Parallel versus serial processing: new vistas on the distributed organization of the visual system

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Recent functional studies question the validity of the hierarchical model of organization for processing visual information in cortical areas. The results of these studies suggest that beyond the primary visual cortex (V1), information is not serially processed through successive cortical areas, but that it is simultaneously processed in several areas. The idea that visual information is functionally segregated into different, parallel channels as it circulates through V1 and V2 towards V4 and the middle temporal visual area is also challenged by recent studies that report a smaller degree of functional specialization within the visual areas than previously thought.

Introduction

Since the early days of single-unit recording in visual cortex, the models of cortical processing have vacillated between favoring a serial (hierarchical) or a parallel organization. The hierarchical model, originally proposed by Hubel and Wiesel, was shaped by the current opinion of the time, which postulated that several successive processing steps should separate sensation from perception (see [1•]). In the cat, these successive steps were represented by cortical areas 17, 18 and 19, and by the simple, complex and hypercomplex functional classes of neurons. Thus, the serial model has two main characteristics: first, processing is accomplished through a cascade of effectors (neuron types or cortical areas), and second, progression in the hierarchy corresponds to an increasing 'complexity' of the effectors.

With the discovery in the 1970s that distinct functional types of neurons exist in the retina and the lateral geniculate nucleus (LGN) of the cat, the parallel model of organization gained recognition. X-, Y- and W-type of retinal ganglion cells appeared to provide the major inputs to different cortical areas [2], and lesions or inactivation (e.g. by cooling) of area 17 did not silence neurons in area 18, as would be expected if these areas operated in an hierarchical cascade [2,3]. Parallel models placed the emphasis on independent and simultaneous processing by modules that are specialized for different aspects of the visual stimulus.

The shift of interest from cat to monkey cortical anatomy and physiology in the 1980s brought back the concept of a hierarchical organization of cortical areas. This followed the early observation of Rockland and Pandya [4] that different types of cortico-cortical connections, later called feedforward and feedback, can be distinguished by the laminar distributions of the parent neurons and target terminal arborizations. Identification of feedforward and feedback connections led to a hierarchical classification of cortical areas by the following criterion: higher-order areas receive feedforward connections and send feedback connections to lower-order areas [5].

At the same period, the idea that magnocellular and parvocellular layers of the LGN process different types of information in parallel became prevalent. In cortex, cytochrome oxidase staining revealed the presence of modules — blobs in cortical area V1 and bands in cortical area V2 — that appeared to operate in parallel.

All these findings lead us to a textbook picture of the organization of the visual system (Fig. 1), which is a hybrid of serial and parallel processing: namely, parallel channels operating within a hierarchy of cortical areas. This review examines recent findings concerning parallel and hierarchical processing in visual cortex, and it will become apparent that this hybrid model does not correspond with reality.

Is there a hierarchy of visual cortical areas?

The major weakness of the hybrid hierarchical/parallel model is that it is based solely on anatomical observations. Functional studies provide little support for a hierarchical (serial) organization of extrastriate cortical areas.

Abbreviations

K—koniocellular; **LGN**—lateral geniculate nucleus; M—magnocellular; **MT**—middle temporal; P—parvocellular; **PMLS**—postero-medial lateral suprasylvian; **V1**—primary visual cortex.
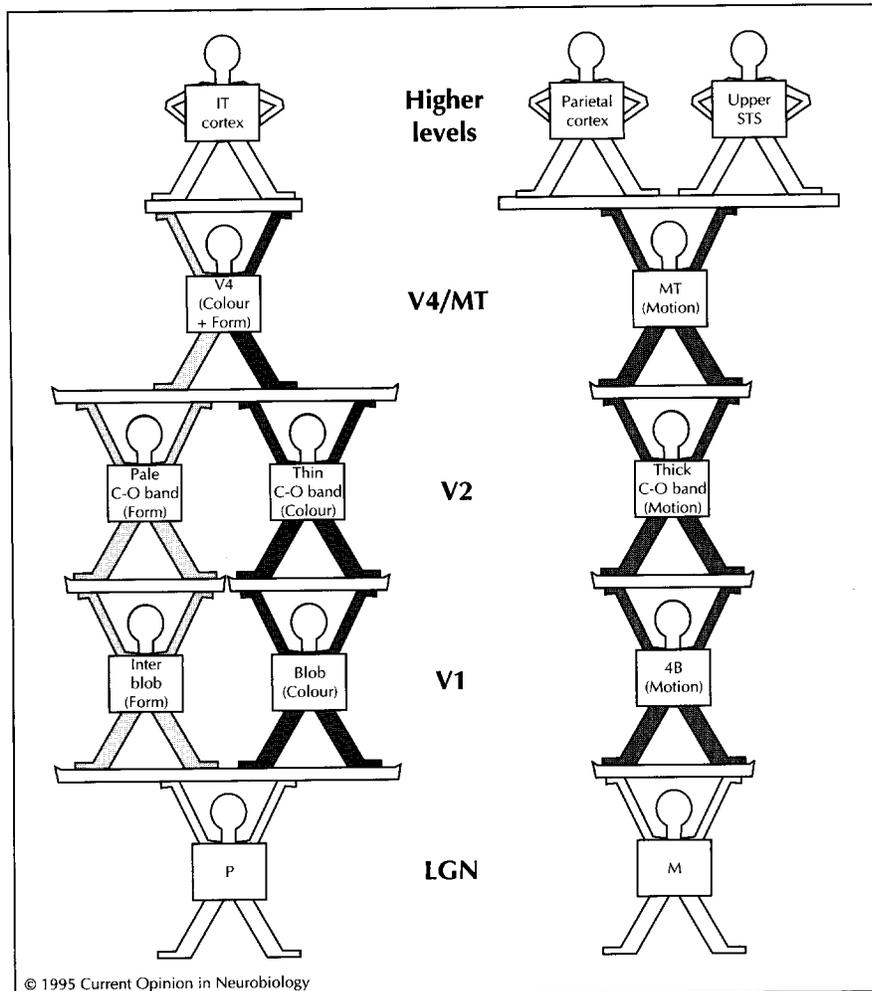
Fig. 1. Cartoon representation of the hybrid hierarchical/parallel model. For a more exact and detailed description, see [5]. Neurons of the parvocellular (P) and magnocellular (M) layers of the LGN give rise to parallel channels that circulate through area V1 and extrastriate cortex towards higher-order areas. The P pathway is supposed to give rise to two channels, one for the processing of color and the other devoted to form. These channels are associated to different cortical territories identified by cytochrome-oxidase (C–O) histochemistry and lead to V4 and interotemporal (IT) cortex. The M channel is supposed to circulate in parallel to the P channels, to be devoted to motion processing, and to innervate area MT, the parietal and upper superior temporal sulcus (STS) cortex. 4B, layer 4B of V1.

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Serial processing: effects of lesions or inactivation of lower-order areas

A serial organization assumes that information is processed at each step before being sent to the next level up. One way to test this mode of operation is to lesion or inactivate a lower-order area to determine whether this silences neurons in higher-order areas. This has only been tested in the V1 area of monkeys, which, when inactivated, silences areas V2, V3, V4 and the inferotemporal cortex [3,6–10]. These electrophysiological results are complemented by behavioural data: lesioning area V1 produces a marked visual deficit (see [11]). Interestingly, it has been shown that with re-training, these V1-lesioned animals can recover some form of vision [12], even though they appear to have no 'conscious' perception of the stimulus they can detect [13•].

A possible explanation for this form of residual vision is that there appears to be some remaining neural activity in other extrastriate cortical areas. Lesioning or inactivation of area V1 decreases the response and lowers the selectivity of neurons in area V3A, the middle temporal (MT) area and the superior temporal polysensory (STP)

area, but does not silence them [14,15]. A similar finding has been reported in humans who have damaged V1 areas; despite the fact that no activity is recorded in the V1 area of these patients, a cortical region corresponding to area MT in monkeys appears to be active [16]. This residual activity in humans may be the functional basis of the phenomenon of blindsight [17,18].

Lesion and inactivation studies have thus confirmed the special status of V1 as the first relay for visual information coming from the thalamus and directed toward the inferotemporal cortex (see Fig. 1). However, this is not the case for the transfer of information directed toward the parietal cortex (see Fig. 1). Beyond V1, area V2 is the second relay of visual information in the hierarchy. Does this mean that inactivation of V2, like that of V1, will silence other higher-order extrastriate areas? This question has not been addressed directly. However, lesioning V2 in monkeys had little consequence on the visual abilities of the animal and only produced a very specific deficit in the detection of pop-out stimuli based on orientation differences [11]. The specificity of the deficit caused by lesioning V2 contrasts with the almost total blindness caused by lesioning V1 [11,13•].
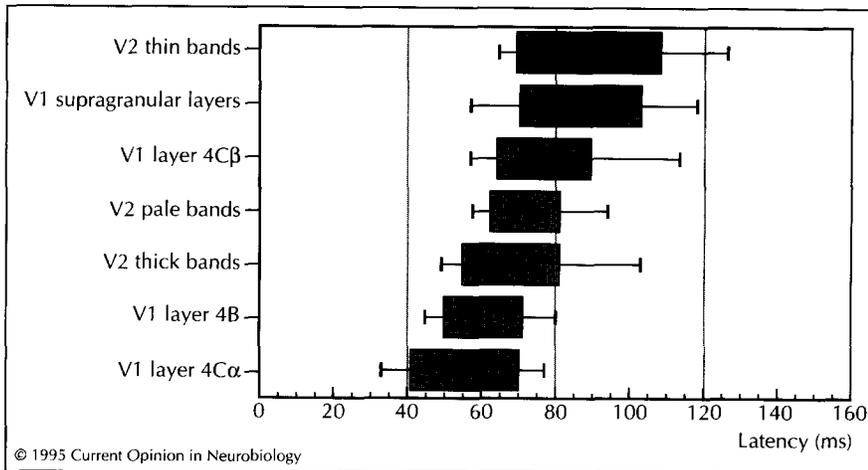
Fig. 2. Latency distribution of neurons in different layers of V1 and V2 responding to visual stimulation. The grey horizontal rectangles represent the range of latencies corresponding to the 25th–75th centile of activated neurons (vertical bars correspond to the median). The small horizontal bars extruding from the left and right side of the rectangles correspond to the latencies for the 10th and 90th centile of activated neurons, respectively. Note that the order of activation does not follow a serial V1-to-V2 order, but is heavily influenced by the type of LGN input (magnocellular to 4Cα and parvocellular to 4Cβ). See [30•,31•] for further details.

This suggests that complete inactivation of V2 will not silence neurons in other higher-order cortical areas, and that, based on the criterion mentioned above, area V2 is not a lower-order area than V3, MT or V4, as proposed by the hierarchical model.

The role of V1 as the major relay of visual information is specific to primates because in non-primate species, lesioning or inactivation of area V1 does not silence other cortical areas. For example, in cats, although inactivation of V1 strongly decreases the responses of most neurons in area 21a, other neurons are little affected [19]. It also has been known for some time that lesioning cat V1 does not silence the responses of neurons of the suprasylvian sulcus [20,21] and that inactivation of V1 does not silence neurons in area 18 [22,23].

The mild effects of area V1 lesions on the activity in other cortical areas of the cat are in contradiction with the predictions of the hierarchical model because, in cats, as in monkeys, area VI occupies the lowest level in the hierarchy [5]. These electrophysiological results are paralleled by the small and specific visual deficits observed in cats after such lesions [24,25]. As has been argued elsewhere [3], the devastating effects of V1 lesions on vision observed in monkeys and humans is a feature unique to primates, which may be related to the more focussed LGN projections to the cortex.

To summarize, lesion or inactivation studies confirm the serial or hierarchical model of cortical processing only in the case of V1 in primates. In other cortical areas and in other orders, it appears that the hierarchical ranking of cortical areas based on the anatomy does not constitute a proper model of the functional visual system.

Serial processing: timing

Another way to test whether cortical areas process information in a serial fashion is to measure the latencies with which neurons in different cortical areas respond to visual stimulation. If information is indeed processed serially, then the latencies of higher-order areas should

be longer than those of the lower-order areas that drive them. Latencies are measured by flashing small spots of light at or by moving stimuli across the receptive fields of visual neurons. Such experiments revealed that there is a very large range of latencies within each cortical area, and that the timing of the latencies overlaps extensively across different areas [26–29].

The latencies in both area V1 and area V2 of the macaque monkey have recently been measured under the same stimulus conditions [30•,31•]. The results show a large overlap of the latency distributions, with V1 neurons activated, on average, 10 ms earlier than neurons in V2. When the neuronal populations of the various channels that stream through V1 and V2 are analyzed separately (see below), it is found that the serial order between V1 and V2 is not the major determinant of the latency differences observed between these areas. Figure 2 illustrates the distribution of latencies in different layers of V1 and different cytochrome oxidase bands in V2, arranged in increasing order (see [30•,31•]). This demonstrates that the earliest activated neuronal populations are in layers 4Cα and 4B of V1 and the thick cytochrome oxidase bands of V2, all territories that are almost exclusively under the control of the magnocellular layers of the LGN (see Fig. 1). After most of the magnocellular-driven activity has left V2 through projection neurons in the thick cytochrome oxidase bands, layer 4Cβ is activated by LGN neurons of the parvocellular layers. This is followed by the bulk of responses in the supragranular layers of V1 and the thin cytochrome oxidase bands of V2.

These results demonstrate that latencies in V1 and V2 overlap extensively and that the latency difference between magnocellular and parvocellular-driven populations is larger (20 ms) than the latency difference between V1 and V2 neurons (10 ms). Although neurons in V2 depend upon V1 for their activation [6,7], there are many neurons in V2 that are active earlier than some V1 neurons; therefore, these 'early' V2 neurons are in a position to drive some of the 'later' V1 neurons. The work of Sandell and Schiller [32] on the inactivation of

V2 confirms that some V1 neurons depend upon V2 for their visual responses.

A few studies have been devoted to the latencies of neurons in area MT. Raiguel et al. [26] found that the median latency of MT neurons is 9 ms longer than that of V1 neurons, and that the shortest latencies in area MT are even shorter than those in V1 or V2. Measuring the latency of the average post-stimulus time histogram of neurons in areas MT and V1, Maunsell [33] concluded that activation of area MT is delayed by 11 ms with respect to activation of the transient neurons in V1. It is interesting to compare these results with those measuring corresponding populations in V1 and V2: the latency difference between the shortest (10th centile) latencies in layer 4Cα in V1 and the thick cytochrome oxidase bands of V2 (10th centile) is 16 ms (Fig. 2). This suggests that MT neurons are activated at the same time as, and possibly earlier than, the neurons in the thick cytochrome oxidase bands of V2, which is in keeping with the results of Raiguel et al. [26] described above. Thus, neurons of the 'second' (V2) and 'fifth' (MT) stages of the proposed hierarchical arrangement of extrastriate areas are activated simultaneously. Therefore, it seems unlikely that MT neurons depend on input from V2 in the same way that neurons in V2 depend upon input from V1. In other words, there is no physiological evidence that MT is a higher-order area than V2.

Measuring latencies in cortical areas of the cat visual system lead to a similar conclusion [34•]. Despite its position as a second-order area in the cortical hierarchy, area 18 contains the earliest activated cortical neurons, some 5 ms earlier than neurons of area 17 [34•]. This probably results from the fact that area 18 is mostly driven by Y cells, which have shorter latencies than X cells in the retina [35]. Thus, in the cat visual cortex, as in the monkey visual cortex, the type of thalamic afferent (X/Y or magnocellular/parvocellular) appears to be a stronger determinant of the latency with which a cortical neuron responds to activation than the supposed rank of the cortical area it belongs to.

In addition, the latencies of activation in the cat visual cortex clearly differ from those predicted by the hierarchical ranking of areas. In the hierarchical scheme, the order of activation should be areas 17, 18, 19, PMLS; however, the order given by the latencies is 18, 17, PMLS, 19 [34•]. This means that the hierarchical scheme is of little help for predicting the temporal sequence of activation of cortical areas.

Is processing done in parallel?

There is strong anatomical and physiological evidence that three separate channels transfer information through the LGN toward visual cortex. These are called M (for magnocellular), P (for parvocellular) and K (for koniocellular) channels. It has been demonstrated by electrophysiological and lesion studies that, although most stimuli activate all three channels, information about color and high spatial frequency is carried by the P channel, and that information about high temporal frequency and low contrast are carried by the M channel [36–40].

It has previously been suggested that the P and M subcortical channels remain separate in cortex [5,41]. The P pathway was supposed to separate into two branches through areas V1 and V2 towards area V4. The first branch, circulating through layer 4Cβ, the cytochrome oxidase blobs in V1 and the thin cytochrome oxidase bands in V2, was supposed to carry color information. The other branch, passing through layer 4Cβ, the interblob regions in V1 and the pale cytochrome oxidase bands in V2, was associated with the processing of form. The M pathway was thought to circulate almost exclusively through layers 4Cα and 4B in V1 and the thick cytochrome oxidase bands in V2, to activate area MT and to be devoted to the processing of motion information. The concept of functional parallel pathways in areas V1 and V2 (Fig. 1) is, therefore, based on two assumptions: first, that pathways remain separate in areas V1 and V2, and second, that the channels in V1 and V2 and extrastriate areas beyond V1 and V2 are specialized processors for certain aspects of the visual stimuli.

Are M and P pathways segregated in areas V1 and V2?

Recent anatomical studies have demonstrated that there is far more convergence of the M and P pathways in V1 and V2 than previously thought. M, P and K channels converge in the cytochrome oxidase blobs, and the M and P channels converge in the interblobs of V1 [42,43,44••]. In V2, extensive interconnections between the different cytochrome oxidase bands have been demonstrated [45••,46••].

Physiological studies using selective inactivations of M and P layers in the LGN confirm that many neurons of V1 receive converging information from M and P pathways [47,48•]. The M and P inputs to the interblobs in V1 may explain why many neurons in pale cytochrome oxidase bands in V2 respond to colored stimuli [49,50••] and at low luminance contrast [50••], and why neurons in area V4 appear to be equally driven by M and P neurons of the LGN [51••]. The similar responses of neurons in V4 and MT neurons to fast moving stimuli [52•] may also result from the strong M channel input into V4.

On the other hand, despite the evidence of a P-dominated layer 4A input to the thick cytochrome oxidase bands and strong interconnections of the bands in V2 [45••], the concept of a relatively pure M channel circulating through layers 4Cα and 4B in V1 and the thick cytochrome oxidase bands of V2 toward MT has been confirmed by physiological studies [52•,53–55]. Responses of MT neurons are little affected by the inactivation of P layers [53]. MT neurons give good

responses to flicker and fast moving stimuli and show high contrast sensitivity [52•] and poor responses to chromatic contrast [54,55], all properties expected from neurons of the M channel. The results of latency studies described above (see also Fig. 2) provide evidence that, in addition, the M pathway is characterized by early activation and fast information transfer.

Functional specialization of channels and cortical areas

One of the strong arguments in favor of a specialized color channel through the cytochrome oxidase blobs in V1 and the thin bands in V2 was the presence of numerous color-selective neurons among the non-orientation selective cells in the blobs in V1 and the thin bands in V2 [41,56,57]. It is clear, however, that color-selective neurons are also present in large numbers in the interblobs in V1 [56,58] and in the pale bands in V2 [50••].

When the receptive field properties of neurons in the different cytochrome oxidase bands in V2 are measured quantitatively, it is found that all types of selectivities are found with varying proportions in each set of cytochrome oxidase bands. Thus color-selective neurons are more numerous in thin and pale cytochrome oxidase bands [49,50••], and orientation-selective neurons are found in larger numbers in thick and pale bands [50••,59]. Direction-selective neurons are more numerous in thick cytochrome oxidase bands ([49,50••]; see, however, [59]). Thick bands also contain larger proportions of depth-selective neurons, as originally proposed by Hubel and Livingstone [41]. However, the earlier report that end-stopped cells are concentrated in the pale bands [41] has not been confirmed [50••,59].

Thus, recent reports do not confirm the original view that form, color, motion and depth are processed in parallel channels in areas V1 and V2. Beyond V2, areas V4 and MT are usually presented as examples of functional specialization for motion and color, as evidenced by the presence of numerous direction-selective neurons in MT and color-selective neurons in V4. A recent report confirms that neurons in MT show little selectivity for color [54]. However, as mentioned above, the responses of neurons in V4 and MT to moving stimuli appear similar in terms of velocity selectivity [52•].

The results of lesion studies suggest that areas V4 and MT are not specialized processors for color, form and motion. Long-term effects of lesions in area MT and the surrounding cortex in the superior temporal sulcus on motion perception are rather mild [60,61•]. In a similar way, lesioning area V4 does not lead to a long-term impairment of color and shape discrimination [60,62]. This demonstrates that motion, color and shape information can be processed in the absence of areas V4 and MT, and that these areas can no longer be regarded as the sole specialized processors for these

attributes of visual stimuli. It should be noted, however, that the short-term effects of lesions on behavior are much stronger [60,63]. The significance of such rapid post-lesion recovery remains to be determined. To circumvent these difficulties related to post-lesion recovery, it is possible to use reversible inactivation methods to test the participation of a given cortical area to visual behaviour. Using such methods, Lomber, Payne and co-workers [64••] have demonstrated a total but reversible deficit in the identification of visual cues masked by moving visual noise when the lateral suprasylvian (LS) area of the cat cortex was reversibly inactivated.

Conclusions

Recent work on the visual system suggests that the organization of cortical areas is neither serial nor parallel. Beyond the well known fact derived from lesion studies that area V1 is a bottleneck for visual information in primates, there is no strong evidence from functional studies that visual information is processed serially through a hierarchy of extrastriate cortical areas. Instead, measurements of visual latencies in different cortical areas suggest two characteristics of processing visual information: first, that the order of activation does not necessarily follow the order suggested by the anatomically defined hierarchy of cortical areas; and second, that there is much more *simultaneity* of processing in the different visual areas than would be expected from a strictly serial organization. This simultaneity suggests that not only feedforward but also feedback connections may play a role in establishing some receptive field properties and, ultimately, in perception, as suggested by recent theoretical studies [65–67]. To further characterize the nature of the information transfers through these connections, one could inactivate specific extrastriate visual areas and measure the responses of neurons in the connected areas. Such studies would help us understand the complexity of the flow of information in visual cortex.

The concept of parallel organization, which implies a segregation of channels and a specialization of cortical areas, has also been challenged by recent studies. First, channels kept separate at the level of the retina and thalamus appear to *converge* on the same cells in area VI and beyond, in the occipito-temporal pathway. Second, information about color, motion or form appears to be distributed among different cortical areas. This *distributed* processing is confirmed by functional studies in humans, which show that not only one, but several cortical regions are specifically activated by one of the parameters (i.e. color, or motion, or form) of the stimulus [68,69]. It is currently postulated that it is through the interactions between these modules that perceptual decisions can be made [65–67,70].

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