Full-length review

A neuronal model of attentional spotlight: parietal guiding the temporal

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Abstract

Recent studies have reported an attentional feedback that highlights neural responses as early along the visual pathway as the primary visual cortex. Such filtering would help in reducing informational overload and in performing serial visual search by directing attention to individual locations in the visual field. The magnocellular (M) and parvocellular (P) subdivisions are two of the major parallel pathways in primate vision that originate in the retina and carry distinctly different types of information. The M pathway, characterized by its high sensitivity to movement and to low contrast stimuli, forms the predominant visual input into the dorsal, parietal stream in the neocortex. The P inputs, characterized by their colour selectivity and higher spatial resolution, are channeled mainly into the ventral, temporal stream. It is proposed that the attentional spotlight originates in the dorsal stream and helps in serially searching the field for conjunction of the relevant target features in the temporal stream, effectively performing a gating function on all visual inputs. This model predicts that a defect limited to the magnocellular or the dorsal pathway can lead to widespread deficits in cognitive abilities, including those functions that are largely based on parvocellular information. For example, the model provides a neural mechanism linking a peripheral defect in the magnocellular pathway to the reading disabilities in dyslexia. Even though there has been strong evidence for a magnocellular deficit in dyslexia, the paradox has been that the cognitive disability seems to be related to P pathway function. The scheme proposed here shows how M input may be vital for controlling sequential attention during reading. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Attention; Visual cortex; Parietal stream; Temporal stream; Dyslexia; Magnocellular pathway

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1. Introduction

Over the last 40 years, we have made considerable progress in our knowledge of the visual pathways, in particular through electrophysiological investigations regarding the trigger features of cells at various levels of the visual system and also from psychophysical studies in humans and other primates. However, the natural world differs substantially from the visual stimuli used in these studies in many ways. One important respect in which it differs is that stimuli in real life rarely occur in isolation and the visual system is often confronted with a multitude of stimuli of different shapes, sizes, colours, depths and speeds of movement. Nevertheless, we are able to focus attention on one object and process just the relevant information, sometimes even doing this covertly while foveating elsewhere. We are also able to employ visual search over a large scene and find, for example, a known face in a crowd fairly rapidly. While doing all this, we can also quite effortlessly bind different features of an object together, so that we can attribute correctly say, the yellow colour to the banana and the red to the apple. One puzzling aspect of this capability is a large body of evidence (see later) which suggests that different stimulus attributes like colour, form and motion may be processed in different areas of the brain. Given this, how is the binding of features made possible? A neuronal model that provides a framework for visual attention should be able to address these questions satisfactorily.

This paper will briefly review some of the psychophysical and neurophysiological studies that are relevant to this problem and propose a neuronal scheme that can explain these data and make testable predictions.

2. A model of attention that incorporates a novel view of convergence of parallel pathways in vision

In proposing a neurophysiological basis for attention, this paper builds upon concepts that have been derived largely from psychophysical experiments over the last 20 years. These ideas and the relevant literature on parallel pathways in vision will be reviewed first.

2.1. Spatial deployment of attention

One of the most influential ideas concerning the mechanisms of visual attention is contained in Treisman's Feature Integration Theory [83]. According to this model, when a target feature leads to unique activity in a feature domain (say, the target being a single green object among a number of red distracters), the detection of the target is done by a parallel process with the number of distracters having no effect. Such pop-out effects in pre-attentive vision have been extensively studied (for reviews, see Refs. [42,63]). In contrast a target lacking a unique feature,

such as its colour or orientation, but which is uniquely distinguished from other objects only by conjunctions of two or more features is detected by a serial process in the visual system (Fig. 1). It is postulated that an attentional
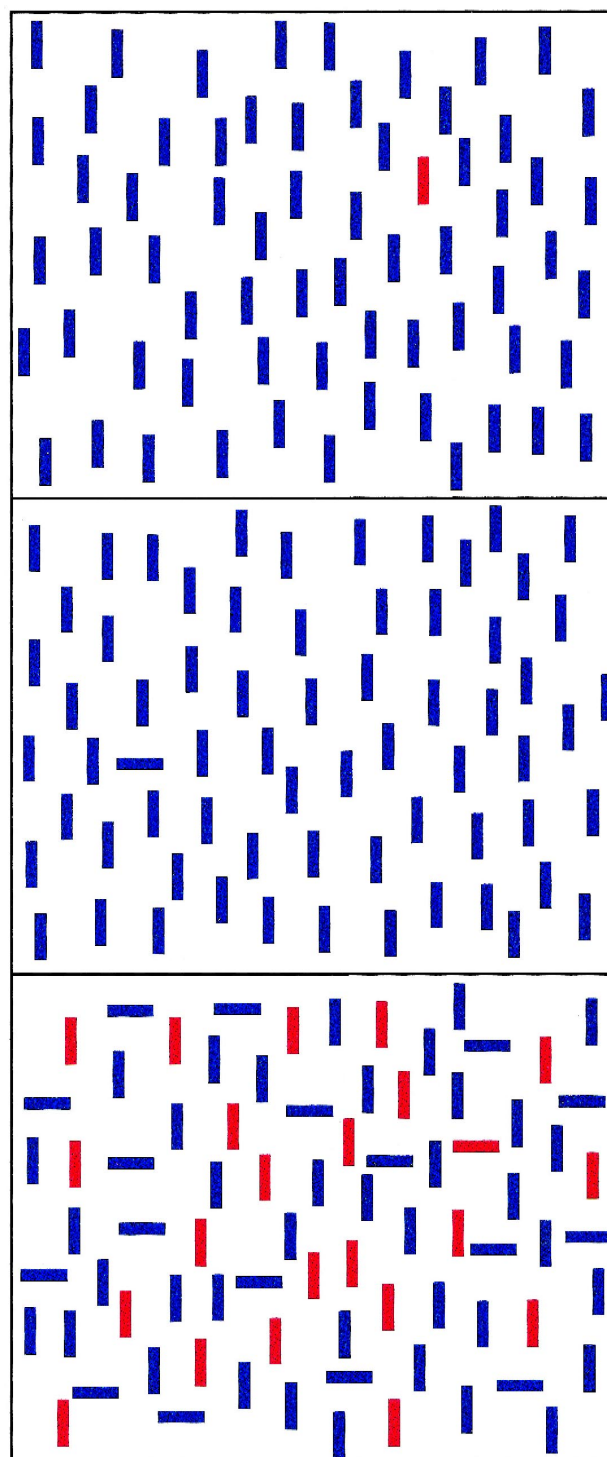

Fig. 1. Parallel vs. serial visual search. In the top two panels, the target, which is a unique feature (colour in the top and orientation in the middle panel) pops out pre-attentively. In the bottom panel, the target (a red horizontal line) does not pop-out, but is detected by a serial search, since the time taken depends upon the number of distracters (after Ref. [83]).

spotlight focuses at each instant of time on a specific location in a fine grain map of the visual world such as that in the primary visual cortex (also known as striate cortex or area V1) and the resulting neural activities in separate feature maps in the higher extrastriate areas allow the unambiguous binding of the corresponding features of the object. It appears that this process is repeated serially through the visual field, since the time taken to detect an object from feature conjunction is positively correlated with the number of distracters. There have been two other important models of attention that have been proposed [29,100]. One of these, the guided search model of Wolfe [100], provides satisfactory explanations for a number of observations that the original feature integration model could not. These will be discussed later, but the basic idea of a spotlight of attention guiding visual search that Treisman proposed is central to the theory advanced in this paper.

2.2. Neural substrates for an early attentional filter

In dealing with the vast amount of information coming in from the retina, it would be more efficient if signals from all over the visual field were not all processed by the different feature systems in parallel. If this is allowed to happen, it would only lead to confusion regarding which features belong to which object ('binding problem', see Ref. [84]) and also impose an enormous and unnecessary computational load on the various neocortical areas. The Feature Integration Theory provides a good solution to this problem by placing attentional selection at an early stage, which, by spotlighting particular locations of interest, reduces computational load and enables features of an object to be bound together. The site of such a spotlight could be as early as visual area V1 before the visual information gets channeled into various feature maps. This seems to be a plausible step when we take into account the anatomy and physiology of the visual pathways. The striate cortex receives massive feedback projections from a number of other neocortical areas (reviewed in Ref. [71]). Even though not much is known about the possible functions of these projections, evidence is emerging that feedback inputs can selectively enhance or suppress responses of neurones in the striate cortex [41,59,93].

The key for the mechanism of attentional selection may lie in the functional subdivisions of the afferent visual pathways. There is considerable evidence that in primates three streams of parallel channels reach the primary visual cortex, namely the parvocellular (P), magnocellular (M) and koniocellular (K) inputs; to some degree these remain separate in their cortical terminations (reviewed in Ref. [13]). Regarding their further projections, since at this moment we know only about the fate of the P and M pathways, this article will not be referring to the K pathways anymore. It is generally believed that a M-dominated dorsal stream that extends from V1 and certain compart-

ments in V2 to middle temporal area (MT or area V5) and further to the parietal cortex is concerned with visual attributes related to space, namely movement, depth and positional relations. On the other hand, the P-dominated ventral pathway extending into areas V2, V3, V4 and the inferotemporal cortex (cytoarchitectonic areas TEO and TE) is concerned with object discrimination based on features like colour, form and texture [46,48,56,88,103]. This dichotomy may not be as clear-cut as originally proposed by Livingstone and Hubel [46] and there seems to exist some cross-talk between the channels at various cortical levels [56,73]. Nevertheless, there is general agreement that the dorsal stream going into the parietal cortex is largely driven by the magnocellular channel. The ventral stream is predominantly driven by the parvocellular channel, although it has substantial magnocellular input [32,33]. The cells in the dorsal stream areas such as MT and the parietal cortex have large RFs, but none the less the regions as a whole do code for spatial position very well. This is so because space is most likely to be coded in each of these areas in the activity of groups of neurones rather than in the responses of single neurones. Unlike the cells in the ventral stream, these neurones do not code for a large variety of forms, and so visual space can be adequately represented by the network without devoting an excessive amount of neural tissue.

I propose that the visual system may exploit this dichotomy of a fast magnocellular/transient channel and a slower parvocellular/sustained channel for the purposes of selective attention. The faster transmission and the spatial coding properties of the dorsal stream are ideal to provide a feedback to one of the earlier stages in the pathway (say, the striate cortex) to selectively facilitate regions of interest before further processing in the ventral stream. This means that, with the initial barrage of visual input, information in the dorsal stream is processed pre-attentively, that is, in parallel over the whole visual field. The information thus extracted about object locations can then be used for spotlighting purposes. Such spatial selection would obviate the need to process information over the whole visual field in the ventral stream. It would also solve the binding problem, since at any one instant only the features that belong to a single object will gain access to the higher areas for processing.

Besides reducing computational load, another good reason for spatial selection of attention to occur at an early stage is the fact that the receptive fields of cells in the ventral stream areas beyond V1 become progressively larger. Thus in macaque monkeys, typical RF sizes of cells in central vision, in areas V1, V4, TEO and TE in the ventral stream, are of the order of 0.2, 3, 6 and 25 degrees, respectively [8,24]. It should however be pointed out that the RFs in areas such as TEO and TE are of a sophisticated nature, so that they often respond only to complex objects, but the object can be presented anywhere within their large receptive fields. Such progression in RF size is

a useful requirement for achieving position invariance in recognizing patterns [90]. Such invariance could also be coded as a network property, but one could safely assume that whatever be the mechanism, position invariance is an essential ingredient of pattern recognition. In any case, with such large receptive fields as have been observed in the temporal neocortex and with each extrastriate area being specialized for a different visual attribute like colour or form, the visual system would be confounded in binding each object's attributes together if a number of small-sized objects are present in the visual world. One solution to this issue is for the system to restrict the inputs to the extrastriate areas to a limited spatial region of interest. If selective attention were to focus serially on specific locations in, say the striate cortex, only those neurones in the inferotemporal cortex that respond to the features present in the object under attention would be excited at any one instant. This may be the basis of perceptual binding of features that belong to one object.

Most electrophysiological investigations in macaques that have sought neural responses related to attention have found significant attentional modulation in the activity of neurones in V4, posterior parietal cortex, MT and inferotemporal cortex [15,16,52,57–61,68,72] [79,87], but they found no such effects in the primary visual cortex [52,57,67]. However, more recently, in paradigms where a number of competing objects were presented simultaneously in the visual field, significant attentional modulation has been shown in some V1 neurones [59,93]. For example, in a paradigm where the monkey had to perform a visual discrimination task at locations in the visual field to which its attention was drawn, a subset of neurones in V1 showed vigorous responses when attention was directed to that location. When attention was directed elsewhere, the responses to the same visual stimuli were absent or very much reduced [93]. In this study, where the cue for directing attention was presented at the same time as the stimulus to be discriminated, the feedback attentional influences on V1 were beginning to be apparent 80 to 100 ms after the stimulus presentation. This latency was consistent with the findings in other studies showing feedback to V1 mediating contextual modulation related to disparity, colour, luminance or orientation cues [104].

It is instructive to compare these results in the striate cortex with the attentional effects observed in V4 and inferotemporal neurones [15,58]. These, latter, extrastriate cells have rather large receptive fields and when two different stimuli fall within the RF, one of them being a good visual stimulus for the cell and the other not, a significant difference in the response to the good stimulus is seen depending upon whether attention is directed to that target or to the other target within the receptive field. This may mean that the RF of the neurone could literally shrink around an attended location. One simple neural mechanism that can achieve this is an attentional spotlight at an earlier level such as V1 allowing only the outputs of

this location to get to higher visual areas like V4. The recent results in V1 [93] thus provide a mechanism for the differential attentional responses seen in the higher areas along the ventral stream.

2.3. Flexibility of the locus for focal attention

The earlier difficulties in demonstrating attentional modulation in neurones of the striate cortex may be partly related to the failure to use a task that would need the fine grain representation of V1. If a visual discrimination task can be performed with the larger RFs of the ventral cortical areas, the feedback need not go all the way to the striate cortex. Attention could be more efficiently and quickly focused on the region of interest at a cortical stage that has the largest RFs which would just perform the task. Thus, only in circumstances where objects clutter the visual field to an extent that the task requires the involvement of V1, would one be able to show attentional influences in V1. Thus, the RF gradient along the ventral stream determines at what level a display of a particular target size is processed by the attentional searchlight (Fig. 2).

This idea is implicit in the dynamic routing of ascending visual signals proposed by Van Essen et al. [90]. Very recently, human imaging studies have also shown that there is a progression of increasing lateral suppression within the visual field from V2 to V4 to TEO which is under focal attentional control [43]. They suggest that this may be related to scaling the attentional effects to the RF sizes along the ventral object vision stream. They were unable to show significant modulation of activity in V1, but this may reflect the technical problem of achieving the
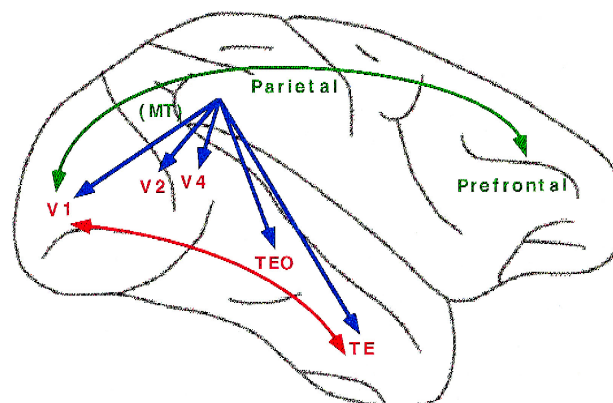
Fig. 2. A model of attentional spotlight. The visual information coming in to the primary visual cortex (V1) is channeled into a dorsal, parietal stream carrying mostly magnocellular inputs and a ventral, temporal stream which is the major pathway for the parvocellular inputs. The attentional spotlight originating in the dorsal stream is directed at the ventral stream for enabling visual search and binding. The level at which it is directed depends upon the size and density of the targets in the visual field. If there are a number of small objects cluttering the visual scene, the spotlight would operate fairly early, say V1. If the targets are larger and fewer, it would be directed at a higher region, V2, V4, TEO or TE.

requisite spatiotemporal resolution with the fMRI technique.

It has also been suggested [22] that an attentional searchlight could be modulating incoming visual inputs as early as the thalamus via the thalamic reticular nucleus (TRN). While the anatomical substrate for this exists and significant cortical influence on thalamic reticular activity has been shown [80], we have to await further experiments to know whether these corticothalamic inputs could be related to attentional selection [37].

2.4. Convergence of parallel streams in visual search

The neural scheme outlined above for focal attention can be applied to visual search functions with a few simple assumptions that are consistent with the known physiology of the visual pathways.

- I propose that the attentional spotlighting described above is necessary only for search and discrimination functions associated with the ventral stream. This is necessary because of the large RFs and the poor coding of spatial relations in the ventral stream. As noted above, the large RFs are an integral part of a system that needs to possess position invariance for consistent object recognition.

- Information on spatial locations of objects for the purpose of spotlighting is provided by the dorsal stream.

- It is suggested that localization of targets and any discriminations based on the specific functions of the dorsal stream, such as disparity or movement, occur in parallel and pre-attentively. Target locations that are so selected could be used for spotlighting for the ventral stream if necessary.

If all the relevant target features that form the conjunction for detecting the target can be processed only in the ventral stream, the dorsal stream would be forced to undertake a serial spotlighting over the entire visual field without any narrowing of the possibilities that occurs when one or more target features could be processed by the dorsal stream. The only tool left for the dorsal stream would be the positional information of objects and a classical Treisman type serial visual search would be undertaken with its typical dependence upon the number of distracters.

On the other hand, if one of the features in the conjunction is one that can be processed by the dorsal stream, the search would be faster. The presence of objects containing this feature would lead to a number of highlighted locations in a spatial map in a part of the dorsal stream, possibly the posterior parietal cortex. These locations of interest that pop-out in the dorsal stream provide the sources for the spotlighting necessary for the ventral stream. If the task involves conjunction of only two features, with one of the features being processed by the dorsal stream, target identification would be rapid without any need for serial search, since within the highlighted array, the unique feature would lead to pop-out in the relevant ventral

stream feature domain. If from among the spotlighted locations, there is no such pop-out, the locations are processed one at a time by the ventral stream.

This theory differs from classical ideas of attentional spotlight in that the dorsal stream can spotlight not just one, but a number of selected locations in V1 (or at the appropriate higher level in the ventral stream) if the particular task makes it possible. Such a feedback would lead to rapid target selection in the ventral stream if among the spotlighted locations a unique feature could pop out. This prediction is supported by the psychophysical findings cited later.

The magnocellular pathway and the dorsal stream can also perform some of the processing functions that are normally associated with the P system. For example, cells in the magnocellular stream, such as those in layer 4B of the striate cortex exhibit orientation selectivity [6]. At least the location of orientation discontinuities in an array of say, a few horizontal and vertical lines among a number of diagonal lines, could be detected by the dorsal stream. However, if the task requires scrutiny and discrimination by the ventral stream of these detected targets, the next step has to be serial search directed by the locations of interest already spotted pre-attentively by the dorsal stream (see also Ref. [70]). On the other hand, if the second feature that forms the conjunction is one that is processed within the dorsal stream itself, the identification would be more rapid.

Thus, according to this model, the two major streams in vision (P and M) converge in the neocortex under special circumstances. This interaction happens because of the filtering function performed by the M dominated attentional spotlight feeding back on to V1, V2 and further along the ventral stream. Thus the faster M input acts as a gate for parvocellular, and possibly other, inputs. The discussion whether this gating function is multiplicative or additive is beyond the scope of this paper and in any case it may be too speculative at this stage. However, it will not be too daring to predict that pure magnocellular deficits can lead to poorer performance in parvocellular mediated visual functions because of the lack of effective M-mediated attentional spotlighting. Such deficits will be detectable only in situations where the density of visual stimuli and of the relevant target features are high enough to require a process of attentional selection.

At this stage, one needs to add an important caveat that interactions between P and M pathways could be quite direct and could occur at an early stage, such as the primary visual cortex. There is certainly the anatomical substrate for such convergence [45,54,101,102] and recently electrophysiological evidence as well [94,95]. There have also been elegant psychophysical studies that have shown how luminance and colour channels could interact with each other to influence detection of single luminance or chromatic targets [17,81]. However, I propose that quite apart from these interactions, the two parallel streams

interact by way of the gating that the M-dominated dorsal stream performs on the information flowing through the various visual stations into the ventral stream—particularly in dealing with real cluttered scenes.

3. Functional implications of the model

3.1. Psychophysical consequences

This neural account of selective attention explains a number of psychophysical observations that have been difficult to reconcile fully with Treisman's original Feature Integration Theory and seem to fit better with its modified version, namely the guided search model [100]. Treisman's early examples [83] of conjunctions that required serial search were features that would be largely processed by the parvocellular pathways and the ventral stream. They in fact showed the typical dependence on target size (i.e., no of distracters) that would be expected in a serial search. However, it has since been shown that conjunctions, where one of the features was movement [55] or disparity [62], could be done much faster than would be expected from a serial search and were little influenced by display size. This may be related to the fact that both movement and disparity are processed mainly in the dorsal pathway [56]. According to my scheme, if a subset of items can be segregated on the basis of a distinct feature by the dorsal stream and these areas are highlighted at the appropriate stage in the ventral stream, the presence of a unique second feature within that array can also be done by a parallel process. This would involve two stages, but at each stage the process is parallel and not influenced by display size. Thus only one of two features in a target defined by a conjunction need to be a feature that can be processed by the dorsal stream to yield flat searches (i.e., slope of Reaction Time × Set Size being flat).

Wolfe et al. [99] found that the Reaction Time × Set size slopes for conjunctions of colour with form, size or orientation were shallower than would be expected from the Treisman model. They proposed that this is consistent with a guided search, where selection of a subset of targets based upon one feature restricts the number of targets to be searched for the second feature. There could be two neural mechanisms underlying the results that are both consistent with the scheme proposed in this paper: (1) Information about the locations of one of the features was made available to the dorsal stream due to a cross-talk between the two streams, or (2) the achromatic feature in these experiments was coarse enough to be processed by the dorsal stream. In either case, with the dorsal stream highlighting the relevant locations of the first feature, the unique second feature would pop-out in the corresponding ventral stream domain.

Wolfe [100] had already suggested that a massively parallel stage possibly precedes a limited-capacity serial stage in visual search. The model I propose clearly identi-

fies the neural pathways involved in such a guided search and given the known properties of these pathways, one can draw further psychophysical implications.

A crucial experimental result that the scheme explains is the following finding by Sagi and Julesz [70]. When a few horizontal and vertical lines were embedded among many diagonal lines, their positions could be rapidly determined by a parallel process. However, identification of each of these lines as vertical or horizontal requires serial search. The patterns used by Sagi and Julesz in this experiment were coarse enough that one could expect that the dorsal stream could extract at least the positions of the orientation discontinuities from the activity of magnocellular driven cells. This would lead to quick determination of the numbers and positions of the targets, but discrimination of each of these lines would, however, need to wait for serial search in the ventral stream guided by the spotlights of attention from the dorsal stream.

The theory also provides a framework for a large number of studies that have shown how visual performance can be enhanced by attending to spatial locations even when the task is likely to involve mainly functions of the ventral stream such as colour and form [26,38,39, 53,64,65].

It is particularly interesting that spatial attention enhanced sensitivity at the attended location more for orientation and form discrimination than for luminance or brightness discrimination [26]. This fall-off of sensitivity from the location was also found to be steeper when stimuli were near each other than when they were farther apart. As explained earlier, in my scheme, the attentional spotlight needs to be brought into play by the system only when the stimuli are close together.

3.2. Clinical implications

The model proposed here would also explain a number of clinical observations, for example, the attentional and binding problems that are associated with parietal cortical lesions [19,34,85]. In addition, the scheme provides a detailed neural mechanism to explain how a lesion in the magnocellular pathways is associated with the reading and attentional deficits of dyslexia [5,7,47,49,78]. In our scheme, the integrity of the dorsal stream is crucial for appropriate conjunctions of features, including those that are entirely processed by the ventral stream and for the extraction of the spatial relationships of the individual items. These functions are crucial in our ability to read effectively. The large RFs of the ventral stream neurones that perform the visual discrimination between the letters cannot possibly order letters of a word or the words of a sentence without the spotlighting aid of the dorsal stream. The dorsal stream may thus be necessary for the smooth flow of attentional focus that helps in the identification of individual letters or words. It is probably no coincidence that average adult readers would read a page of 3000

English characters in about a minute (20 ms per character). This may be directly related to the speed with which the attentional spotlight can be deployed. In fact, the speed of visual search usually cited [40,99] is about 20–30 ms per item. Of course, faster readers might be processing patterns of whole words or parts of words at each moment of attentional focus in stead of single characters.

The most important element in learning to read may be training the attentional spotlight to move sequentially over the letters and words in a line. One would expect this kind of attentional scanning ability to be learned and not innate in the light of a recent experiment by Horowitz and Wolfe [40]. They found that visual search does not keep track of locations that have been inspected and rejected. Such random directing of attentional focus during most visual search situations is a functionally useful strategy to avoid the computational load of keeping track of the search history and also to keep the visual system sensitive to changes in the scene that could occur during the search itself. In the neuronal scheme I have proposed, learning to read will be a special instance of training the dorsal system to perform the spotlighting in a spatially sequential manner. This could well be one of the most challenging tasks for the dorsal stream in modern civilization. One would then expect that abnormal development of the magnocellular pathway could lead to reading difficulties. In fact it has been proposed that in developmental dyslexia, the basic anomaly is a magnocellular defect at the retinogeniculate level [21,23,30,47,78].

While supporting the magnocellular or transient deficit theory of dyslexia [7,47,49–51], the present theory differs from the earlier papers in the mechanism of how the defect leads to the reading disability. It has been assumed so far that in reading, during the saccades between fixations, the magnocellular system suppresses the activity of the parvocellular system so as to prevent interference between the successive sets of parvocellular activity generated during the periods of fixation [11,47,50,51]. This possibility is refuted by the finding [12] that suppression during saccades is selective and targets only the magnocellular system. Further, there is still the problem regarding the processing that occurs within any fixation period. How could the large RFs in the ventral stream, though perfectly capable of seeing small letters, retain the position information within the respective RFs so as to arrange all letters in the text in the appropriate sequence? In the proposed scheme, however, it is the rapid and sequential spotlighting function of the M dominated dorsal system during the fixation periods, that is necessary for the ventral stream to order the letters appropriately.

The fact that magnocellular deficits have not always been demonstrated in dyslexics [36,75] may be due to one of two reasons: (1) In these patients, the lesion may be in the parietal feedback to striate cortex, the afferent magnocellular pathway itself being intact. (2) The magnocellular defect may be so mild that it shows up only in challenging tests where the system has to use the M inputs to sequentially direct focal attention.

The deficits in dyslexia are often also in the auditory system with difficulties in discriminating phonemes in a complex auditory environment. This is possibly related to the subject not being able to detect phase differences between the two ears to localize sounds prior to discrimination. While this could be due to abnormal 'magnocells' in the medial geniculate nucleus [35], it is also possible that the auditory deficit follows from a basic magnocellular lesion in the visual pathway. There is evidence from patients with parietal lesions that a supramodal representation of space may exist in the parietal cortex with convergence of both visual and auditory inputs [31]. There is also ample evidence for multimodal inputs to cells in the parietal cortex [1,2,25,44]. Such a supramodal map of spatial locations may be created during development from synchronized inputs from different modalities such as vision and audition. This map would presumably be used for directing attention in both the visual and auditory worlds. A magnocellular deficit may prevent the development of a proper supramodal map. It is possible that, like in the establishment of the superior collicular maps [82,92,98], the visual input may have a directive role to play in the formation of the auditory map itself. Without the normal spatial maps in the parietal cortex, the attentional spotlighting functions of the brain will be severely compromised, leading to binding and conjunction problems in vision and sound localization errors in hearing. These difficulties will be most easily detectable in tasks like reading and phonemic discrimination in human speech where severe demands would be placed on the attentional spotlighting functions of the dorsal stream. It is recognised that there is little direct evidence for this idea, but it is presented as a heuristic concept.

One would also predict from the scheme proposed in this paper that the development of the focal attentional system through the parietal cortex would be affected in the case of a magnocellular lesion from birth, explaining also the attentional deficits reported in dyslexics [10,69,74,89, 96,97]. In fact, a lesion in any part of the magnocellular channel or the dorsal stream could lead to an attentional deficit, which is a common accompaniment of many neurological disorders. For example, it is being increasingly recognized that the underlying abnormality in schizophrenia may be one of attention [9,14,20] and there is evidence that at least in some schizophrenics, the afferent visual channels, particularly the transient magnocellular pathway, may be affected [76]. There is also evidence showing an intriguing association between schizophrenia and dyslexia [66,77].

3.3. Testable predictions

From the above scheme, a number of predictions can be made. Some of these are the following.

(1) If all the features that define the conjunction in a visual search can be processed by the dorsal stream, no spotlighting will be necessary to perform a serial search. For example, in a variation of the Sagi and Julesz experiment (see Fig. 1 of Ref. [70]), detection of the number of targets and identifying the disparity planes where they lie would both be pre-attentive. The number of distracters would not make a difference unlike in the Sagi and Julesz experiment, where only detection, but not identification of the form of the targets, was done by parallel search.

(2) If the targets are not allowed to be processed by the dorsal stream by making them isoluminant and thus invisible to magnocellular cells, conjunction searches would be much slower than when luminance differences are present between target and background.

(3) Defects in the magnocellular pathway would lead to detectable deficits in parvocellular functions if the task requires the attentional spotlighting functions of the dorsal stream. In searching for targets defined by features that are processed by the P system, reaction times should be longer and conjunction errors common in dyslexics. No parvocellular deficit need be apparent if the test were to directly test a specific parvocellular function without involving distracters. Our preliminary results [96] suggest that reading impaired children perform poorly in conjunction search tasks when a large number of distracters are present.

(4) In glaucoma, where retinal M cells may be selectively lost [3], again reaction times should be longer and conjunction errors common in visual search tasks. Even though the parvocellular system may also be affected in glaucoma [91], the parvocellular deficit would become more obvious when the stimulus is embedded in an environment of a number of other stimuli and a process of visual search is necessary.

(5) Dyslexics who have had auditory deficits, but show no abnormalities in the medial geniculate nucleus at autopsies, might still show lesions in the magnocellular section of the visual system.

4. Relation to other models

The scheme outlined here stresses the importance of spatial selection in visual attention as have some others [19,83,86]. It seems to contradict the alternative idea that attentional selection could be the result of competition between objects for dominance over neural resources rather than due to an early spatial filter [27–29]. This latter model has gained considerable currency in recent years with the finding of within-modality competition in attentional tasks and single unit studies showing priming of neurones that respond to current behavioural targets (reviewed in Ref. [28]). However, a number of studies have shown clearly that spatial selection is an integral aspect of attention and also that there is selective activation of posterior parietal regions in visual search tasks [18,19]. This is further supported by recent studies using transcranial magnetic stimulation, in which disruption of posterior parietal activity delayed search tasks involving conjunction targets, but not those involving pre-attentive pop-out [4]. In Duncan's scheme, activations cannot show such dramatic differences between cortical regions. On the other hand, the above findings and the model proposed in this paper do not necessarily exclude a Duncan type of competitive integration occurring at a later stage of the process [85]. Such competition may be more pertinent to select the appropriate object for the control of behavioural actions and not for the initial selection of objects and binding their features appropriately.

5. Conclusions

In the present scheme, the following factors determine the time taken for visual search.

(1) *Which of the features defining the target can be processed by the magnocellular dominated dorsal stream.* To the extent that one or more defining features can be processed by the dorsal stream, the search would be parallel and therefore faster.

(2) *The sizes and spatial separation of the targets that need to be processed by the ventral stream.* When objects are crowded together in the visual world, the attentional spotlights have to be directed back to an earlier level of the pathway such as V1 (or even the thalamus). This is likely to increase the time taken.

(3) *Number of distracters.* This will be a factor only if the search has a serial component, i.e., if the conjunction of two or more features needs to be identified within the processing modules of the ventral stream with the help of dorsal stream spotlights.

The M dominated dorsal stream plays a crucial part in visual search even if the defining features of the target are all processed by the parvocellular system. The pivotal role of the M system in attention makes the visual system very susceptible to damage of the magnocellular pathway, particularly in tasks where spatially directed attention is an essential component. Reading may well be the most sophisticated application of attentional spotlight in the modern world involving extensive perceptual learning to use the searchlight in a spatially sequential manner. That may be the reason why a magnocellular deficit could underlie the aetiology of dyslexia.

Acknowledgements

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