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Parallel Convergences: A Glimpse To The Magno- And Parvocellular Pathways in Visual Perception

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***Abstract*— The processing of an image, which begins in the retina and continues on the cortex, is provided by two distinct, parallel cellular pathways: the parvocellular (P-) or sustained system, and the magnocellular (M-) or transient system. The P-system is made of small ganglion cells and arranged in receptive fields of small size. In turn, the M-system, is made of larger ganglion cells making up wider receptive fields. Like their anatomical features, also the information carried by the M- and P-cells is different and basically complementary, at least at the subcortical level. A common opinion in the last decades supports the idea that a model based on this parallel M/P complementary processing of the image may account for the various aspects of visual perception. Yet, tracing separately M- and P- information beyond the striate cortex turns difficult due to the diffuse anatomical crossroads, functional intermixing, and to the overlapping of the psychophysical response. The present paper aims at making the point on this issue, pinpointing the already reported caveat for an attractive, albeit probably too simplified (and therefore potentially misleading) schematization.**

***Index Terms*— Color, Contrast Sensitivity, Magnocellular, Motion, Ocular Movement, Parvocellular, Shape. Stereopsis**

I. INTRODUCTION

It is commonly accepted that visual perception relies on two different anatomical and functional domains: the parvocellular and the magnocellular system.

Magnocells make up only about 5-10% of the ganglion population, while parvocells constitute almost 90% of the retinal neurons (1, 2) .

On the retina parvocells, that are specialized for the recognition of stimuli at or around the fixation point, localize mainly in the central region (the macular area) and their number tends to decrease with eccentricity. In turn, the number of magnocells reaches a peak more peripherally (3), so that the topographical transition from one quota to the other occurs in a progressive manner.

It is worth considering that the density of both types of neurons peaks close to the fovea (4), and if the overall amount of P- exceeds the amount of M-cells even in the periphery, the receptive fields of the latter cover a retinal surface 10 times wider (5).

From the retina each of the two systems projects onto specific regions in the lateral geniculate nucleus (LGN). Here the retinal parvocells synapse with the small ganglion neurons located in the four external layers while the magnocells synapse with the large ganglion cells placed in the two most internal layers (Fig.1).

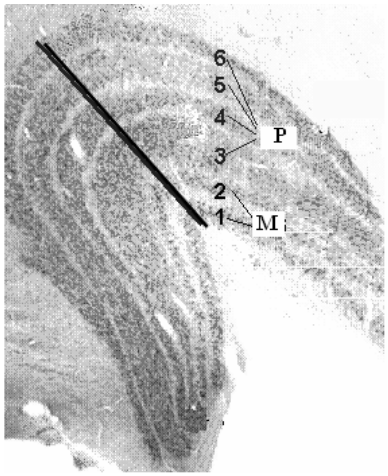

Figure 1. The lateral geniculate body. The inner two layers are composed of M cells, the remaining four external consist of P cells.

From the lateral geniculate body the transmission of the visual input continues and reaches the striate cortex (area V1). Up until this point the information processed by each of the two systems is carried separately (6, 7), so that the M-axons are directed to the lamina 4C and from here to 4B, while the parvocellular projections reach the lamina 4C and from here to the blobs and interblobs (8-10).

From the layer 4B of V1 the magnocellular stream continues towards the thick stripes of the extrastriate area V2 (11), while from the blobs and interblobs the P-pathway synapses with neurons of the thin and pale stripes of V2 (8).

From the thick stripes in V2 the M-pathway carries the information to the middle temporal area (MT, V5 in the macaque), from here to the medial superior temporal area (MST in the macaque), and finally to the posterior parietal cortex (PPC). In turn, the P-pathway connects the thin and pale stripes in V2 to V4 (12, 13). From V4 the signal is projected to the inferotemporal cortex (IT, Fig. 2 and 3).

The P-pathway on the cortex is also known as the temporal or ventral or the "what" stream, being in charge of object recognition, including their fine details, color and shape. In turn, the M-pathway on the cortex is also known as the parietal or dorsal or the "where" stream, being in charge of spatial localization, especially of moving targets.

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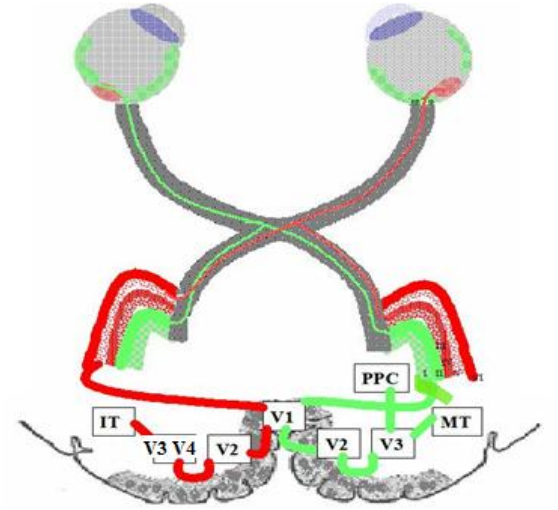

Figure 2. Schematic representation of the visual pathway. In red is represented the parvocellular, system starting on the retina from the small ganglion cells, mainly localized in its central region (the fovea), organized in receptive fields of small size.

The fibers of each P cell are collected in the optic nerve and meet with those of the contralateral eye in the optic chiasm. Here, the outermost portion (temporal) continues its course in the homolateral optic tract while the remaining inner fibers (nasal) cross those of the other side (decussation) and then continue in the contralateral optic tract. At the end of the optic tract both nasal and temporal parvocellular axons project to the lateral geniculate body, a layered structure made up of P cells in the more dorsal portions (layer III, IV, V, VI). Here the transmission of the parvocellular input is transferred to the geniculate P cells and finally reaches the striate cortex, area V1, via the optical radiation. From V1 the stimulus continues in V2, V3 and eventually in the inferotemporal area. In green is the magnocellular pathway beginning from big retinal ganglion cells, mainly localized in the peripheral areas, organized in large receptive fields. The M projections are similar to those described for the P pathway: magnocellular fibers gather in the optic nerve, reach the chiasm where the nasal portion decussates while the temporal one remains on the same side and meets with those of the contralateral eye.From the right and left optic tract, M fibers get to the more ventral layers of the lateral geniculate body (layer I-II). Here the impulse is elaborated by M geniculate receptive fields, along the optical radiations it reaches the striate cortex, area V1, then V2, V3, and finally the mediotemporal area (MT or V5) and the posterior parietal cortex (PPC).

The magnocellular and parvocellular pathway show functional peculiarities that have been extensively investigated in the last decades (e.g. 11, 17-21). Such functional peculiarities make each of the two ganglion systems specialized to separately analyze the features that characterize the stimulus (like speed, spatial frequency, shape, color, texture). Subsequently these decoded characteristics can be integrated according to a cortical hierarchical process.

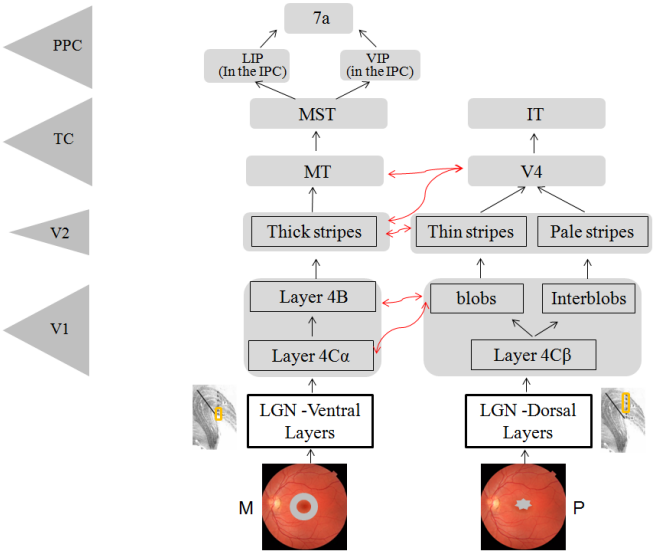

Figure 3. The magnocellular and parvocellular pathway. In red are reported some cross-connections.

In the next pages the characteristics and functions of the two systems will be briefly described, underlining on the one hand the importance of their complementary, cooperative perceptual analysis, on the other hand how some important requisites like the visual persistence or the fine balancing proper of the saccadic/fixation sequence during reading can be explained by their reciprocal inhibitory modulation.

A. Discharge rate and conduction speed

The response of the parvocells to abrupt changes in luminance is tonic (22, 23). In addition, since their axons are scarcely myelinated, parvocells show low conduction speed (22, 24). Due to these characteristics the P-pathway is suitable to process the details of static stimuli: so, the parvocellular system is also referred to as the "sustained system".

In turn, the discharge rate of the M-cells is phasic, showing a peak when a stimulus appears, followed by an abrupt drop of the response to its disappearance. Being highly myelinated, the M-axons show high conduction speed (22). For these reasons, the M-system is defined the transient system, able to process dynamic configurations.

As pointed out by Skottun (25), the terms magnocellular and parvocellular belong to the physiological field, whereas in psychophysics sustained and transient would be preferable. However, the words magnocellular and parvocellular are now customary.

B. Contrast sensitivity

Individually, parvocells are less sensitive to spatial contrast compared to magnocells. The former, in fact, are not able to respond to a contrast less than 10% (26) while the latter are still sensitive to contrasts as low as 2%, (26, 27). Yet, due to the spatial summation among the overwhelming

number of P-cells compared to M-detectors, contrast sensitivity of the sustained system reaches 0.5%, being therefore comparable to that of the transient pathway (28, 29).

Parvocells show best contrast sensitivity at high spatial frequencies and low temporal frequencies, especially in photopic conditions. This fact makes them suitable for the analysis of the details of images projected onto the foveal region, but (as a consequence of their tonic response) unsuitable for the detection of rapid temporal changes (motion perception). On the contrary, especially at low luminance levels, the M-system shows higher contrast sensitivity at low spatial frequencies and high temporal frequencies, which makes it less sensitive to details and highly sensitive to rapid changes over time (27, 30- 32).

Important contribution for understanding the functions of the two ganglion subsystems has been provided by deprivational studies focused on the lateral geniculate body of the cat and monkey. The selective destruction of the inner layers of the LGN, pertaining to the M system, revealed reduced contrast sensitivity when serial configurations were displayed at very low spatial and high temporal frequencies (33, 34): for example, gratings of 1 cycle/degree flickering at 10 Hz (33). In this experimental condition a consistent functional segregation of the M pathway is expected, whereas presenting stationary stimuli or gratings with low temporal frequency does not prevent from the concomitant stimulation of the P pathway, irrespective of the spatial frequency adopted.

The same occurs with gratings of high temporal frequency but with spatial frequency not low enough (28, 35, 36).

In turn, reduced contrast sensitivity at high spatial and low temporal frequencies after lesions of the parvocellular pathway confirms the P-pathway is preferentially activated by stimulations belonging to this spatiotemporal domain (28, 33, 36).

Still, after selective destruction of the geniculate parvocellular layers Merigan and Eskin found defective contrast sensitivity with stationary gratings also at low spatial frequencies (as low as 0.5 c/deg), that is to say in the magnocellular spatial domain (28). This finding confirms that even in the magnocellular domain the P-system takes part in the processing of the stimulus. The parvo-mediated deficit, however, is shown to fade as the temporal frequency is increased.

It follows that in viuew of the fact the P-response is saturated for spatial frequencies of about 1 cycle/degree and temporal frequency beyond 10 Hz, (with due caution) a grating with spatial frequency lower than 1 cycle/degree and temporal frequencies equal or higher that 10 Hz should be considered as the most effective combination to segregate the magnocellular function.

The normal contrast sensitivity function (CSF) and the contribution provided by the magnocellular and parvocellular system is shown in Figure 4.The curve depicted in the left panel is the result of the joined activity of the M system, mainly effective at the lowest spatial frequencies and of the P system, especially sensitive to the highest spatial frequencies. The optimal cutoff to differentiate the P/M function in the spatial frequency domain is set around 1.5 cycles/degree (37) or between 0.2 and 3.5 cycles/degree (38).

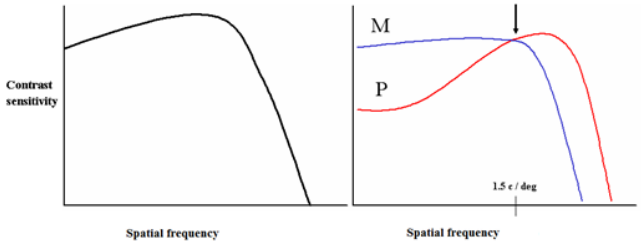

Figure 4. Left: CSF for spatial frequencies from 0.75 cycles/degree to 18 cycles/degree. Right: individual CSF of the M- and P system, sensitive to low and high spatial frequencies, respectively.

The transition point is set around 1.5 cycles/degree and marked by the arrow. Above this value of spatial frequency, the P system is mainly active, under this value it depends on the M system.

From the figure it can be deduced that reduced contrast sensitivity at low luminance for gratings with spatial frequency less than 1.5 cycles/degree is sign of prevalent malfunction of the M system, because the P activity is weaker in these conditions of stimulation. However, the result of the combined M+P functions shows that even when processing very low spatial frequencies the magnocellular system is joined by the parvocellular activity to a certain amount so that, due to this large overlap of the M/P functional architecture, this cutoff must be considered with caution. The selectivity of the M system can be increased presenting stimuli not stationary, but shifting or reversing at high temporal frequency, even more under low mean luminance levels.

A main reason why as a matter of fact segregating the transient from the sustained function is difficult, is that even if the activation level of each P-cell is lower compared to the M cells, due to spatial summation the cumulative activation threshold of the parvocellular system is lower compared to the magnocellular pathway (21, 26, 31): as a consequence the former tends to respond to a broader spectrum of frequencies than expected based on the CSF.

Indeed, selective lesions of the P-system reduce contrast sensitivity not only at the higher spatial frequencies, but less selectively and to a certain extent even at the lower ones (1 cycle/degree: 35, 39; 2 cycles/degree: 36). In other terms, as pointed out by Skottun, the effect of the sustained pathway is overwhelming, so that its deprivation ends up suppressing not only the response in its own domain but even in the transient spectrum (25).

C. Visual Acuity

In a lesion study selective parvocellular damage determined tree-four-fold reduction of visual acuity, while M-ablation did not achieve any appreciable effect (36). Yet, contrary to what expected, the spatial resolution of individual P- and M-cells is similar irrespective of the eccentricity (40), despite at any eccentricity the receptive fields of parvocells have smaller centre (and less diffuse dendritic spreading: 41) than the magnocellular units (31, 42,, but see 7, p. 374 for

counter-evidences). So, the superiority of the parvocellular system in processing visual acuity is believed to depend on the higher parvocellular density (43) (P vs M density: 8:1 according to Perry et al (44).

D. Color

Color perception stems from the L ("red"), M ("green"), and S ("blue") cones in the retina, showing a peak wavelength respectively at 562, 535, and 440 nm. After transduction, their wavelength is processed by red-green (L- vs M-cones) and blue-yellow (S- vs L+M-cones) color-opponent receptive fields on the retina, then on the lateral geniculate nucleus, and finally on the striate cortex.

Color perception is probably the most effective marker of the parvocellular activity, since P- but not M-cells show color opponency: in other terms parvocells (but not magnocells) respond selectively to isoluminant colored stimuli (31). As a matter of fact, lesions of the parvocellular pathway lead to loss of color perception (35, 45).

On the cortex the ventral stream is in charge of color perception trough the blobs in V1, the thin stripes in V2 and finally V4 (e.g. 46; see also 7).

As recalled by Roe et al (47), if the generation of color perception depends on the wavelength-selective cones and the subsequent color-opponency processing provided by dedicated parvocellular receptive fields, for the perception and ability to discriminate the hues the thin stripes in V2 play a fundamental role (48).

The pivotal function of V4 in color perception has been claimed since the early Seventies (49) and further supported by experimental evidences (50-52). Even if lesions involving bilaterally V4 demonstrated slight (albeit permanent) deficit in color perception (53, 54), the contribution of V4 in this respect seems crucial and far more complex than believed. On the analogy of the blob-color sensitive neuronal clusters of V1, the regions (several millimeters wide) of V4 narrowly tuned for hue, therefore functionally associated with color processing, have been named by Conway et al "globs" (it follows that the "interglobs" are the interleaved no-glob regions: 55).

V4 is advanced to be essential for color constancy that is to correctly judge the color of an object under different environmental illuminations. Difference in the illumination, in fact, can change the wavelength composition of the light reflected by the object: in other terms, as exemplified by Roe et al (47), thanks to V4 "a red apple remains red whether it is in shadow or under sunlight" The goal would be obtained since V4 color-responsive neurons would shift their spectral tuning as a function of the illumination of the environment (46, 56). As a matter of fact, neurons in the globs are found to be tolerant to luminance variation (55).

In addition, V4 is sensitive to forms defined by equiluminant color-contrast borders (57).

The processing of color would be integrated beyond V4, since also in the inferotemporal cortex (IT) the majority of the neurons are found to be sensitive to color (see for example: 58).

E. Shape

Shape perception is considered a function processed by the parvocellular system, that takes place on the cortex in the thin and pale stripes in V2, continues in V4 and ends in the inferotemporal cortex. Lesions involving bilaterally V4 demonstrated to a certain extent deficit in shape and texture discrimination (53, 54). In the so-called "interglob" regions of V4 (55) neurons are sensitive to orientation (59): as recalled by Roe et al (47), since curvature processing is considered as an integration of the orientation response of the neurons whose receptive field (2-10 deg wide) receives the input, interglob neurons in V4 can be regarded as contour analyzers and, finally, as shape detectors (60). Unlike lower-level orientation tuned neurons, in V4 detectors respond optimally to acute convex and concave curvatures (61), with a marked bias toward the former (60). In addition, at a higher cortical level, the inferotemporal cortex (IT) is found to be particularly sensitive to specific shapes like snakes, flowers-like forms, hands, and even faces, as well as textures (62).

F. Motion

Motion perception is considered as the most effective marker of the magnocellular activity.

As expected from its high sensibility to temporal contrast, the transient system, indeed, plays a pivotal role in processing dynamic configurations. A selective lesion of the transient system in the inner (M-) layers of the lateral geniculate body reduces motion sensitivity of the macaque (33-35, 39, 63). As a matter of fact, Schiller found a deep loss of motion perception after ablation (obtained by injecting ibotenic acid) of geniculate M-neurons of the macaque but not after destruction of geniculate P-cells (35, 39).

Motion processing on the cortex follows the dorsal stream and starts from the thick stripes in V2, a magnocellular domain where direction selective neurons have been found (64).

As far as we know, the higher-level processing regions of motion perception are the mediotemporal area, also called MT or V5, and the middle superior temporal area (MST: 65), both characterized by the large size of their magnocellular receptive fields.

Studies in macaques showed that about 90% of the cells of MT are direction sensitive (66), so that a selective lesion of the transient system on the mediotemporal (MT) and medial superior temporal cortical region (MST) makes the animal less sensitive or insensitive to dynamic configurations (65, 67, 68).

It has been suggested that the relationship between motion perception and magnocellular system simply depends on the fact that the M-cells see (that is detect) better fast moving stimuli compared to the parvocells. Based on this property, the judgment of the position of the target over time provided by the magnocells would be more accurate, so it would be the perception of its movement (7). If it were the case, according to Merigan & Maunsell, it follows that "the M pathway is not

specialized for motion perception, but is specialized for the transmission of middle and high velocity stimuli that are important to some functions of the parietal visual stream" (7, p.394).

According to a more sophisticated perspective motion perception in MT derives from a mechanism of signal integration in both the temporal domain and visual space: Mikami, in fact, showed in monkeys that neurons in MT are sensitive to motion when it is simulated by using a high number of presentations, while they do not respond if just two kinematograms are displayed (69).

At a higher cortical level (area MST) neurons of the M-system are found to respond to complex types of motion, like the rotatory and translational components of the optic flow (70).

Even if motion has been considered as a function mediated by the transient system, a body of research suggests the ventral stream may play a role as well.

Directions selective neurons have been found not only at the early stage of the dorsal stream, that is in the thick stripes of V2, but (to a lower extent) even in the pale stripes of V2, that is in a cortical station along the ventral stream (64). Moreover, at a higher cortical level up to one third of the neurons in V4 are found to be directionally selective (71).

Yet, the meaning and role of motion processing provided by the ventral stream is argued to be substantially different from the classical information coded by the dorsal pathway: V4 would process not motion per se, but more strictly motion differentiation, being suitable for detecting difference in the dynamic component of a moving object compared to the (static) environment. Accordingly, motion differentiation can be regarded as the way to discriminate a moving figure from the background. In the final analysis, directionally selective neurons in V4 make motion a tool for the recognition of the characteristics of dynamic stimuli (71, see also 47).

G. Stereopsis

Stereopsis or depth perception derives from the small positional differences between the corresponding visual features projected to the two eyes. Even if such binocular disparity has been found as early as in neurons of the striate cortex (in the cat: 72), the relative disparity signals used in depth perception are constructed outside area V1 (73). In V2 neurons selective for binocular disparity are prevalent in the thick stripes, leading to the conclusion that depth perception is a magnocellular function (e.g. 21).

Still, as recalled by Roe, neurons selective for binocular disparity have been found also along the ventral stream, in the thin and pale stripes of V2, and at a upper stage in V4. Some researchers advanced the existence of two different types of stereopsis: a coarse stereopsis, processed along the dorsal pathway, in charge of depth perception by processing large, absolute retinal disparities (0.5-10 deg) relative to low spatial frequencies of moving targets, and a fine stereopsis, coded by the ventral stream, in charge of depth perception by processing small, relative, retinal disparities (less than 0.5 deg) in presence of high spatial frequencies of stationary or quasi-stationary objects (see 47). As a confirmation the parietal and temporal pathway underlie differential stereoscopic domains, microstimulation of V4 and MT led, respectively, to impaired fine (but not coarse) and coarse (but not fine) depth perception (74, 75)

H. Visual attention

Visual attention is the function that allows selecting the information of interest from the information globally available. The selection of the information may involve a portion of the visual space (visual attention) or a particular feature of a stimulus (feature attention). Spatial attention can be modeled as a spotlight encompassing a region of the visual space where the neuronal activity is enhanced. Feature attention, in turn, acts picking out relevant items of a visual configuration, be it a scene or an object (see 47). There is strong evidence that V4 underlies both spatial and feature attention (e.g. 76), modulating feedback projections coming from the temporal cortex as well as from the frontal eye fields (FEF) located in the Broadmann area 8 (77-79). As a matter of fact, visual attentive-related neuronal enhancement has been recorded in V4 and at a higher hierarchical level, in IT (see for example 80-82). Moreover, V4 cells can alter their modulation pattern according to the tuning characteristics of the neurons stimulated by the feature of the object that is capturing the visual attention of the observer (83).

Alongside these findings suggesting the area V4 to be the visuoattentive region par excellence, another strand of research ascribes a relevant part to the dorsal stream. In fact, the posterior parietal cortex is found to play an important role in processing spatial attention (84-86). Moreover, spatial attention would not be modulated just by the higher hierarchical structure of the dorsal pathway, as suggested by Britten (87), but it would involve the magnocellular pathway as early as at MT area as well, with a magnitude of the effect comparable to V4 (88). According to the model proposed by Vidyasagar, visual attention depends on the two-stages serial cooperation of the dorsal and ventral stream: the faster transient system would preattentively process (in parallel) the visual scene, allowing subsequently the sustained system to concentrate the attentional focus on the spatial region of interest (86).

I. FEMs control

The dorsal stream at the level of the posterior parietal cortex is found to be involved also in modulating the saccadic control: More specifically, the main regions in charge of the saccadic control are the Parietal Eye Field (PEF), the mediotemporal area and the medial superotemporal area (e.g. 89-93). Interestingly, visual attention has a modulatory effect on the triggering of saccadic movements (94-97) and the cortical regions along the dorsal stream responsible for visual attention and saccadic control are found to be the roughly the same or to overlap consistently (see for example 92).

J. Integration vs competition: the case of visual persistence and saccadic/fixation rhythm during reading.

Evidently, the dorsal and the ventral stream cooperate in integrating the perceptual processing required by the different characteristics of a visual scene or in focusing and orienting visual attention.

Still, antagonistic activity of the parvocellular and magnocellular pathway has been theorized to explain the perceptual phenomenon of visual persistence and an important physiological mechanism, namely the saccadic/fixation alternation required to perform a lexical task.

i- visual persistence: visual persistence (VP) is the response to a visual stimulation that continues after its disappearance and that is indistinguishable from the response occurred during its presence: so, due to visual persistence, two targets displayed in quick succession are perceived as a single image if their temporal separation is below a given limit (98).

A strand of research suggests visual persistence is modulated by the inhibitory effect of the M-pathway on the sustained activity of the parvocells. In effect VP time increases with the spatial frequency of the target (99-101), and is found to be higher in dyslexic subjects (101, 102-108), who are hypothesized to suffer from a magnocellular deficit (e.g. 108-111).

ii- Oculomotor pattern during reading: it has been advanced that the rhythmic alternation of saccades and fixations during reading is driven by the inhibition of the P- over the M-system and vice versa. According to such "pull and push" or "competition-interaction" model, the foveal parvocellular center is in charge of maintaining stable foveal fixation on a syllable whereas the magnocellular system drives the saccadic triggering. The P-system, fully activated at the early phases of the foveal fixation, is progressively inhibited by the peripheral magnocellular center that in turn is activated by the presence of a extrafoveal syllable. When the magnocellular activation is preponderant, i.e. the parvocellular center is maximally inhibited, the saccadic triggering occurs (see also 112).

During the saccadic "jump", the process reverses: the parvocellular activation rises progressively, suppressing more and more the magnocellular center. When the activation level of the latter drops below a threshold, the "jump" comes to an end: as a consequence the "landing" of the saccade takes place, generating the fixation (113, 114).

II. Conclusion

When dealing with visual perception, Nature seems to have simplified the matter by adopting two formally separate visual pathways, each carrying its own, specific information. The functional selectivity of the parvo- and magnocellular systems makes their projection toward the cortex a parallel, segregated stream of data. In their review (7), Merigan & Maunsell concluded stating that, even if incomplete, M/P segregation does exist along the visual pathway not only at a subcortical (retino-geniculate-striate) level, but (to a certain extent) even on the cortex: in effect, after injecting tracers in the inferior parietal and inferotemporal cortex the dorsal and ventral streams remain morphologically separated along their way from the magnocellular-/parvocellular portions of V1 till to the upper cortical areas (respectively the posterior parietal cortex [PPC] and the inferotemporal area [IT]: 115, 116). But if the existence of two specialized and separated anatomofunctional systems would help accurately process the individual characteristics of the object, evidently at a certain level of the cerebral hierarchy the characteristics of the visual stimulus, elaborated so far along two different channels, need integration to provide the observer with the final percept: so, the convergence of the two parallel pathways cannot be other than the final, crucial step. In effect, from the striate cortex the dorsal and ventral input tends to merge, converging onto the extrastriate parietal (dorsal) and temporal (ventral) pathway, Interestingly, such extrastriate merging would be asymmetric, so that the parietal stream would be made almost exclusively of magnocells, while in the temporal stream the contribution of the two cellular types would be equivalent (7, 117).

The functional (and anatomical) integration of the two streams is supported by the existence of striate and extrastriate cross-connections between the parvocellular and magnocellular stations. Cross-connections have been documented as early as in V1 between the layer 4B and 4Cα and the blobs; in addition, the striate parvocellular system (namely blobs and interblobs) is found to receive magnocellular projections, since a blob and interblob residual activation state persists even after disruption of the P-pathway in the lateral geniculate nucleus (118). Finally, as recalled by Merigan & Maunsell (7), the magnocellular layer 4B of V1 is found to some extent responsive to color: a function closely related to the ventral stream.

At a higher level, beyond V1, reciprocal projections have been documented between MT and V4 (119).

Evidently, such cross-connections end up reducing the precortical M/P segregation of the magnocellular and parvocellular pathways, yielding their convergence and integration.

Yet, the results of the experiments aimed at clarifying first the stages of segregation and then the mechanisms of integration of the two systems are often conflicting, since the functional P-/M-spectrum of response at the cortical level overlaps to a certain extent; in addition, the spatial and probabilistic summation make the cumulative response of a class (the P) of neurons far different from that expected by single cell recordings (consider for example contrast sensitivity). Evidently, all these peculiarities make the results of the surveys (especially lesion studies) not univocal.

As a matter of fact, even if cortical localized (selective) lesions may generate quite specific functional M-P deficits, these deficits are small and overall transitory. Such small and transitory functional effect after destruction of the parietal or temporal cortical stream may depend not only on the distributed pattern of M/P visual processing (120), but also on the (so far obscure) substitute action of other visual areas (65).

The cross-connections are therefore the substrate for the functional interaction between the transient and sustained system: in some cases, like the modulation of the saccadic/fixation rhythm, such interaction does not integrate the separate M/P complementary inputs (7), but acts

competitively.

In conclusion, in order to fully achieve the perception of an object the parallel, segregated parvocellular and magnocellular pathways require subsequent anatomofunctional convergence onto the cortex. The way and extent of such "parallel convergence" is still matter of debate.

Evidently, Nature made things more complicated than expected, and the notion of a parallel processing system of the individual features of the visual stimuli albeit captivating very likely suffers from excessive schematism. No doubt further investigations are required to better understand the process of segregation and subsequent integration underlying visual perception.

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