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Leonardo Chelazzi

Serial attention mechanisms in visual search: A critical look at the evidence

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Abstract Until a few years ago, visual search tasks were of exclusive pertinence to psychophysicists and cognitive psychologists trying to understand the operating principles and computational constraints of visual perception and visual selective attention. In recent years, cognitive neuroscience, with its powerful tools, has started to explore more directly the neuronal mechanisms underlying search performance in humans and macaques, aiming at the same general goals. New observations from a number of cognitive neuroscience approaches are promising a near future of great excitement in this field of research. This article offers a critical review of some of these recent contributions and highlights some of the interpretational problems that they pose.

Introduction

Especially over the last twenty years or so, visual search tasks have been extensively used by psychophysicists and cognitive psychologists as a means to explore the operating principles and underlying mechanisms of visual perception and visual selective attention (e.g., Wolfe, 1998). One notion that has emerged from this wealth of research is that visual perception proceeds through two distinct computational stages: a first, preattentive stage where elemental features (e.g., colors and local contours) are registered across the entire visual scene in parallel; and a second stage where the elemental features are properly conjoined with the aid of focal attention, allowing the perception of multidimensional objects (e.g., Treisman & Gelade, 1980). The hallmarks of this second stage, or level, of processing are: (1) that the perceptual analysis of complex visual objects depends critically on focal attention, and (2) that it can only occur for one object at the time, that is, it proceeds serially.

In the last decade the above dichotomy between *parallel* and spatially *serial* operations in visual search has been seriously challenged by other, contrasting psychological models suggesting that all kinds of search tasks can be solved by a parallel, competitive architecture (e.g., Duncan & Humphreys, 1989).

More recently, a fundamental distinction between these two alternative processing mechanisms of search performance has also been assessed using a variety of cognitive neuroscience techniques, including functional brain imaging, transcranial magnetic stimulation, scalp recording of evoked electrical potentials, and the study of individuals with localized brain damage[1]. In addition, some research has started to address the same issues by recording the activity of single neurons from the brains of behaving macaques.

In what follows, I review and discuss a set of selected contributions that have begun to explore in a systematic fashion the mechanisms underlying visual search performance in humans and macaques. Specifically, I will try to examine to what extent the available literature demonstrates beyond any reasonable doubt the intervention of serial attention mechanisms in some types of search tasks. In spite of the encouraging findings provided by some of these studies, I believe we still have a long way to go before we can come to any final conclusion.

Perhaps, partially in line with some recent "hybrid" models, visual search may almost invariably rely on the dynamic interplay and co-operation between parallel mechanisms and focal attention.

L. Chelazzi
Department of Neurological and Vision Sciences,
Section of Physiology, University of Verona,
Strada Le Grazie 8, I-37134, Verona, Italy;
Tel.: +39-45-8098149; Fax: +39-45-580881;
e-mail: Leoche@borgoroma.univr.it

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[1] Although of great interest, for this article I have actually decided to leave out the visual event-related potential literature bearing on these themes. For selected readings, see Luck, 1994, Girelli & Luck, 1997, and Luck & Girelli, 1998.

The classical view

In visual search, observers are asked to report the presence or absence of a pre-specified target element embedded in an array of nontargets. For instance, a subject may be asked to detect a single red circle among green circles, or a randomly oriented letter T among randomly oriented Ls.

Several years ago it was proposed that a dichotomy existed between two classes of visual search mechanisms. With certain types of search arrays – typically, when the target differs from the nontargets along a single perceptual dimension (e.g., a red circle among green ones) – search was thought to be solved by preattentive mechanisms operating in parallel across the entire stimulus array. With other types of arrays – for instance, when the target differs from the nontargets on the basis of a combination of features (e.g., a red vertical bar among red horizontal bars and green vertical bars) – search was thought to require the serial, attentive scrutiny of each array element in turn (Treisman & Gelade, 1980; Treisman & Gormican, 1988; Treisman & Sato, 1990).

The notion that distinct mechanisms account for search performance with different types of stimulus arrays was largely based on the diagnostic use of the so-called search function. If the experimenter systematically varies the number of elements in the array (the set size) and then plots the time taken to find the target in the array (or to signal its absence) as a function of this number, one may observe flat or steep functions depending on the type of array used. In particular, with targets defined by single features (e.g., the red circle among green circles) the function is virtually flat, whereas with conjunction-defined targets (e.g., the red vertical bar among red horizontal bars and green vertical bars), the slope of the function turns out in the order of several tens of milliseconds per element (e.g., Treisman & Gelade, 1980). As noted above, the interpretation was quite straightforward. With feature-defined targets, search is accomplished by a mechanism that is insensitive to the number of array elements, that is, that operates in parallel across the entire array. In contrast, with conjunction-defined targets, search depends on a serial, time-consuming mechanism that scans individual elements in the array (or small groups of them) in turn: The larger the number of elements, the longer it takes, on average, to "hit" the target with this postulated mechanism (Treisman & Gelade, 1980).

I should note that targets defined by a combination of two visual properties (e.g., color and shape) are not the only ones that produce non-flat slopes. For instance, searching for a T character embedded among L characters yields significant slopes as well (Beck & Ambler, 1973; Bergen & Julesz, 1983; Fiorentini, 1989; Saarinen, 1997). In this case it has been argued that, since the letters T and L are composed of the same line elements (features) – a horizontal and a vertical segment – these two features must be combined in a specific spatial arrangement for either of the two letters to be correctly perceived.

Also, research in recent years has described numerous exceptions to a rigid distinction between feature and conjunction search. In fact, search for feature-defined targets has sometimes been shown to yield non-flat slopes (e.g., Treisman & Gormican, 1988; Nagy & Sanchez, 1990; Wolfe, Friedman-Hill, Stewart, & O'Connell, 1992; Verghese & Nakayama, 1994), and sometimes the search for conjunctions of two or more features has been shown to yield very shallow or even flat slopes (Egeth, Virzi, & Garbart, 1984; Nakayama & Silverman, 1986; Pashler, 1987; Steinman, 1987; Treisman, 1988; McLeod, Driver, & Crisp, 1988; Wolfe, Cave, & Franzel, 1989; Duncan & Humphreys, 1989; Treisman & Sato, 1990). Finally, parallel search (i.e., flat slopes) has also been shown for "high-level" features, such as depth from shading (Ramachandran, 1988; Kleffner & Ramachandran, 1992), three-dimensional structure (Enns & Rensink, 1990), surface representation (He & Nakayama, 1992), and, finally, differential familiarity on the part of the subject for the target and the nontarget elements (Wang, Cavanagh, & Green, 1994; Johnston & Schwarting, 1997).

These exceptions to the dichotomy between feature and conjunction search are certainly of great interest for the understanding of search mechanisms in general. In the following discussion, however, I will not focus on these exceptions. Rather, I will take feature and conjunction search tasks as prototypical task examples that have often been demonstrated to produce flat and non-flat search functions, respectively, and that supposedly do and do not involve serial mechanisms. Finally, and most relevantly to the spirit of this article, I will focus on "traditional" feature and conjunction search tasks because of their wide use in recent cognitive neuroscience studies.

However, what could be the neuronal mechanisms underlying visual search performance with feature-defined and conjunction-defined targets, that is, with arrays yielding flat and non-flat slopes, respectively? To explain search for feature-defined targets, authors have often referred to the known functional architecture of the primate visual system, in particular to the fact that different properties of the visual scene (color, edge orientation, texture, motion, and depth) are at least partly represented in specialized, retinotopically organized maps (De Yoe & Van Essen, 1988; Livingstone & Hubel, 1988; Zeki & Shipp, 1988; Desimone & Ungerleider, 1989). Within each of these independent maps, simple features are supposedly registered in parallel across the entire visual scene.

Moreover, one property of neurons at several (perhaps all) stages of the visual system may be sufficient to account for feature search. Visually responsive neurons tend to discharge more vigorously to an effective stimulus in their receptive field (RF) when this stimulus differs from stimuli in the RF surround (i.e., in the "local" background) (Blakemore & Tobin, 1972; Maffei

& Fiorentini, 1976; Fries, Albus, & Creutzfeldt, 1977; Nelson & Frost, 1978; Allman, Miezin, & McGuiness, 1985a, 1985b; Schein & Desimone, 1990; Gilbert & Wiesel, 1990; Knierim & Van Essen, 1992; Lamme, 1995: Raiguel, Van Hulle, Xiao, Marcar, & Orban, 1995; Zipser, Lamme, & Schiller, 1996; Xiao, Raiguel, Marcar, & Orban, 1997). Starting in the retina, neurons throughout the visual hierarchy code some form of contrast between one region of the visual field and the neighbouring regions. In our example, units in some feature map responsive to the red target will benefit from chromatic contrast (the red circle is surrounded by green circles), while the neuronal response to any green circle will be relatively attenuated by the lack of chromatic contrast (any green circle is largely surrounded by other green elements). Feature (or pop-out) search can then be explained by the fact that units responsive to the target (e.g., the red circle) will be more active than any of the units responsive to the nontarget elements in the array (e.g., the green circles). In different terms, units coding the red target will produce a local maximum in the feature map sensitive to the color of the elements. This local maximum is not reduced by increasing the number of array elements; hence the independence from this number of the time needed to complete feature search. Indeed, it has been shown that search for a feature-defined target may even benefit from a higher density of the array, which can be accounted for by the fact that a higher array density may strengthen the feature contrast, or local mismatch, signal (Sagi & Julesz, 1987; Bacon & Egeth, 1991; Bravo & Nakayama, 1992).

This account of feature search is entirely in terms of center-surround interactions in the visual system, producing an enhanced signal for the target relative to the signal for any of the nontargets. I should note, however, that the original proposal by Treisman (Treisman & Gelade, 1980) was that feature targets could be effectively detected by simply monitoring the pooled activity in the feature map selective for the feature value distinguishing the target from the nontargets. Simply put, in order to decide whether an array of green elements contains a single red element (the target), it is sufficient to assess whether any above-baseline activity is present in the feature map for the color red.

I should also point out that, although search for feature-defined targets proceeds in parallel without the involvement of limited capacity processing, this need not imply that spatial attention is not ultimately aimed at the target location, once preattentive mechanisms have extracted the target from the multielement array. In fact, by presenting a post-array probe stimulus at varying locations, it has been shown that focal attention is summoned to the target location in a reflex-like fashion soon after the onset of a pop-out display (Kim & Cave, 1995, Luck & Hillyard, 1995). Furthermore, focal attention to the target may actually be necessary for the subjects to produce a conscious, deliberate response (e.g., Duncan, 1985; Riddoch & Humphreys, 1987; and see below).

The explanation for the search of conjunction-defined targets was straightforward as well. In this case, search was thought to be time consuming because it requires serial deployment of spatial attention to the individual elements in the array (Fig. 1, A & B).

More specifically, it was proposed that perception of certain types of targets – notably, targets defined by conjunctions of elementary features (e.g., color and shape) – can only proceed within the focus of spatial attention. Focal attention was thus suggested to be critical for the binding of the constituent features of an object. Conjunction targets are extracted from the array only when the scanpath of focal attention intersects their location, allowing the correct combination of features. This is the core of Treisman's "Feature Integration Theory" (Treisman & Gelade, 1980; Treisman & Sato, 1990; Treisman, 1993).

An alternative view

Although appealing in several ways, the above dichotomy between parallel and serial mechanisms underlying different forms of visual search has been disputed in recent years (e.g., Duncan & Humphreys, 1989; Wolfe, Cave, & Franzel, 1989; Duncan, 1996). One alternative view is that all kinds of search task can be solved by a parallel, competitive mechanism (Duncan & Humphreys, 1989; Duncan, 1996). This mechanism, whether engaged for the search of feature-defined or of conjunction-defined targets, is based on mutual inhibitory interactions among units activated by the various elements in the array (objects in the visual scene).

I have noted above that pop-out search can be accounted for with reference to center-surround interactions at several stages of the visual system. More specifically, the degree of activation attained by neurons responsive to the target (the red circle) will be higher than the degree of activation attained by neurons responsive to any green element in the array. If we accept the hypothesis that array elements must compete to access perceptual awareness (visual short-term memory) and to gain control of overt behavior, this imbalance in the degree of activation will result in a relative competitive advantage of the "red units" over the "green units."

Let us now imagine that an observer has to find a red vertical bar embedded among green vertical bars and red horizontal bars. Let us also accept that color and orientation are coded in separate feature maps. Contrary to what happens with a pop-out array, in this case none of the array elements (including the target) will automatically gain supremacy over the other elements due to its uniqueness. None of the elements will stand out as a feature singleton. Competitive models can nevertheless explain how the target is selected in such an array.

The fundamental proposal is that units within a feature map with contrasting stimulus preferences are part of a reciprocal inhibitory network. Any gain in relative

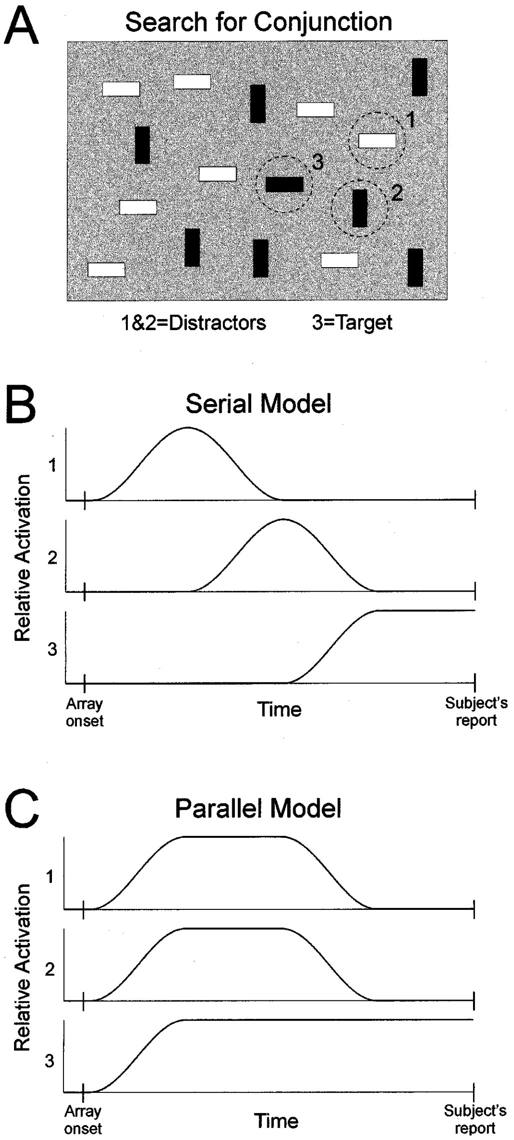

Fig. 1 Example of a conjunction search array and schematic illustration of two alternative neuronal mechanisms which might underlie target detection with such an array. **A** Search array where the target element, a black horizontal bar, is presented among white horizontal and black vertical nontargets. The target is therefore defined by a specific conjunction of its "color" and orientation properties. The numbers *1* and *2* indicate two nontarget elements, one of each type, while the number *3* corresponds to the target in the array. These numbers also indicate three hypothetical RFs (*dashed circles*), each including one array element. **B** Schematic description of the underlying neuronal mechanisms according to the serial model. The three panels, from 1 to 3, show the firing behavior of the corresponding neurons, whose RFs are indicated in Fig. 1A. On the x axis is the time from array onset and until the subject's report. On the y axis is the relative degree of activation in arbitrary units. In this example, nontargets *1* and *2* are sequentially assessed before focal attention is directed to the target *3*. Correspondingly, activity of neuron *1* is high soon after array onset, followed by activation of neuron *2*, in turn followed by persisting activation of neuron *3* due to focusing of attention onto the target location. Here I do not make any specific commitment to which visual structures, cortical and/or subcortical, might display such a neuronal behavior. The only assumption is that neurons in the hypothetical structures would show much greater activation for an attended than for an unattended effective RF stimulus, a property that, for instance, has been documented in areas of posterior parietal cortex of the behaving macaque (Lynch et al., 1977; Robinson et al., 1978; Bushnell et al., 1981; Steinmetz et al., 1994; Robinson et al., 1995; Colby et al., 1996). **C** Schematic description of the neuronal underpinnings according to a parallel, competitive model. The three panels again illustrate the activity of the three neurons whose RFs are indicated in Fig. 1A. According to parallel models, neurons responsive to any of the array elements become concurrently active shortly after stimulus onset, and activity remains high for a certain period of time. Then, as competition among the array elements starts to resolve, only the neuron coding the target element continues to fire, while all other neurons are progressively suppressed. Although not shown, it might well be that, as neurons coding the various nontargets start to be suppressed, the neuron coding the target undergoes further enhancement, now being released from the inhibitory action exerted by neurons responsive to the nontargets

degree of activation for some groups of units will then result in a relative disadvantage for other groups of units. The competitive interactions among units with contrasting stimulus preferences can be biased by a top-down signal specifying task-relevant information, like the feature composition of the searched-for target. As a consequence, in our example all the red elements and all the vertical elements in the array will gain a relative supremacy in the color and orientation maps, respectively.

In addition to the effects exerted on the competitive interactions by the top-down, biasing signal, the combination and interplay of grouping and figure-ground segmentation principles should be a good predictor of the extent to which different stimuli in the visual scene (i.e., different neuronal populations within a map) will enjoy mutual support or suffer mutual antagonism (Duncan & Humphreys, 1989). This scheme can explain competition within each feature map and within-map selection. However, how can this relative advantage of red and vertical selective units resolve in an overall supremacy of the conjunction-defined target over all nontarget elements?

The second property of the postulated competitive mechanism is that units coding the individual features of an object in separate maps support each other (Duncan, 1996). This can arise, for example, because the different features of an object share the same or a similar spatial location. In a sense, shared location acts as a common feature that preattentively binds together the different properties of an object through a mechanism of co-ordinated activity across separate feature maps. Shared location may be just one of the factors that determine conjoined representation ("common fate") of the different features of an object. Here, too, grouping and figure-ground segmentation principles may determine whether or not certain features in the scene (and the corresponding units in the feature maps) belong together to form a perceptual object (see, e.g., Driver & Baylis, 1989; Baylis & Driver, 1992; Baylis, Driver, & McLeod, 1992).

Because units in different feature maps with corresponding RF locations are proposed to support one another, only units responsive to the features of the target will benefit from a double advantage – the advantage for redness in the color map and the advantage for verticality in the orientation map. Within the network of multiple feature maps, units coding for the different properties of the target will eventually gain overall supremacy relative to all other units activated by the different properties of the nontargets (Fig. 1C). According to this model, the degree of activation for any given element in the array, and its competitive weight, will be proportional to the overall degree of similarity between its properties and the advance description of the target.

Although I have outlined the computational scheme of this competitive model using a typical conjunction search task, one central aspect of this model is its extreme flexibility as to the kind of information that can control target selection. Any simple feature, feature conjunction, global object property, or categorical class, acting as a target template, is supposedly able to bias competitive interactions among the elements in the array. Thus, for instance, in my previous analysis of the mechanisms for detecting a simple feature target I have emphasized a pure bottom-up mechanism, which entirely rests on the computation of a feature contrast (or local mismatch) between the target and the surrounding nontargets. In light of the competitive scheme just described for conjunction search, however, it is clear that top-down signals are bound to influence feature search as well. The advance description of the distinguishing property is likely to give the feature target an additional competitive advantage over nontarget elements in the array. It is clear by now why competitive models of this sort challenge the concept of a fundamental distinction between feature and conjunction search.

Also, a recent report by Joseph and his colleagues (Joseph, Chun, & Nakayama, 1997; see also Rock, Linnett, Grant, & Mack, 1992) stands against a strict dichotomy between effortless feature search and attention-demanding conjunction search. They had their subjects search a circular array centered on fixation for the presence of a pop-out target (an oriented Gabor patch among Gabor patches of orthogonal orientation) and at the same time identify a white letter element presented at the center of gaze in a rapid stream of otherwise black letters. Contrary to the idea that pop-out search is not reliant on attentional resources, engaging the subjects in the letter identification task produced a marked decrement in search performance (percentage of correct reports), with target letter-to-search array stimulus onset asynchronies of up to about 500 ms. This result seems to indicate that even simple feature search depends critically on attentional resources. However, we should be cautious in interpreting this finding. It is one thing to say that feature defined targets can be *extracted* from the search array without the intervention of focal attention to the individual array elements, or even without distributed attention to the entire display area; it is a completely different thing to recognize that (focal or distributed) attention to the preattentively extracted target may be necessary to produce a deliberate report about its presence (Duncan, 1985; Riddoch & Humphreys, 1987). As Treisman puts it, "Preattentive processing cannot directly affect responses or experience; it is an inferred stage of early vision which I attribute to the separate feature modules. Before any conscious visual experience is possible, some form of attention is required..." (Treisman, 1993, p. 13). This corresponds to saying that even in feature search, attention may act as the gateway to a post-perceptual processing stage of phenomenal awareness and response selection.

The slope of the search function and the "dwell time" of attention

Non-flat search functions provide *prima facie* evidence for the involvement of a serial mechanism in certain kinds of visual search. However, arguments against this interpretation come, among others, from the following data and considerations. First of all, search slopes have been found to vary in a continuous manner from a few to over one hundred milliseconds per added item (Treisman & Gelade, 1980; Quinlan & Humphreys, 1987; Wolfe, Cave, & Franzel, 1989; Duncan & Humphreys, 1989). Variability per se is not too problematic for serial models. The time needed to complete the perceptual analysis of each item might well increase as the elements in the array become more complex, or better as the target becomes increasingly more similar to the nontargets (and the nontargets more heterogeneous; e.g., Farmer & Taylor, 1980; Carter, 1982; Treisman & Gormican, 1988; Duncan & Humphreys, 1989). Nontargets that are highly homogeneous and easily discriminable from the target can be rejected more rapidly than nontargets sharing one or more properties with the target.

More difficult to accommodate within the framework of serial models is the fact that sometimes search slopes for conjunction-defined targets can be of only 10 or less ms per item (e.g., Wolfe, Cave, & Franzel, 1989). According to the serial scanning model, processing of each item should involve the following steps: (1) focusing of spatial attention onto its location, (2) completion of the perceptual analysis of the item, (3) comparison of the perceptual representation of the item to a memory template, and (4) shift of spatial attention to a new location. Intuition tells us that these four cognitive steps, however fast, should engage brain activity for a somewhat longer period of time than 10 ms or so. However, apart from intuition, an abundant literature now suggests that attentive processing tends to remain locked onto a single visual object for a time period in the order of hundreds rather than tens of milliseconds. For instance, when subjects are asked to attentively process two visual targets presented at the same or a different spatial location with varying interstimulus intervals, processing efficiency of the second target in the sequence is reduced for interstimulus delays of up to ~500 ms (see literature on the so-called "attentional blink" and "dwell time" of attention: Broadbent & Broadbent, 1987; Raymond, Shapiro, & Arnell, 1992; Duncan, Ward, & Shapiro, 1994; Ward, Duncan, & Shapiro, 1996). This seems to indicate that, when assigned to a given stimulus, resources for the attentive processing of a second stimulus are not entirely free for a long period of time, certainly much longer than any study of search would have predicted on the basis of the slope of the search function. If attentive processing of a visual stimulus can take up to several hundreds of milliseconds, how can serial scrutiny of search arrays take only a handful of milliseconds per added item?

Several counter-arguments can be raised against these objections. First, as suggested by a number of authors (e.g., Treisman, 1982, 1988; Pashler, 1987; Treisman & Gormican, 1988; Treisman & Sato, 1990; Poisson & Wilkinson, 1992), with certain arrays the focus of spatial attention might encompass several elements at a time. Perceptual analysis could then proceed for all these elements in parallel. In this case, search slopes would represent only a very crude estimate of the serial component of the search operations. Related to this proposal, it has also been suggested that parallel mechanisms could first parse array elements into perceptual groups, on the basis of their feature composition, and then reject *en block* one or more of these groups for their dissimilarity to the feature composition of the searched-for target (Farmer & Taylor, 1980; Bundesen & Pedersen, 1983; Egeth, Virzi, & Garbart, 1984; Wolfe, Cave, & Franzel, 1989). Serial scrutiny would thus be restricted to just the elements that have survived this initial, parallel stage of processing (Wolfe, Cave, & Franzel, 1989).

In addition, one might argue that findings on the "dwell time" or "attentional blink" are not directly pertinent to the interpretation of the search slopes. For instance, even though attentional resources are not *entirely* free for a new visual object for several hundreds of milliseconds with temporally dispersed displays (i.e., with sequential presentation), deployment of attention and perceptual analysis might be carried out much more efficiently with spatially dispersed displays (i.e., with simultaneous presentation).

One possibility might be that the interplay between the four aforementioned cognitive steps in serial scrutiny be optimized by partially overlapping them in time. This is reminiscent of the *overlap model* put forward some years ago by Harris and her colleagues (Harris, Shaw, & Bates, 1979; Harris, Shaw, & Altom, 1985). At any given moment, for example, perceptual analysis and matching to a mnemonic template might be carried out for one element in the array while spatial attention is already shifted and engaged onto another element for taking up and queuing new information to be processed. After all, different cognitive operations are at least in part carried out by different brain structures and circuits, and what appears as an orderly temporal sequence of cognitive operations might well correspond to a partially concurrent activation of the responsible neural circuits, optimally orchestrated to achieve maximal task performance. However elaborate it may sound, this possibility is plausible and should be tested experimentally. Building interpretations and drawing conclusions about the mechanisms underlying one type of behavior (visual search) on the basis of data and concepts derived from other tasks ("dwell time" or "attentional blink" tasks) seems risky at best.

However, how can the competitive model outlined previously account for non-flat search functions? Such a model asserts that target selection results from competitive interactions among the neural populations coding the various array elements. The model can easily explain non-flat search functions and, most importantly, search functions varying in a continuous manner between a few to over 100 ms per added item. The basic concept is that within a competitive network, the time taken for the competition to resolve in favor of the target element depends on the combined effects of three factors: the degree of similarity between the target and the nontargets, the degree of homogeneity among nontargets, and, finally, the number of elements in the array. At one extreme, when target and nontargets are very dissimilar and nontargets are identical to one another (like in pop-out), the number of array elements has no effect because each added nontarget will in no way increase "noise" in the system and will not prolong the competition process. The target representation acquires immediate dominance over the nontarget representations. At the other extreme, when the target and the nontargets share several properties and the nontargets are very diverse from one another, any added nontarget will greatly increase the amount of noise in the system and substantially prolong the competition. Many nontargets in the array will in fact benefit from a certain degree of activation (competitive weight), due to their similarity to the target template. These issues have been treated in great detail by Duncan and Humphreys (1989) and will not be further discussed here.

This kind of parallel, competitive model has one additional tenet that helps explain non-flat slopes with certain kinds of arrays. The starting-point is that in a competitive network, the total amount of activation is constant. If the processing of the array elements depends on a fixed-capacity pool of resources, then increasing the number of elements will lead to a greater fractionation of the resources available for the processing of each individual element, which will in turn lead to increased time needed to complete the analysis of the entire array and for competition to resolve (Atkinson, Holmgren, & Joula, 1969; Duncan & Humphreys, 1989; Bundesen, 1990; Townsend, 1990).

However, there exists a further piece of behavioral data supporting serial models. When searching for a conjunction-defined target, subjects typically take longer to decide that the target is absent than to decide that it is present, and sometimes this difference is expressed by a ~2:1 ratio of the relative search slopes (Treisman & Gelade, 1980). This is perfectly compatible with serial search models. If search is assumed to be self-terminating (i.e., it is interrupted upon detection of the target) with target-present arrays, on average, the target will be found after scrutiny of one half of the array elements. In contrast, subjects will not be able to decide that a target is absent from the whole array before scrutiny of all the elements in it: hence the two-to-one ratio. We should again be cautious with this interpretation, however. First, a two-to-one ratio has not been found in all studies (e.g., Wolfe, Cave, & Franzel, 1989), and the truly robust finding is that it usually takes longer to decide for the absence than for the presence of a target. Second, such a result can easily be explained without calling into play any serial mechanism. Let us consider any kind of difficult search, be it search for a conjunction-defined target or something else, which produces a non-flat slope. According to parallel competitive models, resolving the competition takes increasingly longer with the number of elements because of the added noise to the system introduced by any added element and the greater fractionation of the limited capacity resources (Duncan & Humphreys, 1989; Bundesen, 1990). In other words, perceptual evidence for the presence of a target builds up more slowly as the number of elements is increased. Conceivably, subjects might also have to wait longer before they can decide for the absence of a conjunction-defined target than for its presence, much for the same reason. Deciding for the presence of a target relies on a signal that emerges from a noisy background of neural activity; deciding for the absence of a target relies on the absence of such a signal and more specifically on the ability to discard any random fluctuation of the background neural activity (noise) as a potentially meaningful signal. In a variety of non-search perceptual tasks requiring subjects to report the presence or absence of a given signal, reaction times are significantly longer in the latter condition.

All the issues we have discussed in this section leave several questions unanswered. Are non-flat search slopes indicative of serial scrutiny, or can they be accommodated within the framework of parallel competitive mechanisms? Does the attentive processing of a visual object take tens of milliseconds, or hundreds? Can steeper slopes for target-absent than for target-present arrays be taken as evidence in favor of serial scrutiny? Obviously, more empirical data or new ways of reasoning are still needed.

Evidence from functional brain imaging and transcranial magnetic stimulation studies

So far, we have reviewed and discussed some findings and notions largely based on behavioral observations with human subjects. In the following sections we turn to recent studies using a variety of cognitive neuroscience approaches and methodologies. Once more, while a number of findings from these more recent studies might seem to indicate that some search arrays require the intervention of serial scrutiny, others recommend caution with this conclusion.

In a recent experiment using positron emission tomography (PET), local changes in cerebral blood flow were measured while human observers searched visual arrays for targets defined by color, by speed of motion, or by a conjunction of color and speed of motion (Corbetta, Shulman, Miezin, & Petersen, 1995). Search slopes were flat for feature-defined but not for conjunction-defined targets. The main finding in the study, however, was that search for conjunction-defined targets, but not search for feature-defined targets, led to a blood-flow increase in a region of the posterior parietal lobe (superior lobule), particularly of the right hemisphere. Even more importantly, this local activation matched very closely the activation of the same region obtained in a previous study (Corbetta, Miezin, Shulman, & Petersen, 1993) in which subjects were to perform successive shifts of spatial attention. Thus, the same neural machinery appears to be involved both in a task requiring covert shifts of spatial attention and in a task requiring search for a conjunction-defined target. The authors inferred that, if this parietal region was active during shifts of spatial attention, then the reason why it was also active during conjunction search must be that conjunction search also involves shifts of covert attention. Hence comes the conclusion that conjunction search does presumably involve serial scanning of the array elements with spatial attention (Corbetta, Shulman, Miezin, & Petersen, 1995).

Two recent studies cast doubts on the notion that activation of posterior parietal cortex (superior lobule and intraparietal sulcus) is such a unique signature of spatial attention shifts. In one preliminary report by Wojciulik and her colleagues (Wojciulik, Kanwisher, & Driver, 1997), subjects were asked to monitor a rapid stream of letter stimuli presented at fixation in order to detect the onset of a target letter. In different trial blocks, subjects searched either for a conjunction or a feature target, while their brain activity was measured using functional magnetic resonance imaging (fMRI). Monitoring for conjunction targets resulted in increased blood flow in the intraparietal sulcus bilaterally. Thus, even when spatial shifts of attention are not implicated, attentive processing of certain types of stimuli may be accompanied by activation of posterior parietal cortex.

Related to the previous study, Vandenberghe and his colleagues (Vandenberghe et al., 1997) using PET have recently shown a robust activation of posterior parietal cortex, particularly in the right hemisphere, when subjects were required to discriminate the orientation or the relative location of a grating stimulus presented in the periphery of the right or left visual hemifield. In addition to a widely distributed network of cortical areas, this activation included both the intraparietal sulcus and the superior parietal lobule. When both properties of the same grating stimulus were to be reported, several of the areas activated during the discrimination of either individual property were further enhanced, notably right superior parietal cortex, left superior parietal cortex, and left intraparietal sulcus. The authors of this study put forward two accounts of the parietal activation. On the one hand, as already demonstrated in a previous PET experiment (Vandenberghe et al., 1996), parietal activation may be associated with maintained attention to extrafoveal targets, as opposed to central targets, arguing for a role of parietal cortex in the attentive processing of peripheral events. On the other hand, activation in the same general region during nonspatial tasks suggests that parietal cortex may have a general, non-spatial role in maintaining cognitive readiness or alertness (Pardo, Fox, & Raichle, 1991; Coull, Frith, Frackowiak, & Grasby, 1996). Again, as in the study of Wojciulik et al. (1997), consecutive shifts of attention do not appear to be a critical factor to produce parietal activation.

In summary, while the research of Corbetta and his colleagues (Corbetta, Shulman, Miezin, & Petersen, 1995) points to a critical role of posterior parietal cortex in conjunction search, other functional brain-imaging studies (Wojciulik, Kanwisher, & Driver, 1997; Vandenberghe et al., 1997) suggest that such a role in conjunction search may not necessarily relate to the execution of sequential shifts of visuospatial attention. An increased processing effort (whether foveal or peripheral), and/or sustained focal attention to peripheral stimuli might be sufficient to engage circuitry in posterior parietal areas.

In the macaque, the pattern of anatomical connectivity along with the physiological properties of the neurons have led to a subdivision of the posterior parietal cortex into a number of areas (e.g., Andersen, Asanuma, Essick, & Siegel, 1990; Colby, Duhamel, & Goldberg, 1993; Andersen, Snyder, Bradley, & Xing, 1997). Each of these areas is specialized both in terms of its dominant sensory input and its competence with respect to motor output (e.g., eye vs. arm movements). Most certainly, a similar constellation of areas also exists within the homologous cortex in humans, not to speak of the complicating factor of hemispheric specialization. Thus, in addition to disclosing the critical task variables that activate posterior parietal cortex, a primary goal for future functional brain imaging research will be to separate the cognitive operations contributed by the different subdivisions within this general region.

The results of a recent study with transcranial magnetic stimulation (TMS) are consistent with an involvement of posterior parietal cortex in tasks requiring detection of a conjunction-defined target (Ashbridge, Walsh, & Cowey, 1997). The rationale for the experiment was similar to the rationale underlying the study of Corbetta et al. (1995). Again, subjects were asked to search visual arrays for a target defined by color, by orientation, or by a combination of color and orientation. Non-flat search slopes were obtained only in the conjunction search condition. At various times after onset of the array, single pulses of magnetic stimulation, known to produce temporary dysfunction of the stimulated tissue, were applied to the right (and left) parietal region of the experimental subjects. When applied at a specific time after array onset (100 ms after the onset of target-present arrays and 160 ms after the onset of target-absent arrays), TMS of right posterior parietal cortex impaired performance in conjunction search but not in feature search. Impairment consisted of an increase in RT but was not accompanied by an increased error rate.

At first glance, these findings might seem compatible with the idea that serial scanning of the array elements, impaired by TMS of right posterior parietal cortex, is crucial to perform conjunction search. The story, unfortunately, is a little more complicated. In discussing their findings (with target-present arrays), the authors of this study entertain three possible explanations for the disruptive effect of right parietal stimulation. Obviously, the first account suggests that TMS interfered with the control mechanisms that shift an attentional window to the different array elements. However, as the authors recognize, "if the increase of RTs caused by TMS were due to delaying individual shifts of attention, the efficacy of TMS should be relatively evenly spread across all stimulation times." There remains a possibility – however remote – that the specific time at which TMS produced its effects corresponded to a critical phase during which the scanpath of the attentional shifts was first programmed or started. The second, somewhat fuzzy, interpretation is that TMS interfered with the "tuning of the spatial attention mechanism," that is, with setting up a spatial attention process which operates with a fine spatial resolution, as required by conjunction search. This possibility is more consistent with the finding of a narrow time window during which TMS was effective. Also, it predicts that perhaps the number of array elements should have little or no effect on the placement of this time window. The third interpretation is that TMS may disrupt the normal interplay between areas of the "what" occipito-temporal stream of cortical visual processing and areas of the "where" occipito-parietal stream (Ungerleider & Mishkin, 1982). In particular, areas in the ventral stream might send weighted signals corresponding to the feature composition of the various array elements to instruct spatial attention mechanisms in parietal cortex about the likely target locations. TMS might disrupt the delivery to right parietal cortex of such weighted signals.

Contrary to what was suggested by the authors (Ashbridge et al., 1997), however, I argue that this hypothesis predicts that increasing the number of array elements, as well as increasing the target-nontarget similarity and the nontarget-nontarget heterogeneity, should affect the critical time of TMS. All these factors should in fact increase the time needed to compute "likelihood" weights in occipito-temporal areas and delay delivery of these weighted signals to posterior parietal cortex.

At any rate, the possibility of drawing firm, general conclusions from this study is seriously limited by two features of the experimental design. First, TMS was only applied at time delays of 0–200 ms post-array onset, even though the subjects' average reaction time to report the presence of a conjunction-defined target was over 700 ms. What would have been, if any, the effect of TMS at 200–700 ms post-array onset? Second, TMS was only applied in trials with an array size of eight elements, thus preventing us from knowing whether the sensitive period for TMS would have been invariant across different array sizes.

Whichever the specific nature of the contribution given by parietal circuitry to visual search, the general concept of a tight link between (right) posterior parietal cortex and (conjunction) search tasks yielding non-flat slopes is strengthened by a subsequent TMS experiment by Walsh and his colleagues (Walsh, Ashbridge, & Cowey, 1998). Efficiency of search has sometimes been shown to increase with extensive practice (Schneider & Shiffrin, 1977; Steinman, 1987; Ellison & Walsh, in press), as indicated by a substantial decline of the search slopes. Walsh et al. (1998) confirmed this finding. They had their subjects search arrays of 3, 8, or 16 elements for the presence of a green vertical bar among green horizontal and blue vertical bars. Subjects performed the task for about 500 trials per day, usually for five consecutive days. Improved performance with practice was revealed by a reduction of the search slope from an average of 24 ms/item on the first day to 8 ms/item on the last day of testing. More importantly, while TMS of the right parietal cortex had a significant impact in the initial phase, when subjects produced relatively steep search slopes, it later became completely ineffective, once practice had taken place and search slopes had become very shallow. The effect was strictly stimulus-material specific. After extensive exposure to a given set of array elements, leading to flat slopes and insensitivity to right posterior parietal TMS, switching to a new set of array elements reinstated both non-flat search slopes and sensitivity to TMS of the critical right parietal locus.

In general, brain imaging and TMS studies strongly support the notion of a specific and critical involvement of posterior parietal cortex (particularly of the right hemisphere) in tasks requiring detection of a conjunction-defined target. The evidence is still very questionable, however, that this involvement is distinctively related to the putative role of posterior parietal cortex in controlling serial shifts of visuospatial attention. It seems indeed wiser, at present, to entertain this possibility along with several others, some of which have already been considered. I would like to make one final comment on these results from functional brain imaging and TMS studies. The available data seem to indicate a qualitative distinction between search tasks using feature- and conjunction-defined targets. This distinction might be more apparent than real. Future attempts to explore with these methods the neuronal mechanisms underlying visual search might gain deeper insight from manipulating task difficulty in a parametric fashion, as attested by the slope of the search function. Contrary to the notion of a qualitative difference between feature and conjunction search (Duncan & Humphreys, 1989), using search tasks of increasing difficulty might, for instance, reveal a progressively more important recruitment of parietal tissue.

Findings from brain-damaged patients

One central tenet of Feature Integration Theory is that the constituent features of an object are correctly combined only with the aid of focal attention. In keeping with this notion, several studies have shown that the constituent features of simultaneously presented objects (e.g., a red square and a blue triangle) can be miscombined (subjects report seeing a red triangle or a blue square) if focal attentive processing is prevented, for instance with short exposure duration and/or a secondary, attention-demanding task (Prinzmetal, 1981; Treisman & Schmidt, 1982; Prinzmetal, Presti, & Posner, 1986; Eglin, 1987; Cohen & Ivry, 1989; Cohen & Rafal, 1991; Ivry & Prinzmetal, 1991; Lasaga & Hecht, 1991; but see Johnston & Pashler, 1990; Tsal, Meiran, & Lavie, 1994).

In addition, illusory conjunctions can be a consequence of brain lesions which disrupt the normal functioning of spatial attention (Arguin, Cavanagh, & Joannette, 1994; Friedman-Hill, Robertson, & Treisman, 1995). Perhaps the most dramatic demonstration of illusory conjunctions in a brain-damaged patient is contained in a recent report by Friedman-Hill and her colleagues (Friedman-Hill et al., 1995). In this study, a patient with Balint's syndrome following bilateral parieto-occipital damage was presented with pairs of colored letters, and the patient's task was to report the identity and color of the first letter he saw. The rate of illusory conjunctions was 13%, even in the absence of any competing, attention-demanding task, and even when display duration was as long as 10 s (see also Robertson, Treisman, Friedman-Hill & Grabowecky, 1997, for a more systematic description of this patient's cognitive deficits). Similarly, Arguin and his colleagues (Arguin et al., 1994) reported a particularly high percentage of illusory conjunctions (~25%) in the right hemifield of a group of eight left-hemisphere damaged patients. These same patients had previously been shown to have a severe deficit in attending to contralesional stimulation.

Several studies have also directly investigated performance in visual search tasks following localized brain damage accompanied by visuospatial attention deficits (e.g., contralesional hemineglect). What would one predict to be the consequence of an altered control of spatial attention on search for feature and conjunction targets?

If one accepts that conjunction search is critically dependent on serial attention shifts, while feature search is not, one might predict a very severe impairment in the former task but not in the latter. Specifically, one might predict that conjunction search be seriously affected on three grounds. First, the slope of the search function for conjunction-defined targets might become much steeper than normal, due to a very laborious deployment of focal attention to the individual array elements in turn. Second, search might become fallacious due to a deficit in the correct binding of the features belonging to the individual items (see above). Third, detection of conjunction-defined targets presented contralaterally to the lesion might be impaired due to an overall reluctance to orient toward the contralesional half space (and/or an abnormal difficulty to disengage attention from ipsilesional items). These predictions are only partially supported by findings in brain damaged patients.

Riddoch and Humphreys (1987) tested search performance for single-feature and feature-conjunction targets in three patients with contralesional neglect following a right hemisphere lesion. As in normal humans, the rate of search for a feature target was independent from the number of array elements, both in the right and in the left hemispace. Also, no clear difference in search latency was observed between feature targets presented in the ipsilesional versus contralesional half of the display. However, patients incurred many more misses for detecting feature targets contralateral than ipsilateral to the lesion, indicating that attention may play a critical role even with feature-defined targets. As suggested by the authors, attention may have to be drawn to the information specified by preattentive vision, for its conscious detection to occur (Duncan, 1985; Joseph et al, 1997).

When tested with conjunction targets, patients displayed the typical set size effect (i.e., an increase of RT to detect the target as a function of the number of array elements). The slope of the search function, however, was steeper for contralesional than for ipsilesional targets. Finally, more targets remained undetected when shown in the contralesional compared to the ipsilesional half of the array. The last two results are in accord with the notion that serial shifts of attention may be necessary to support the perceptual analysis of conjunction-defined array elements. This conclusion is nevertheless put into question by the effect of one additional manipulation tested in the study. When the patients were cued to orient contralaterally to the lesion by being asked to identify a letter stimulus presented at the left edge of the display, all the signs of impairment substantially ameliorated, both for feature and for conjunction targets. This indicates that, once an overall reluctance to orient to the side contralateral to the lesion (and/or abnormal difficulty disengaging from the elements on the ipsilesional side) is overcome, even search for conjunction-defined targets can proceed almost normally in these patients. One caveat about this study is that head/eye position was not controlled, and cueing may have instigated overt orienting responses to the side opposite the brain lesion, thus bringing the whole search array into the intact half space.

In addition, the results from the study of Eglin and her colleagues (Eglin, Robertson, & Knight, 1989) pose some difficulty for the simplistic notion that search for conjunction-defined targets, but not feature-defined targets, depends on the normal functioning of spatial attention. They assessed search performance in a group of seven patients showing severe contralesional hemineglect following a unilateral brain lesion. Patients were presented with search arrays confined to either half space or across the midline, and containing a feature-defined or a conjunction-defined target. First of all, at variance with the behavior of control subjects, search for feature targets yielded non-flat search functions. Second, search rates to locate both a feature- or conjunction-defined target, although lower than normal, were the same on the two sides of space as long as no distractors were present on the opposite side. Adding distractors on the ipsilesional side, however, severely disrupted search of both types of contralesional targets, while distractors on the contralesional side had no effect on search performance in the ipsilesional half space. The overall pattern of results seems to suggest that (a) locating both feature and conjunction targets may require attentional processing, albeit to a different extent, and (b) the deficit with both kinds of search array is better understood in terms of difficulty in disengaging attention from the ipsilesional array elements rather than a fundamental inability to process array elements appearing in the contralesional half space (Posner, Walker, Friedrich, & Rafal, 1984). Again, it should be noted that, since patients were allowed to move their eyes and head, hemispace did not correspond to visual hemifield, and this might have affected performance, especially with arrays confined to either half of the display area.

A very careful study of the search deficits deriving from unilateral brain damage was performed by Arguin and his colleagues (Arguin, Joannette, & Cavanagh, 1993). They tested a group of three patients with left-brain damage who had previously been shown to have difficulty in directing spatial attention to the contralesional right hemifield. In contrast to the previous studies of Riddoch and Humphreys (1987) and of Eglin et al. (1989), central fixation during stimulus presentation was controlled in this study. Search arrays containing a varying number of elements (1, 2, 3, or 4) were presented to each hemifield in isolation, and the target was defined either on the basis of a single feature (orientation, Exp. 1, or color, Exp. 2) or of their conjunction (Exp. 3). These patients showed a marked deficit in conjunction search for displays presented to the contralesional right hemifield, compared to their performance with displays in the opposite left hemifield and compared to the performance of two control groups: one of age-matched neurologically intact individuals, and a second group of left-hemisphere damaged patients without signs of attentional deficit. Slopes for conjunction search in the right visual hemifield were more than two times as steep in the patient group with the attention deficit than in the two other groups (168.8 vs. 67.1 and 68.9 ms/item). Search for feature-defined targets presented to either visual hemifield was completely unaffected in the same patients.

Following a set of arguments, the authors maintain that the most likely explanation of their main finding is "an increase in the time necessary to integrate the features of a contralesional item once attention is focused at the location it occupies." Thus, they obviously favor an interpretation in complete accordance with Feature Integration Theory. This very thorough study thus stands in strong support to the view that focal attention may be critical for the perceptual processing of conjunction-defined stimulus elements. It now becomes crucial that these findings be replicated by other authors, in particular to see whether they would hold true in *right* parietal damaged patients with contralesional attention deficits (hemineglect and extinction).

In summary, only the study by Arguin et al. (1993) suggests a qualitative difference between search for feature and conjunction targets. The other two studies reviewed here (Riddoch & Humphreys, 1987; Eglin et al., 1989), in contrast, suggest that performance in both kinds of search task deteriorates, though to a different extent, following a brain lesion accompanied by attentional deficits (neglect). Once more, there seems to be ground to suspect that feature and conjunction search tasks might simply represent the extreme cases on a continuum of task difficulty. Neuronal mechanisms based in posterior parietal cortex might just become progressively more critical as task difficulty increases.

An account of the behavioral deficits following localized brain damage in terms of a parallel, competitive model of attentional selection can be found in recent reviews by Desimone and Duncan (Desimone & Duncan, 1995; Duncan, 1996; and see below).

Taken together, the aforementioned results from functional brain imaging and TMS studies, as well as the observations with brain-damaged patients, do not appear to resolve the long-standing question of the involvement of serial mechanisms in some forms of visual search. I believe that evidence for this involvement is still quite inconclusive. What these findings rather invariably demonstrate is simply a critical contribution of posterior parietal tissue in tasks requiring search for a conjunction-defined target and the likely critical role of focal attention in these tasks. However, what could be the role of attention mechanisms, other than the serial scrutiny of the array elements? I will come back to this question in a later section.

Can the answer come from single-cell recording studies in behaving monkeys?

A few years ago we conducted a series of studies on the neuronal mechanisms underlying search for complex visual objects in the inferior temporal (IT) cortex of the behaving macaque monkey (Chelazzi, Miller, Duncan, & Desimone, 1993; see also Chelazzi, 1995; Chelazzi, Duncan, Miller, & Desimone, 1998). Animals were trained to search an array of 2–5 elements for the presence of a target stimulus that matched a previously presented cue and to make a saccadic eye movement to it. The location of the target in the array was varied randomly from trial to trial, so that the animal had to find it based on its non-spatial attributes. Stimuli consisted of complex objects, like colored patterns, human body parts, plants, and fruits. Search for this kind of stimuli resulted in non-flat search functions, with a slope of ~25 ms/element for target-present arrays. While the animals were performing the task, the activity of single neurons was recorded extracellularly from the most anterior and ventral portion of IT cortex.

Two main findings were obtained (Fig. 2). First, many cells that were selectively responsive to a particular cue stimulus at the beginning of the trial continued to discharge at a higher-than-baseline rate during the delay interval of 1.5–3.0 s between cue offset and onset of the search array. Second, many cells showed large and sustained responses to their effective sensory stimulus in the array when this was the target in a given trial (as it matched the preceding cue), while responses to the same stimulus were profoundly suppressed in trials where it was a nontarget. Particularly important, the response to the effective sensory stimulus in the array, depending on it being a target or a nontarget in different trials, did not differentiate for the first 200 ms or so post-array onset. In this early phase, responses to targets and nontargets were on average indistinguishable. Beginning at about 200 ms post-array onset, however, which was about 100 ms before the animals made the saccade to the target in the array, responses to nontargets started to be suppressed, and suppression continued to develop through the time of saccade execution. Recordings from the extrastriate area V4 have revealed a similar modulation of neuronal responses to targets and nontargets (Chelazzi & Desimone, 1994). These results imply that, some time before the animal delivers its behavioral response, the neuronal representation of nontarget stimuli in areas of the occipito-temporal stream of cortical visual processing becomes progressively weaker, while at the same time these areas convey information almost exclusively about the stimulus of interest. This information, available in visual cortex much prior to the saccade, could then be passed on to structures more directly implicated in the programming and execution of eye movements, such as the frontal eye field and the superior colliculus, where target-related activity has also been documented (Glimcher & Sparks, 1993; Schall & Hanes, 1993; Schall, Hanes, Thompson & King, 1995).

Findings from this study have been taken to support a Biased Competition model of visual search for complex objects (Chelazzi et al., 1993; Chelazzi, 1995; Desimone & Duncan, 1995; Desimone, 1996; Duncan, 1996; Duncan, Humphreys, & Ward, 1997; Luck, Chelazzi, Hillyard, & Desimone, 1997; Chelazzi et al.,

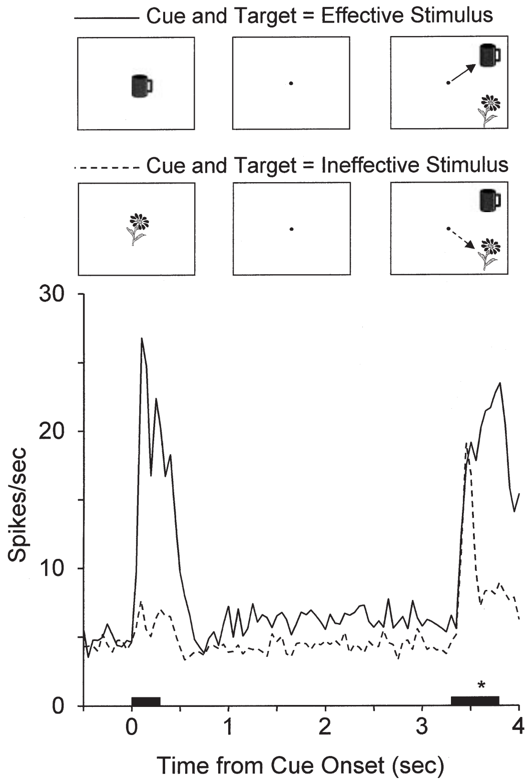

Fig. 2 Schematic illustration of the task design and results in the study of Chelazzi et al. (1993). As shown in the two sets of panels on top, each trial began with presentation of a cue stimulus at the center of gaze, which the animal had to retain in short-term memory. After a blank delay interval, an array was presented in the periphery of the visual field at random locations, and the monkey was rewarded for making a saccadic eye movement to the stimulus in the array that matched the initial cue. For the data shown here, the search array consisted of only two stimuli, but arrays of 1, 3, and 5 stimuli were used as well. The cue and target corresponded to the effective sensory stimulus for the recorded cell (exemplified by the cup) in some of the trials (first set of panels at the top), while in other trials the cue-target stimulus was the ineffective sensory stimulus (exemplified by the flower; second set of panels from the top). As shown in the histograms below, average responses to the cue stimulus of a group of 20 IT neurons were much higher when the cue was the effective than the ineffective stimulus. Also, after the cue had been extinguished (the black horizontal bar at the bottom left of the plot indicates cue duration), cells maintained a higher level of sustained firing following the effective than the ineffective cue. Finally, when the array was presented (the black horizontal bar at the bottom right of the plot indicates array duration), the initial neuronal response was about the same whether the effective stimulus in the array was the target or the nontarget. Starting about 200 ms post-array onset, however, which is about 100 ms prior to saccade onset, neuronal activity remained high only when the effective stimulus was the target, while it dropped to near baseline level when the ineffective stimulus was the target and the effective stimulus was the nontarget. The asterisk indicates average saccade latency. Modified from Chelazzi et al., 1993

1998). As noted previously, the biased competition model asserts that stimuli in the visual field compete for limited-capacity processing. Competition in visual cortex can be biased by top-down signals coding task-relevant information, like the advance description of the searched-for target. The single-unit data fulfil all the criteria required for this competitive model (Fig. 3).

The elevated firing during the delay interval of units selective for a given cue stimulus can be viewed as the neuronal correlate of a mnemonic template of the searched-for object. This signal, in addition to storing a mental representation of the cue-target stimulus in a given trial, might also prime cells to react differently to the subsequent stimuli in the search array. More specifically, as the neuronal populations coding the various elements in the array engage in the competitive process, cells that have been activated by the cue stimulus – and are again activated by the target – might be positively biased against cells that are activated by the nontarget elements in the array. If, say, a given neuron produces a vigorous response to a red apple presented as the cue and also maintains a higher firing rate during the delay period, then when a search array is presented comprising the red apple along with one or more additional stimuli, this neuron might enjoy a competitive advantage against the neurons activated by the nontarget stimuli. In other words, the mnemonic signal reflected in the sustained activation during the delay might tip the balance of the competitive interactions in favor of the cell populations coding the different properties of the target. This view obviously points to a very tight functional link between active memory signals (working memory) and the attentional selection of task-relevant stimuli at the expense of task-irrelevant ones (Desimone, 1996). Specific models of this general computational scheme have been developed in recent years (e.g., Phaf, van der Heijden, & Hudson, 1990; Usher & Niebur, 1996).

However, why are these findings in line with a parallel, competitive model of target selection? The competitive model predicts that the multiple objects present in a complex scene will activate, in parallel, their respective neuronal representations in visual cortex. Then, as the competition among these representations starts to resolve in favor of the target, only the target representation will remain active, while neuronal populations contributing to the representations of the nontarget stimuli will become more and more suppressed. Our findings that *initial* responses in V4 and IT are the same regardless of whether the effective sensory stimulus for the individual cell is the target or a nontarget in the array suggests parallel, initial encoding of all the array elements. Then, the fact that *later* only cells responsive to the target continue to discharge supports the idea that the target representation wins the competition against the representations of the nontargets.

This interpretation is rather appealing, for it can parsimoniously account for visual search of complex visual objects with mechanisms that are entirely manifest at the level of a single neuron: the mnemonic coding of task-relevant information during the delay, and the gradual suppression of responses to nontargets. The data, as they stand, can nonetheless be interpreted otherwise. In order to explain this, I need to go into some

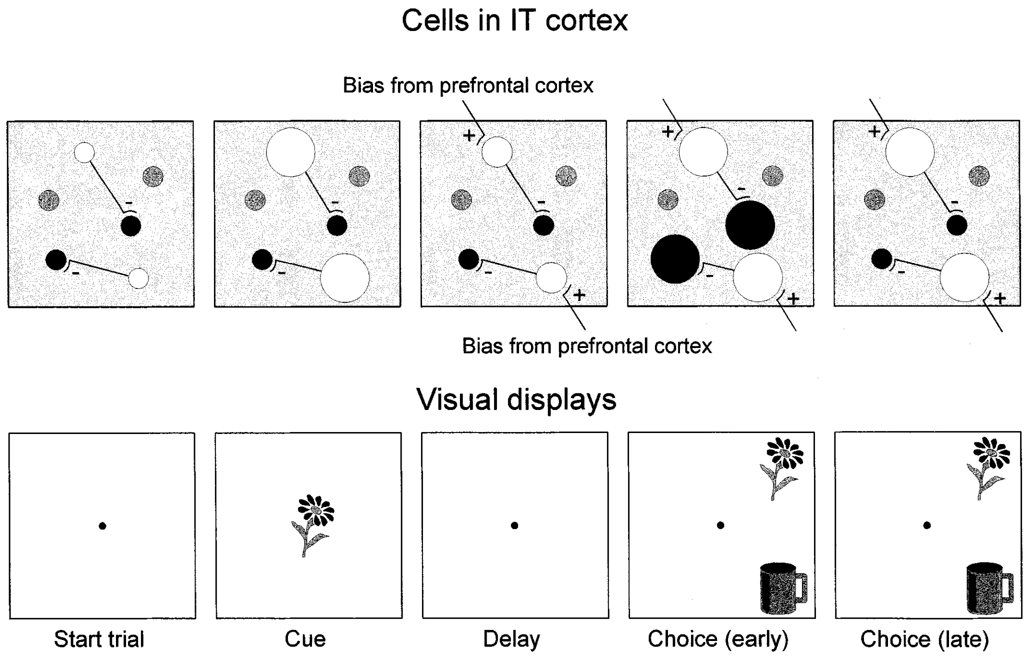

Fig. 3 Schematic description of the main phases of the search task with two-stimulus arrays confined within the hemifield contralateral to the recording side, and of the pattern of activity in a representative population of IT neurons. The lower diagrams illustrate the visual displays during the relevant portions of the task. Each dot in the upper diagrams represents an individual neuron, and the size of the dot indicates relative firing rate. A specific cue (here exemplified by the flower) activates the subpopulation of IT cells tuned to any of its features. During the delay period, this subpopulation maintains a higher level of sustained activation, relative to other cells that are not fired by the cue stimulus. When the search array is first presented, both the target and the non-target initially activate neurons for which they represent effective sensory stimuli. Later, starting about 100 ms prior to saccade onset, the cells tuned to the properties of the target stimulus remain active, whereas cells tuned to the properties of the nontarget are suppressed. This late divergence in activation may depend on competitive interactions within IT cortex, here schematically depicted by the inhibitory influence from cells activated by the view of the flower onto cells activated by the view of the cup. This inhibitory influence is obviously reciprocated by one running in the opposite direction, that is, from cells activated by the view of the cup onto cells activated by the view of the flower (not shown). Also, we hypothesize that competitive interactions within IT cortex are under the top-down control exerted by projections from prefrontal cortex (see Chelazzi et al., in press). In a given trial these projections give a competitive advantage (positive bias) to cells in IT coding the cue-target stimulus in that trial, at the expenses of cells coding the nontarget. Reprinted with permission from Chelazzi et al., 1998

details of the experimental strategy we followed to study the effect of target selection on neuronal activity in IT.

Since the majority of IT neurons have large RFs that comprise most of the central visual field, it was impractical to have only one array element falling within the RF boundary and then compare the activation elicited by the stimulus when it was a target versus when it was a nontarget. For this reason we adopted a strategy first developed by Moran and Desimone (1985) to study the effects of spatially selective attention on the activity of IT cells. According to this strategy, even when two or more stimuli are simultaneously presented inside the individual RF, only one stimulus is rendered “visible” to the cell under study, while the other stimuli are rendered essentially “invisible” to the same cell. This is achieved by respectively selecting stimulus properties to which a given cell is either responsive or unresponsive. To this aim, as we proceeded to investigate any individual neuron, the first step was to measure the neuronal response to a predetermined set of stimuli in order to select one stimulus that could drive a vigorous response from the cell (an effective sensory stimulus) and one or more additional stimuli that were completely ineffective. Let us, for instance, take the simple case of an array composed of only two elements. This array was obtained from the combination of the effective and one of the ineffective stimuli for the recorded cell (Fig. 2, panels at the top right). The excitatory response elicited by such an array reflected only the processing of the effective stimulus. Therefore, we could test the effects of target selection by measuring the response of the neuron when the effective sensory stimulus in the array was the target in a given trial versus when it was a nontarget. That is, we compared responses to the same, identical array when this had been preceded by the effective versus the ineffective sensory stimulus as the cue. Typically, we had about 20–30 trials per condition (per cell) for this comparison.

Now the question is: how different are the predictions made by the serial and parallel models regarding this comparison? I indicated earlier which predictions are made by the parallel model. Initially, as the representations of the two array elements are activated in parallel, the response elicited by the array should be the same, regardless of whether the effective sensory stimulus is the target or the nontarget. Later, as the competition resolves in favor of the target, the neuronal response to the array should remain high when the effective sensory stimulus is the target, while it should become suppressed when the target is the ineffective sensory stimulus in the array. As already noted, this is exactly the pattern of results that we observed in our IT and V4 recordings. However, are we really in the position to reject the predictions made by the serial models?

According to serial models, array elements are assessed in temporal sequence. At any given time, only the neuronal representation of one element is active (except for the processing stage, in which elemental features are preattentively registered), with the representation of the target always being active last, before the behavioral response. Given the simplified array of two elements, which in fact we used for much of our recordings, serial models predict that on half the trials, on average, the target should be sampled first (and last), while on the other half of the trials the nontarget should be sampled first, followed by the target. Let us now imagine, for the sake of the argument, that a serial mechanism was at work in our study.

We know from the work by Moran and Desimone (1985) that spatial attention gates the responses of IT neurons, such that the firing rate of a given cell reflects primarily the RF stimulus corresponding to the current attentional focus, while other stimuli within the same RF are filtered out. Extrapolating to our paradigm, one can imagine that neuronal activity should have been high whenever focal attention was aligned with the effective stimulus in the array and low whenever it was aligned with the ineffective stimulus. As schematically illustrated in Fig. 4, two types of serial scanning sequences (scanpaths) might have occurred, both in trials where the effective stimulus was the target (Fig. 4A) and in trials where the ineffective stimulus was the target (Fig. 4B). Specifically, when the target was the effective sensory stimulus, there might have been a mixture of trials where focal attention was first directed to the ineffective stimulus and then the effective one, and trials where focal attention was directed to the effective stimulus at first, with no need for additional shifts. Similarly, when the target was the ineffective stimulus, there might have been a mixture of trials where focal attention was first aligned with the effective stimulus and then with the ineffective one, and trials where focal attention was directed to the ineffective stimulus at first, again with no need for any additional shift.

In neurophysiological experiments of this sort it is customary to average firing rates across all available trials collected in any specific condition in order to reduce the intrinsic, random variability in the activity of nerve cells. The histograms shown in Fig. 2, for instance, were obtained by averaging both across a population of IT cells and, for each contributing cell, across all the available trials. As stated previously, the histograms appear consistent with the tenets of the parallel, competitive models. However, it is clear by now that averaging might have arbitrarily combined trials in which the scanpath of attention, and consequently the pattern of

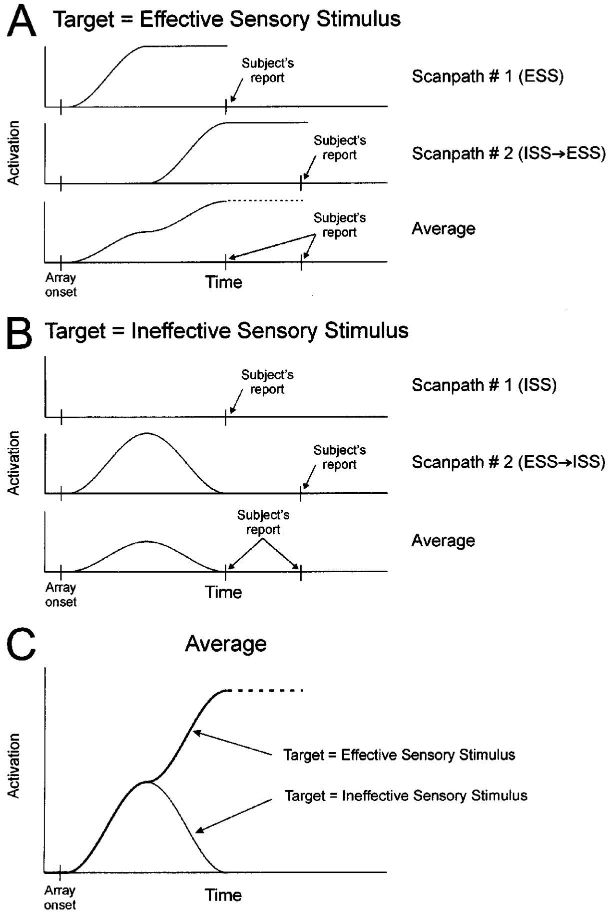

Fig. 4 Schematic illustration of how across-trial averaging might conceal a serial component in the response of IT neurons to the search array, thus mimicking a pattern of activity more compatible with a parallel, competitive mechanism. **A** The two panels on top describe the activity of the same hypothetical IT neuron recorded during the course of two different trial types in which the effective stimulus was the target. In the upper panel the effective sensory stimulus (ESS) is sampled first (and last) by the focus of attention. Consequently, neuronal activity is high through the time of the behavioral response. In the second panel from the top, the scanpath of attention first intersects the ineffective sensory stimulus (ISS), followed by the effective one. Activity starts to build up only after an initial period of suppression. Note that during this initial period, in spite of the fact that an effective stimulus is present inside the RF, activity remains low because the effective stimulus falls outside the focus of attention (Moran & Desimone, 1985). The bottom panel shows the pattern of activity obtained after averaging the data recorded during scanpath #1 and #2. **B** The same logic as in Fig. 4A is applied, but now for trials where the ineffective sensory stimulus is the target. In the upper panel the ineffective sensory stimulus is sampled first and last. In the second panel from the top the ineffective stimulus is sampled only after the effective one. The bottom panel shows the pattern of activity obtained after averaging the data recorded during scanpath #1 and #2. Note that in all cases where the ineffective stimulus is being sampled, activity is made equal to baseline, even though in the study of Moran and Desimone (1985), as in other studies of spatial attention in visual cortex (e.g., Luck et al., 1997), ignoring an effective RF stimulus does not typically cause the activity of the neurons to drop to the baseline level, that is, suppression is never absolute. **C** The bottom panels from Fig. 4A and Fig. 4B are superimposed for comparison. The average neuronal activity, obtained after pooling together simulated trials with differing scanpaths of serial scanning, mimics the pattern of response observed in our study of IT neurons during visual search (Chelazzi et al., 1993)

neuronal activity and the behavioral performance, were different.

Following this reasoning, we indeed looked for the existence of two distinct populations of trials in both experimental conditions, that is, in trials where the effective stimulus was the target and in trials where it was the nontarget. We did this both for the neural data and the saccadic reaction time (sRT) data. In neither case were we able to discern any sign of bimodal distribution. While these negative findings might stand in further support of a parallel, competitive model, caution is obligatory. Other sources of random variability across trials in neural as well as sRT data might have smeared the underlying, putative bimodal distributions into a unimodal appearance.

One might wonder at this point how a single-unit recording experiment could ever overcome the aforementioned difficulties and provide results that help understand the mechanisms of visual search. If the hypothesis to be tested is that some types of search array require serial scanning, one general approach to avoid the problems outlined above might be for the experimenter to infer or to control the scanpath of attention. If this were feasible, analysis of the neuronal responses as a function of time could reveal a pattern of activation consistent with the orderly deployment of focal attention to the various elements along the scanning path. An additional general strategy might be to try to reduce as much as possible the inter-trial variability, such that neural and behavioral data might tend to fall into as many distinct populations in the distribution as there are elements in the array. Also, future single-unit recording experiments might test to what extent the results obtained in our study generalize to search arrays made of other types of stimuli, such as the more traditional feature- and conjunction-defined arrays. Finally, in addition to measuring neuronal activity in areas of the occipito-temporal stream of cortical visual processing, like V4 and IT, it would be of great interest to record from areas of the occipito-parietal stream of processing, such as areas LIP and 7a, which have long been implicated in the control of spatial attention (Lynch, Mountcasle, Talbot, & Yin, 1977; Robinson, Goldberg, & Stanton, 1978; Wurtz, Goldberg, & Robinson, 1980; Bushnell, Goldberg, & Robinson, 1981; Colby, 1991; Steinmetz, Connor, Constantinidis, & McLaughlin, 1994; Robinson, Bowman, & Kertzman, 1995; Colby, Duhamel, & Goldberg, 1996).

One attempt to provide direct neurophysiological evidence for the existence of a selection mechanism operating in parallel across the visual field has been contributed by a recent single-cell recording study by Motter (1994a). In this study a circular array of four or six oriented bars was presented around fixation. Half of the bars were of a certain color (or luminance) and the other half of a different color (or luminance). The color (or luminance) of the fixation target, serving as a selection cue, indicated which of the two stimulus subsets was relevant in a given trial and which was irrelevant: the subset having the same color as the fixation target was relevant, the other one was irrelevant. After a variable delay, only two stimuli in the peripheral array remained visible, one from the relevant and the other from the irrelevant subset. At this time the monkey had to discriminate the orientation of the bar stimulus of the relevant color (or luminance).

The main result in the study was that, in the delay interval during which the entire array was still visible, responses of V4 neurons to a bar presented inside their RF were much larger if such stimulus was part of the relevant subset than if it was part of the irrelevant subset. Interestingly, this effect was engendered both by a continuously available selection cue (Motter, 1994a) and by the memory of the same cue, briefly presented at the beginning of the trial and then turned off (Motter, 1994b). These findings imply that in a complex visual scene, multiple spatially dispersed stimuli can be selected in parallel when they are all potentially relevant to the task at hand. In the particular task design used in this study, selection of multiple relevant stimuli was based on color or luminance features, but an analogous selection mechanism might be accessible for any other type of feature or even for feature conjunctions.

Several considerations limit the general contribution of this study. First, as acknowledged by the author (Motter, 1994b), one might conjecture that during the delay period the monkey was actually scanning the multiple relevant stimuli in the array with a focal attention mechanism, instead of selecting all of them in parallel. Note that with arrays of four or six total elements, only two or three elements were relevant in any given trial, so that the hypothetical focal mechanism did not have to be diverted away from any one of them for much of the time. Motter argues that this is unlikely, since the neuronal response to the relevant RF stimulus appeared to maintain a constant level, without any major interruption. It is rather difficult to assess the validity of this statement from simple inspection of the published histograms (Motter, 1994a, 1994b). One way of directly testing this possibility would be to measure the response to a relevant RF stimulus, averaged across the entire delay period, as a function of the total number of relevant elements in the array. By definition, an unlimited-capacity parallel mechanism does not predict any reduction in the average response to a relevant RF stimulus as a function of this number. The opposite prediction is made by a serial scanning model (or a limited-capacity parallel mechanism). For instance, with arrays comprising two or three relevant elements, focal attention should be aligned with any such element one-half and one-third of the time, respectively (ignoring the time spent "in flight" between elements), and the average firing rate of the neurons should be reduced in proportion to this fraction. More generally, the averaging of single-unit data across trials may pose interpretational difficulties as to the neuronal mechanisms underlying a variety of perceptual and motor tasks (e.g., see Basso & Wurtz, 1997, for a similar potential artefact).

There might be an additional problem in the experiments of Motter (1994a, 1994b), as pointed out by Newsome in a recent review article (1996). In a typical neurophysiological experiment examining a retinotopically organized visual area, RF location remains pretty much constant across weeks or months (or years!) of daily data collection. This is because, in a given monkey, access to the cortical region of interest is usually constrained by the initial positioning of the recording chamber and the limited opening of the overlying skull. As a consequence, the animal tends to receive much more frequent visual stimulation in the area of the RF, relative to the rest of the visual field, if only for the painstaking procedure of mapping its boundaries. This, in turn, might encourage the animal to develop a consistent positional bias in favor of the RF location. If this were the case, what appears as a selection mechanism operating in parallel across the visual array could instead be explained with a tendency to direct focal attention toward the stimulus in the RF. There are two ways around this potential, albeit unlikely, artefact. One would be to avoid any positional bias in the experimental procedure. A second one would be to record from multiple electrodes simultaneously and measure the activity of neurons whose RFs cover distant elements in the array. If the selection mechanism were genuinely parallel, then neurons responding at different locations in the visual field would display an identical pattern of activity.

However, even if the effect reported by Motter (1994a, 1994b) was indeed generated by a selection mechanism operating in parallel across the entire visual field, it remains to be established what role it might play in visual search. Typically, visual search tasks require the subject to locate a single target in a multielement array, whereas in the experiments of Motter, the animals were to "preselect" a number of potential targets and to filter out the other elements in the array. The preliminary, attentional parsing of the visual array in relevant and irrelevant elements based on their feature composition is likely to represent a critical stage of processing (e.g., Wolfe, Cave, & Franzel, 1989). However, search performance might often involve an additional stage where, either by means of a serial or of a parallel, competitive mechanism, selection must eventually settle on a single target among the preselected stimuli of interest.

Notably, as in our study of V4 and IT neurons in visual search (Chelazzi et al, 1993; Chelazzi & Desimone, 1994; Chelazzi et al., 1998), also in this study by Motter (1994a), responses of V4 neurons were initially unaffected by whether the RF stimulus was of potential relevance or not. Although the selection cue was available well in advance, responses started to correlate with selection of the RF stimulus only 150–200 ms post-array onset, in keeping with the idea that competition among neuronal representations may take a significant amount of time to resolve in favor of task-relevant information. One might actually regard this temporal delay before the competition settles as an adaptive mechanism evolved to allow task-irrelevant information to gain temporary access to central processing mechanisms and, if advantageous, to "interrupt" the existing stimulus processing schedule.

As with the evidence from cognitive neuroscience approaches in humans, also the single-unit recording studies discussed in this section do not allow a decision whether serial attention mechanisms are implicated in visual search tasks yielding non-flat slopes. In fact, although some potential problems with analysis of the neuronal data recommend caution, the results of Chelazzi and his colleagues from recordings in area V4 and IT seem more compatible with a Biased Competition Model of target selection. Once more, future experiments will have to provide additional evidence against or in favor of this preliminary interpretation.

Summary and general discussion

In this section I will first summarize the main conclusions derived from the cognitive neuroscience work discussed in this article. Then, I will try to fit these conclusions to serial and parallel accounts of effortful visual search, thereby suggesting conceptual constraints for the development of these models. Thus, what have we learned from the survey of the cognitive neuroscience literature?

The lesson from single-unit experiments in behaving macaques (Chelazzi et al., 1993, 1998) can be summarized here in a sentence. Although the available evidence is fully compatible with a parallel, competitive model of target selection, methodological constraints have so far limited our ability to demonstrate or to disprove the involvement of serial mechanisms in visual search. More experimental work is needed.

As shown by the study of Corbetta et al. (1995) with PET, posterior parietal activation, particularly in the right hemisphere, is specific to effortful, conjunction search, as opposed to simple, feature search. As indicated by other imaging studies (Wojciulik et al., 1997; Vandenberghe et al., 1997), however, an analogous parietal activation can also be observed in the absence of sequential shifts of visuospatial attention. Increased processing effort (whether foveal or peripheral), and/or sustained focal attention to peripheral stimuli lead to recruitment of circuitry in posterior parietal cortex, as well.

Similar considerations can be made about the studies with TMS. The reports by Ashbridge et al. (1997) and by Walsh et al. (in press) demonstrate that normal functioning of (right) posterior parietal cortex is critical in conjunction search tasks yielding non-flat search functions. A detailed analysis of their results, however, does not support the idea that this involvement is related to the execution of serial shifts of attention. TMS impairs performance only when delivered in a very narrow sensitive period after array onset, and this seems incompatible with the view that it prevents the orderly shifts of focal attention to individual array elements in turn.

Let us finally turn to the observations with brain-damaged individuals. In general, these data are quite difficult to combine into a coherent picture, as is often the case in neuropsychology for a number of factors (e.g., variability in the precise location and extent of the lesion). In general, visual search performance in the contralesional hemispace is seriously altered following brain damage leading to attention deficits (neglect). A clear-cut dissociation between feature and conjunction search, however, is reported in one study (Arguin et al., 1993) but not in others (Riddoch & Humphreys, 1987; Eglin et al., 1989). Also, both in the study of Riddoch and Humphreys and in the study of Eglin et al. (1989), efficiency of search within the contralesional hemispace becomes virtually normal once an overall reluctance to orient to that space is overcome by experimental manipulations. As with the data from brain imaging and TMS, it seems reasonable to infer from the neuropsychological evidence that posterior parietal cortex, and presumably the attention mechanisms to which it contributes, are perhaps more critical in certain types of search tasks than in others. It does not readily follow that the role of parietal tissue is to control sequential shifts of focal attention to the array elements.

In conclusion, the results from functional brain imaging and TMS, and from the study of brain damaged patients, do not prove the intervention of serial shifts of attention in visual search. They do, however, demonstrate very forcefully that some search arrays, typically those yielding non-flat slopes, require the intervention of mechanisms located in the (right) posterior parietal cortex.

How can some of the existing models of visual search accommodate these findings? I will first consider the parallel, competitive model described in this article.

This model has proven very successful at explaining a large body of behavioral data, including positive search slopes varying in a continuous manner between a few to over 100 ms per added item (Duncan & Humphreys, 1989). Also, it can easily explain why performance can be greatly facilitated when observers are allowed to use feature information to restrict search to a subset of the array elements (Farmer & Taylor, 1980; Bundesen & Pedersen, 1983; Egeth et al., 1984). Further support for the competitive model comes from experiments showing that feature and conjunction search tasks may not be inherently different, and both rely on limited-capacity resources (Duncan, 1985; Duncan & Humphreys, 1989; Joseph et al., 1997).

We have also seen that, albeit with an important caveat, neuronal data from extrastriate and inferotemporal areas of the behaving monkey are fully consistent with a Biased Competition Model of target selection (Chelazzi et al., 1993, 1998; Chelazzi, 1995; Desimone & Duncan, 1995; Duncan, 1996). The neuronal representations of competing objects become active at the same time after array onset. As the competition starts to resolve, however, only task-relevant information continues to be represented in visual cortex.

At least in part, the parallel, competitive model can also explain the pattern of behavioral deficits observed in brain-damaged patients. As argued by Desimone and Duncan (1995; Duncan, 1996; Duncan et al., 1997), the attentional deficit found in these patients is the consequence of an enduring competitive imbalance against visual stimuli normally represented in the lesioned part of the brain. This, for instance, would explain why the patients in the studies of Eglin et al. (1989), and of Riddoch and Humphreys (1987) perform virtually normally in the contralesional hemifield, once a strong ipsilesional bias is overcome. Any loss in the representational strength (competitive weight) for some of the stimuli in the scene necessarily results in a gain of dominance by the other competing stimuli. This imbalance can be reverted by a number of factors (Duncan, 1996).

Problems for the competition model come, I believe, from the functional brain imaging and TMS results discussed previously, which point to a specific involvement of posterior parietal cortex in effortful search. According to this model, the computational machinery responsible for selecting a relevant visual object among other, irrelevant objects in the scene is distributed across most (if not all) of the visually responsive structures in the brain (Desimone & Duncan, 1995; Duncan, 1996). One of the central tenets of the model is that there is no such thing as an attentional center or even an attentional network. Attentional phenomena are the result of a distributed property of the brain. Specifically, they are built on the pervasiveness in the central nervous system of a competitive (i.e., reciprocal inhibitory) network architecture. It is therefore hard for the model to explain why in the more demanding search tasks, but not in the easier ones, posterior parietal cortex seems to play such a critical role.

The fact, in itself, that posterior parietal cortex takes part in target selection in visual search is not at odds with the competitive model. This was made especially clear in recent formulations by Duncan (1996; Duncan et al., 1997). We know that the primate cortex contains twenty and more visual areas, in the occipital, parietal, and temporal lobes, and that they are partly specialized for the analysis of different properties of the retinal input (De Yoe & Van Essen, 1988; Livingstone & Hubel, 1988; Zeki & Shipp, 1988; Desimone & Ungerleider, 1989). In addition to areas that are primarily visual, several additional regions of cortex are activated by visual input – for instance – the premotor cortex and frontal eye field. Finally, visually related activity is recorded in a number of subcortical structures, including the superior colliculus, the basal ganglia, and the pulvinar. In his Integrated Competition Model, Duncan (1996; Duncan et al., 1997) suggests that, when a given stimulus in the scene becomes the object of attention, its neuronal representation gains supremacy against all other stimuli across most of the visually activated areas, cortical and subcortical, visual and premotor. It comes as no surprise, then, that posterior parietal cortex is involved in tasks requiring selection of task-relevant information. What is not accounted for by the model is why this involvement should be specific, for example, to more demanding visual search tasks.

Difficult to accommodate within the framework of the competitive model is also the increased probability of illusory conjunctions in patients with unilateral (Arguin et al., 1994) or bilateral (Arguin et al., 1994; Friedman-Hill et al., 1995) brain damage, including the parietal lobe, and leading to attention and visuospatial deficits. The difficulty stems from the fact that, according to the model, the proper conjoining of elemental features occurs preattentively. Common location or other grouping factors automatically parse the objects in the scene from one another and from the background.

It seems to me that future formulations of the parallel, competitive model of target selection will have to account for the more recent cognitive neuroscience data and will presumably have to ascribe some specific computational role to posterior parietal cortex.

Let us now turn to Feature Integration Theory. Since it was first proposed almost 20 years ago (Treisman & Gelade, 1980), this theory has continued to enjoy great popularity among cognitive psychologists and cognitive neuroscientists, as this article testifies. The success is probably due to its being relatively simple, yet at the same time broad enough to offer a general account of visual perception and visual selective attention. As stated at the outset of this article, hallmarks of this model are (1) that the perceptual analysis of complex visual objects, as opposed to simple features, depends critically on focal attention, and (2) that it can only occur for one object at the time, that is, it proceeds serially. It is especially on the latter property that I have focused the foregoing discussion, and it is on this same property that I will focus the analysis below.

As already stated several times, recordings in area V4 and the inferotemporal cortex of the behaving macaque reveal a pattern of neuronal activity fully compatible with a parallel, competitive model of target selection (Chelazzi et al., 1993, 1998; Chelazzi, 1995). At present, it would nevertheless be unwise to conclude that these findings are sufficient to rule out a serial mechanism in search tasks producing non-flat slopes.

Partly consistent with Feature Integration Theory, on the other hand, are the findings with brain damaged patients. First, patients with an attention deficit resulting from brain lesions including the posterior parietal cortex produce an abnormally high percentage of illusory conjunctions (Arguin et al., 1994; Friedman-Hill et al., 1995). Second, especially one study (Arguin et al., 1993) demonstrates a clear dissociation between feature and conjunction search, only the latter being severely disrupted following posterior parietal lesions accompanied by an attentional disorder. As pointed out by the authors (Arguin et al., 1993), several accounts of this finding, all in line with Feature Integration Theory, are tenable.

Although other functional brain imaging studies recommend caution with the more obvious interpretation, the work of Corbetta et al. (1995) can be interpreted in strong support of the Feature Integration Theory and, specifically, of the involvement of serial shifts of attention in conjunction, but not feature search.

At first glance, the results of Ashbridge et al. (1997; see also Walsh et al., 1998) also lend support to the Feature Integration Theory, insofar as they indicate a critical involvement of posterior parietal cortex in conjunction but not in feature search. A closer look at the specific nature of the TMS results, however, shows that they are actually rather incompatible with the notion that conjunction search requires serial attentional scanning of the array elements.

In general, a large proportion of the cognitive neuroscience data reviewed in this article *can* be interpreted in favor of the Feature Integration Theory. It is the behavioral results from normal observers, collected by several authors over the course of many years, that have instead forced a modification of the original theory (Wolfe et al., 1989; Treisman & Sato, 1990; Treisman, 1993). On the one hand, the observation that conjunction search can result in almost flat slopes has challenged the strict dichotomy between two different kinds of search tasks: effortless feature search proceeding in parallel across the visual field, and effortful conjunction search requiring a sequential assessment of individual array elements (Egeth et al., 1984; Nakayama & Silverman, 1986; Pashler, 1987; Steinman, 1987; Treisman, 1988; McLeod et al., 1988; Wolfe et al., 1989; Duncan & Humphreys, 1989; Treisman & Sato, 1990). Similarly, a re-evaluation of the theory has been compelled by numerous observations showing that feature information, applied in parallel across the stimulus array in a top-down fashion, can effectively improve performance in search for a conjunction target (Farmer & Taylor, 1980; Bundesen & Pedersen, 1983; Egeth et al., 1984; Wolfe et al., 1989).

Prompted by these behavioral findings, the more recent developments of Feature Integration Theory, like Wolfe's Guided Search Model (Wolfe et al., 1989; Cave & Wolfe, 1990; Wolfe, 1994; see also Treisman & Sato, 1990; Treisman, 1993), have incorporated and emphasized the important role played by parallel mechanisms of selection even in conjunction search (see below). In a sense, in order to explain some of the available data, serial models of conjunction search have had to incorporate properties of the parallel, competitive models. Indeed, the main reason to maintain a serial stage of processing in these modified versions of Feature Integration Theory – apart from personal preference – is any observed deviation from complete flatness of the calculated search functions. This diagnostic use of the search slopes, however, might once more be flawed, since non-flat slopes may be explained in several other ways (Townsend, 1990; Bundesen, 1990).

Nevertheless, if "hybrid" models like the Guided Search Model of Wolfe (Wolfe et al., 1989; Cave & Wolfe, 1990; Wolfe, 1994, 1996; see also Hoffman, 1978, 1979) can account for behavioral data that instead posed serious problems to the original Feature Integration Theory, then these models seem to represent the best alternative to entirely parallel, competitive models of visual search and should be considered in some detail.

Hybrid models of conjunction search

The Guided Search Model is discussed here as the more popular example of a hybrid model of visual search (Wolfe et al., 1989; Cave & Wolfe, 1990; Wolfe, 1994, 1996). As noted before, it was initially motivated by the observation that search for a conjunction target sometimes produces very shallow slopes, and also by the observation that search for triple conjunctions proceeds more efficiently than it does for simple conjunctions (Wolfe et al., 1989). In addition, it was motivated by the finding that feature information can be used in parallel to restrict search to a subset of the array elements (Farmer & Taylor, 1980; Bundesen & Pedersen, 1983; Egeth et al., 1984; Wolfe et al., 1989). In essence, the model asserts that parallel processes can guide serial, focal attention processes to the location of likely targets.

The basic architecture of the model includes a set of feature maps, just like in Feature Integration Theory, and an Activation Map, also similar to Treisman's Master Map (and Kock & Ullmann's, 1985, Saliency Map). Focal attention is directed to the array element that corresponds to the maximally activated location in the activation map. The fundamental development, compared to Feature Integration Theory, is that the degree of activation at any given location in the activation map, that is, for any array element, depends on the combined inputs from the feature maps to the activation map for that location. In turn, the level of activation in the feature maps for any given element is a function of the degree of similarity between the features of the element and the features of the target. Similar to the competitive model discussed previously, this happens because feature maps are under the control of top-down signals specifying the target features.

For instance, when a subject is instructed to search for a conjunction target, say a red X among red Os and green Xs, all the red elements in the color map and all the X elements in the shape map will attain a higher degree of activation than the green elements and the O elements. As a consequence, the summed amount of excitation in the activation map will be higher for the target than for any nontarget. According to this scheme, any parallel, feature map cannot extract a conjunction-defined target; nevertheless, it can divide the array elements into those that could be the target and those that could not.

If this mechanism were perfect, Wolfe's reasoning goes, attention would be immediately directed to the target location, and search slopes should be independent from set size. More typically, however, several locations in the activation map will pass a certain threshold, and several shifts of attention will have to be made to candidate targets before the target is found.

In summary, according to this model, search for conjunctions is serial, that is, it depends on focal attention to individual array elements in turn, but it is not random. Each time the spotlight of attention is shifted, it goes to the most likely target location, as identified by the ongoing parallel processes. Importantly, for this model there is no qualitative difference between feature and conjunction search. In both cases the parallel processes guide attention to the target. The difference is that in feature search the signal from the feature maps is very strong, and attention is immediately directed to the target. In conjunction search, on the contrary, attention will be directed to more than one location in the array before the target is found, because the signal-to-noise ratio is not as large.

At this point someone might actually wonder what is the reason for hybrid models like Guided Search to maintain a serial stage in their computational architecture? Basically, the reason is to explain the slope, however shallow, of the search functions. As already argued, if the guidance of attention by the parallel processes were perfect, then no serial operation would be necessary, and search slopes would always be flat. This logic, however, is all but compelling. We know that, even if locating the target in the array depended entirely on parallel, competitive processes, several reasons could still account for non-flat slopes, other than the occurrence of serial shifts of attention (Duncan & Humphreys, 1989; Townsend, 1990; Bundesen, 1990). Thus, the question remains of why in the Guided Search Model a serial stage is at all necessary.

Although the motivation to maintain a serial stage of processing seems questionable, it is important to assess to what extent the Guided Search Model can fit the cognitive neuroscience data discussed in this article.

Guided Search is in an enviable position to account for the physiological data collected in the behaving monkey. We have seen that the pattern of neuronal activity from areas V4 and IT is fully compatible with the Biased Competition Model of target selection (Chelazzi et al., 1993, 1998). However, as I have pointed out, caution is mandatory, since the participation of serial attention phenomena might have been concealed by the averaging procedures. Whether or not future single-unit recording experiments were to demonstrate the intervention of serial mechanisms in visual search, the data could easily be accommodated by the Guided Search Model. According to this model, the difference in response to targets versus nontargets can equivalently be viewed as the expression of the parallel selection mechanism operating in the feature maps, or of the consequential focusing of attention onto the candidate target. In the former case, the result would support the idea that top-down information influences the representational strength (weight) for each element in the array according to its similarity to the target. In the latter case, the result would support the idea that focal attention further enhances the neuronal activity related to the target.

Guided Search can also explain the search deficits observed in some brain-damaged patients. For instance, if one were to hypothesize that the Activation Map is implemented in posterior parietal cortex (which seems to be a reasonable guess; see, e.g., Gottlieb, Kusunoki, & Goldberg, 1998), then the impaired search performance in the contralesional space could be explained in several ways. For instance, one could reason that the level of activation for the array elements ipsilateral to the lesion is consistently higher than the level of activation for the array elements on the contralesional side. This would lead to an enduring inability to orient focal attention to a contralesional target. In addition, one could reason that a posterior parietal lesion prevents the normal delivery to the activation map of the weighted signals from the feature maps, thus making the serial attention process wander at random around the stimulus array. Finally, the model can also accommodate the observation that both feature and conjunction search, though to a different extent, suffer from a posterior parietal lesion accompanied by attentional deficits. According to the model, focusing of attention onto the target location is a critical step for all kinds of targets.

For the Guided Search Model, feature and conjunction search tasks are not intrinsically different. The difference that is typically observed in the subjects' performance can be attributed to a different signal-to-noise ratio in the weighted signals fed from the various feature maps to the activation map. As a consequence, conjunction search requires, on average, a greater number of serial shifts before the activation map correctly directs focal attention to the target element. In this perspective, the model could explain why the PET experiment of Corbetta et al. (1995) found activation of posterior parietal cortex in conjunction, but not in feature search.

Finally, the Guided Search Model can perform well at accounting for the results with TMS. TMS, for instance, may disrupt conjunction search because it prevents the delivery to the activation map of the weighted signals computed within each feature map. This, as we saw, is indeed one of the interpretations of their own results offered by the authors of the TMS study (Ashbridge et al., 1997).

In conclusion, both the Biased Competition Model and the Guided Search Model can explain many of the recent findings from the cognitive neuroscience work reviewed in this article. In fact, while the observation that posterior parietal cortex is critically involved in time consuming search tasks poses an interpretational problem for the competitive model, this same finding can be easily accommodated by Wolfe's hybrid model of target selection (see also Treisman's recent developments of Feature Integration Theory: Treisman & Sato, 1990; Treisman, 1993). However, given the remarkable explanatory power of the competitive model (including its account of non-flat slopes), and despite the apparent success of Guided Search, it may be worth conceiving a computational scheme that combines properties of the two classes of models. This is what I will endeavor in the section below.

A personal view

The present article was primarily intended as a critical review of some literature on visual search and especially of some recent attempts to shed light on the mechanisms underlying search performance using a variety of cognitive neuroscience techniques like functional brain imaging and transcranial magnetic stimulation. Nevertheless, I would also like to propose a personal view that tries to move beyond a fundamental dichotomy between parallel, competitive mechanisms and spatial attention (i.e., serial) mechanisms. The hypothesis was prompted by the results discussed previously and was inspired both by the Biased Competition Model of target selection and by Wolfe's Guided Search Model. From the former, it inherits the idea that target selection results from a competition scheme implemented in the distributed representation of incoming visual inputs. The competition is controlled, or biased, by the advance description of the target-distinguishing features. Similar to the competitive model, it also abandons the idea that non-flat search slopes are diagnostic for serial scanning operations. From the Guided Search Model, it inherits the concept of an activation map which controls the orienting of focal processing resources to potential targets. In my view, however, it is the distributed competitive network (rather than the individual maps working independently) that feeds the activation map with inputs specifying the location of the potential target(s).

Thus, the hypothesis that I would like to put forward is that any kind of search task may require the co-operation of parallel, competitive mechanisms and of focal, spatial attention mechanisms. In particular, the hypothesis is that spatial attention mechanisms are recruited to focus processing resources onto *one* candidate target element extracted from the multielement array by the competitive mechanisms.

According to the competitive model, evidence for the existence of a pop-out target accrues very rapidly and efficiently, while it typically accrues slowly and less efficiently with conjunction-defined targets. In the former case, as I have already said, focal attention is automatically engaged onto the target location and may even be indispensable to support phenomenal awareness and explicit report, but is not necessary to extract the target from the multielement array. I propose the term "attentional glimpse" for this rapid alignment of focal attention with a pop-out target. In the case of conjunction search, on the contrary, as some perceptual evidence has accumulated for the presence of a candidate target, and given the relatively slow build-up of this accumulation, focal attention is directed and maintained onto its location for preferential and sustained analysis. More specifically, the intervention of spatial attention would serve to amplify the outcome of the ongoing parallel, competitive mechanism, that is, to augment separation in the strength of neuronal representation between the target and the nontargets, thus allowing the target to enter perceptual awareness and to gain complete control of overt behavior.

According to the present proposal, some recent findings using PET and TMS might be taken to demonstrate that in conjunction search, posterior parietal cortex (especially of the right hemisphere) and the spatial attention mechanisms to which parietal cortex participates may be recruited to perform *not many but one* final shift of focal attention to the candidate target and to maintain focal processing resources on it until the subject produces his or her response. The degree of posterior parietal cortex activation might simply be a function of the processing effort required for the perceptual analysis of the candidate target, that is, of the amount of time during which focal attention is diverted from the center of gaze and maintained onto its location. This could be sufficient to explain the greater activation of posterior parietal cortex in conjunction than in feature search tasks.

There are two main notions in this proposal. One is that the advance description of the searched-for target, by influencing the distributed neuronal populations activated by the various array elements, will invariably have some degree of success in biasing the competitive interactions in favor of the neurons contributing to the representation of the target. This bias, however weak, will tend to make the representation of the target dominant over the representation of the nontargets. The second notion is that, as this dominance develops, and inasmuch as the representation of the candidate target embodies spatial information, the resulting spatial signal will trigger the orienting of focal attention onto its location. This state of affairs presumably involves an interplay between areas of the occipito-temporal stream of cortical visual processing and circuitry in posterior parietal cortex. The former would be responsible for coding the various stimulus features (Desimone & Ungerleider, 1989) and can be thought of as the *battlefield* of the competitive interactions between the target and nontarget representations. The latter, as part of a widely distributed network of brain areas, would be responsible for directing attention in space (e.g., Corbetta et al., 1993; Nobre et al., 1997).

According to the present proposal, in most instances of time-consuming visual search, focal attention is neither instantly captured by the extracted target, like in the effortless pop-out tasks, nor serially shifted to the individual elements of a conjunction search array for an item-by-item perceptual assessment. Focal attention is instead oriented to the one candidate target which is emerging out of the competition process taking place among all the elements in the array. The possibility should not be excluded, of course, that when the similarity between target and nontargets is very high, and the nontargets are very dissimilar to one another, the efficiency of the competitive mechanisms can be so low as to provide no clear signal about the presence and location of a single candidate target element for focal scrutiny. Under these circumstances, search might indeed proceed only through the serial assessment of multiple array elements. This could nevertheless represent more the exception than the rule. In more typical conditions, competitive mechanisms may be successful at providing one candidate target, which is then processed with the aid of focal attention.

In essence, there are three main conceptual differences between Wolfe's Guided Search Model and the present proposal. One is that, in line with competitive models of visual search, my account does not take nonflat search slopes as direct evidence in favor of serial deployment of attention to individual array elements. The second is that, also in accordance with the competitive model discussed in this review, top-down information related to the identity of the target does not necessarily act upon independent feature maps. The competition process takes place simultaneously across multiple feature maps contributing to the representation of the array elements, in a distributed and co-ordinated fashion, and is under the biasing influence of the target template. A third and final aspect in which the present proposal departs from the Guided Search Model, and instead favors the Biased Competition Model, is that the latter rests on a much more thorough and comprehensive treatment of the factors in a search array that make a target easy or difficult to find (e.g., target-nontarget similarity, grouping: Duncan & Humphreys, 1989). On the other hand, the main difference between the present proposal and the Biased Competition Model regards the idea of a critical contribution of parietal cortex, and of the attentional mechanisms housed in it, to effortful search tasks.

Concluding remarks

In this article, I have reviewed and discussed a number of recent contributions bearing on the question of whether subjects engage serial scanning operations to search for conjunction-defined targets. This question, as I have pointed out several times, still remains to be answered. Only converging findings from a broad range of approaches and methodologies will allow us to resolve this long debated issue in cognitive psychology and cognitive neuroscience.

As a working hypothesis, I have outlined a proposal that inherits features of the Biased Competition Model and of the Guided Search Model, thus moving beyond a strict dichotomy between these two alternative accounts of the mechanisms underlying visual search. Following the Biased Competition Model, I have suggested that target selection depends on a competition scheme implemented in the distributed representation of incoming visual input. However, in line with the Guided Search Model, I maintain that, as soon as the competitive mechanism extracts one candidate target (or a few) from the multielement array, a spatial attention control mechanism intervenes to allow focal processing of its properties and to funnel its identity to perceptual awareness (working memory) and to response selection stages.

Following the competitive model, this view can easily accommodate a large body of behavioral data, while at the same time it also offers a possible explanation for the growing evidence in favor of a critical involvement of (right) posterior parietal cortex in effortful search tasks. As suggested by a number of findings, spatial attention is eventually oriented to the target element both in feature and conjunction search. This orienting, however, may correspond to what I have called an "attentional glimpse" in feature search and to a more intensive and sustained focal processing effort in highly demanding search tasks. Without necessarily calling into play the execution of consecutive shifts of attention in tasks producing non-flat slopes, this account could nevertheless explain why posterior parietal cortex appears to be more critical in "difficult" than in "easy" search tasks.

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