1989) and colleagues, who have pushed the study of cognitive processes to the single cell level, by demonstrating how the responses of single cells in V5 can affect decision making processes. They have thus also shown that complex cognitive functions can coexist with simple analytical ones in the same cortical area.

My colleagues and I have also used brain imaging techniques to identify V5 in the human brain (Zeki *et al.* 1991*b*) and have shown that it falls within territory that, when lesioned, results in the syndrome of cerebral akinetopsia (i.e. motion imperception) (Zihl *et al.* 1983; Zeki, 1991*a*). Another significant demonstration was that the 'phenomenal' motion seen in some works of art, as in Leviant's *Enigma*, is generated by cortical activity within V5 without engaging V1 differentially (Zeki *et al.* 1993). This raised the possibility that V5 can mediate a conscious perception of fast motion without parallel activation of V1 from which it receives such a major input. This was not altogether outrageous, since Riddoch (1917) had already shown, in a study effectively dismissed by Holmes (1918), that patients blinded by lesions to V1 were still capable of perceiving consciously motion in their blind fields, and anatomical studies had shown that there is a retinal input to V5 that by-passes V1 (Cragg, 1969). Our studies of patient GY (Zeki & ffytche, 1998), since confirmed, have indeed shown that a patient with extensive damage to V1 is capable of perceiving fast motion consciously within the 'blind' field, and that whether he perceives motion or not depends upon the level of activity within V5.

Thus, from demonstrating functional specialization in the visual brain to laying the grounds for the study of complex cerebral functions including consciousness, V5 has proven to be a mine of critical information about the way that the primate visual brain functions. Of course, if I had not discovered and characterized it, others would have in due course. So it was nice to be in the right place at the right time.

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