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Contributions from cognitive neuroscience to understanding functional mechanisms of visual search

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We argue that cognitive neuroscience can contribute not only information about the neural localization of processes underlying visual search, but also information about the functional nature of these processes. First we present an overview of recent work on whether search for form–colour conjunctions is constrained by processes involved in binding across the two dimensions. Patients with parietal lesions show a selective problem with form–colour conjunctive search relative to a more difficult search task not requiring cross-dimensional binding. This is consistent with an additional process—cross-dimensional binding—being involved in the conjunctive search task. We then review evidence from preview search using electrophysiological, brain imaging, and neuropsychological techniques suggesting preview benefits in search are not simply due to onset capture. Taken together the results highlight the value of using converging evidence from behavioural studies of normal observers and studies using neuroscientific methods.

Over the past decade there has been a substantial growth in the number of studies that use methods from cognitive neuroscience to analyse cognitive processes. These methods either use measures of brain activity (e.g., the

magnitude of the BOLD response in fMRI, the magnitude of a specific component of a stimulus-evoked response potential in ERP recordings), or procedures that intervene with processing at a neural level (e.g., transcranial magnetic stimulation or effects of brain lesions), to provide new data on the neural substrates of cognition. Studies using these techniques to assess visual search have provided important new data on both which neural systems mediate search, and on their time course of operation. For example, experiments using functional brain imaging in humans have consistently demonstrated that search is dependent on a frontoparietal network that overlaps with the neural circuitry involved in the control of eye movements (e.g., Corbetta & Shulman, 1998, 2002). The processes that direct search can also be complemented by the top-down preactivation of other brain areas, from those mediating high-level pattern recognition (e.g., Chelazzi, Duncan, Miller, & Desimone, 1998; Chelazzi, Miller, Duncan, & Desimone, 1993), to the priming of early visual areas when spatial expectancies for targets can be developed (Ress, Backus, & Heeger, 2000; see Kanwisher & Wojciulik, 2000, for a review). However, in addition to throwing light on which brain regions are engaged during search, do such studies provide constraints on under-standing the *functional* mechanisms of search—how search might operate in terms of *algorithms* as well as neural processes? This is the question that we review here. We address the issue through studies of two issues—whether the need to "bind" information from different visual dimensions constrains search (e.g., in search for conjunctive targets; cf. Treisman & Gelade, 1980), and whether the benefit from previewing distractors in search is due solely to the capture of attention by new items (cf. Donk & Theeuwes, 2001, with Watson, Humphreys, & Olivers, 2003). In both cases, we argue that data derived from cognitive neuroscientific studies contribute to our under-standing of the functional mechanisms of search.

BINDING AND VISUAL SEARCH

In 1980, Treisman and Gelade published a now classic paper demonstrating a clear difference between search for targets defined by a feature contrast relative to distractors (a difference in shape or colour) and search for targets defined by a conjunction of features from different dimensions (for example, both their shape and their colour, e.g., a red circle target presented amongst red squares and blue circles). Although search for targets defined by single features was little affected by the number of distractors present (and so was likely based on spatially parallel processing), search for form–colour conjunctions was linearly affected (consistent with spatially serial, attentive processing). This result was the foundation for one of the central tenets of Feature Integration Theory (FIT), that search is constrained by the need to

bind together visual features that are processed independently (form and colour, in this instance). According to FIT, the binding of independently processed features is dependent on attention being allocated to the locations of stimuli, effectively filtering out irrelevant features (from other stimuli) from the binding process. This assertion has received support from physiological studies showing that attention modulates the receptive fields of cells in area V4, which appear to contract around the location of an attended stimulus (Moran & Desimone, 1985).

Although FIT provides a functional account of the difference between so-called feature- and conjunction-defined targets, it is by no means the only theory put forward to explain the behavioural data. For example, Guided Search (Wolfe, 1994), like FIT, holds that search is constrained by the need to bind independently processed features, but it allows for search to be guided in a top-down fashion to salient features defining a particular conjunction. This provides an explanation of why search for form–colour conjunctions can be efficient when feature values defining the stimuli are very different from one another (e.g., Wolfe, Cave, & Franzel, 1989). Other theories, though, make no qualitative distinction between the processing of independent features and of feature conjunctions. Attentional Engagement Theory (AET; Duncan & Humphreys, 1989, 1992) holds that both independent features and conjunctions of features are processed in parallel, but search is constrained by the similarity relations between (1) the target and the distractors, and (2) the distractors themselves. High target–distractor similarity slows search, whereas high distractor–distractor similarity can facilitate search by enabling distractors to be grouped and rejected together. In terms of their similarity relations, conjunctive targets may be difficult to select in search because they share features with distractors, whereas distractors can have different features from one another. When conjunctive targets are presented amongst homogeneous distractors, however, distractor–distractor grouping may be stronger than target–distractor grouping, with efficient search emerging from the parallel rejection of distractors (e.g., Duncan & Humphreys, 1989; Humphreys, Quinlan, & Riddoch, 1989). For AET the processes leading to the selection of feature- and conjunction-defined targets may differ quantitatively but they are not necessarily qualitatively different.

These contrasting theoretical accounts have been extremely difficult to separate from behavioural data alone. For example, although the finding of linear effects of the number of distractors on search is consistent with FIT's position that conjunctive search should involve serial attention to each item, the data can also be accommodated by models in which conjunctions are coded in parallel (e.g., Heinke, Humphreys, & Tweed, 2006 this issue; Humphreys & Müller, 1993; Townsend, 1971). Likewise, effects of grouping on search match the predictions of AET, but they can also be explained by

FIT if additional processes are allowed to contribute to search, such as the inhibition of feature maps common to distractor but not target features (e.g., Treisman & Sato, 1990). Can data from cognitive neuroscience help here— for instance, by indicating that an additional process of binding is involved when participants search for form–colour conjunctions rather than feature-defined targets?

There have been several attempts made to address this question. For example, Donner et al. (2002) measured brain activity using fMRI when participants searched either for form–colour conjunctions or for feature-defined targets that were as difficult to detect as the conjunctions. In this case, any enhanced activity in the conjunction search task should not simply reflect the increased difficulty of conjunction search. They found that there were areas of overlap across the conjunction and hard feature-search tasks, relative to an easy feature-search baseline (e.g., in posterior regions of the intraparietal sulcus; IPS), along with some areas where activity was greater in one task than the other. For example, the area joining the IPS to the transverse occipital sulcus, plus also the frontal eye fields, showed greater activation in the conjunction than in the hard feature-search task. On the other hand, there was greater activation in the hard feature-search task, relative to the conjunction task, in the anterior IPS. Given that search difficulty was matched in the hard-feature and conjunction conditions, these differences suggest that some distinct processes were recruited in the two tasks. Nevertheless, it is unclear what these processes might be. For example, areas showing increased activation in the conjunction task may reflect the unique need for feature binding in this condition. Alternatively, however, they might reflect greater top-down guidance of search (e.g., guiding search to items of the target's colour; Wolfe, 1994). If there was top-down guidance of conjunction search, then areas showing increased activity in the hard feature-search task might reflect additional serial scanning of attention in that condition relative to the (guided) conjunction search condition.

Somewhat different imaging results were reported by Nobre, Coull, Walsh, and Frith (2003). They orthogonally manipulated search difficulty with whether the target was defined by a single feature or a conjunction of features (including both hard and easy versions of both feature and conjunction search). They found that, in general, activation increased in the hard search conditions irrespective of whether search was for a feature- or a conjunction-defined target (particularly in the superior parietal lobule and the right IPS). In contrast, there were only sparse increases in activity in the conjunction tasks relative to the feature search tasks, and these took place in regions of parietal cortex that also showed sensitivity to search difficulty (i.e., that showed increased activity in hard search tasks relative to easy search tasks). These results suggest that feature and conjunction search tasks may not differ qualitatively, but there are quantitative effects of search

difficulty, perhaps reflecting increased competition for selection when targets and distractors are similar (cf. Duncan & Humphreys, 1989, 1992). On the other hand, null effects are typically difficult to interpret. Also, it is possible that the need for binding was not stressed in these conjunction search tasks. For example, in different, difficult conjunction searches targets were defined by colour and motion direction, and by velocity and form; there is behavioural evidence that participants may employ parallel filtering of motion-defined targets in visual search (e.g., McLeod, Driver, & Crisp, 1988; Nakayama & Silverman, 1986). If one set of distractors can be filtered in parallel, then it might not be necessary to bind all features to find the target amongst the remaining subset of distractors.

A different approach is to examine the behavioural consequences when brain activity is disrupted in regions putatively involved in binding and search. Several studies have demonstrated that damage to parietal cortex can lead to problems in feature binding, so that patients make abnormal numbers of illusory conjunction responses, where they appear to bind attributes belonging to different stimuli (see Friedman-Hill, Robertson, & Treisman, 1995; Humphreys, Cinel, Wolfe, Olson, & Klempen, 2000, for evidence from effects of bilateral parietal lesions; see Cohen & Rafal, 1997, for evidence from effects of unilateral parietal damage). Parietal patients are also frequently worse at conjunction search than at search for feature-defined targets, consistent with their problem in binding having a differential impact on conjunction search (e.g., Eglin, Robertson, & Rafal, 1989; Friedman-Hill et al., 1995; Riddoch & Humphreys, 1987). However, it is also the case that parietal patients can manifest abnormal effects of search difficulty even for feature-defined targets, as the saliency of such targets is decreased (Humphreys & Price, 1994; Humphreys & Riddoch, 1993). Studies where conjunction and feature searches have been directly compared in neuropsychological patients have not matched the conditions for search difficulty, making it impossible to assess whether the effects of parietal lesions are due specifically to impaired binding or to more general problems associated with difficult search.

Other intervention studies have used transcranial magnetic stimulation (TMS) to assess temporary effects of parietal stimulation on feature and conjunction search tasks. Ashbridge, Walsh, and Cowey (1997) first reported that TMS applied to the right IPS disrupted conjunction search more than feature search, but again search difficulty was not equated. More recently Ellison, Rushworth, and Walsh (2003) contrasted TMS effects on both easy and hard versions of both feature and conjunction search tasks (cf. Nobre et al., 2003). They found the TMS applied to right posterior parietal cortex selectively disrupted the conjunction relative to the feature search tasks. This fits with the idea that some extra process, such as feature binding, might be modulated by the posterior parietal cortex and might play a selective role in

conjunction search. However, the hard feature task was more difficult than either conjunction task, so that an additional process, such as top-down guidance of search, might have influenced performance with conjunctions. This additional process (rather than binding) could have been disrupted by TMS. Furthermore, the difficulty of the hard feature task could have effectively limited any further disruptive effects on search.[1]

Hence, prior cognitive neuroscience research on this issue has been suggestive but inconclusive. Recently we (Humphreys & Hodsoll, 2006) investigated the same issue using a neuropsychological approach, comparing a small group of five patients with inferior parietal lesions with age-matched control. Search for a (relatively easy) form–colour conjunction target (a green "X" amongst green "O"s and red "X"s) was assessed in comparison with a more difficult feature search task (the target was a white shallow line, sloped 33° either up or down from the horizontal; the distractors were steeper white lines, sloped 66° either up or down from the horizontal). The target was either present or absent, and when present it fell either in the left or right visual field. The backgrounds were always black and there was a single display size of 16 items (8 in the left field and 8 in the right; see Figure 1 for examples of the displays). In order to avoid ceiling or floor effects, and the difficulty in interpreting the slow RTs that can be found with neuropsychological patients, the stimulus exposure was limited with the durations set to generate a level of about 80% correct performance across the feature and conjunction search tasks (for the patients and controls alike). On trials where the subject decided that the target was present, they were asked to state whether it fell in the left or right field. Performance was scored as correct when both the present/absent decision and the localization decision were accurate.

The data for target present trials are shown in Figure 2. For both the controls and the patients performance on absent trials was around 90% correct, for both tasks (control mean $=91\%$ for conjunction search and 87% for feature search; patient mean $=90\%$ for conjunction search and 88% for feature search). When incorrect, the controls had no bias to report a target in the right versus the left field (46% vs. 54% of the false alarms, averaged across the tasks). The patients had a bias to their contralesional field (72% of the false alarms were localized in the contralesional field, averaged across the tasks). On present trials the overwhelming numbers of errors were target misses rather than mislocalizations (95% for controls, 94% for patients). For

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[1] Reaction times (RTs) were measured. When there are slow RTs in search, there may be some rate-limiting factor (e.g., the ability to discriminate the target from a distractor) that constrains performance even if TMS had an effect on other processes (e.g., the speed of serially selecting each stimulus for subsequent discrimination). For example, if the time to discriminate the target from the distractor is sufficiently long and variable, then there may be negligible effects due to changing the speed of selecting each item for discrimination.
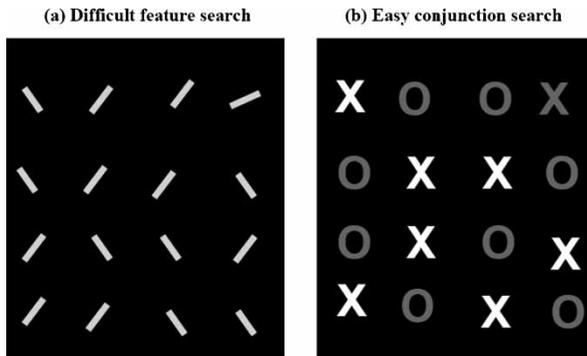
Figure 1. Example displays used by Humphreys and Hodsoll (2006). (a) Hard feature search (target =shallow, distractors =steep); (b) easy conjunction search (grey =green in the displays, and white =red; target =green "X"). For each type of search we depict a "present" trial with the target in the top right location.

the controls there was an overall advantage on present trials for the (easy) conjunction task over the (difficult) feature search task, and this held irrespective of whether the target appeared in the left or right visual fields (Figure 2a). This advantage could reflect any of several processes: (1) Easier matching to memory, since there was only a single conjunction target but two possible feature targets (shallow line oriented either right or left); (2) greater feature-based guidance of search in the conjunction condition, since the features making up the conjunction target were relatively salient

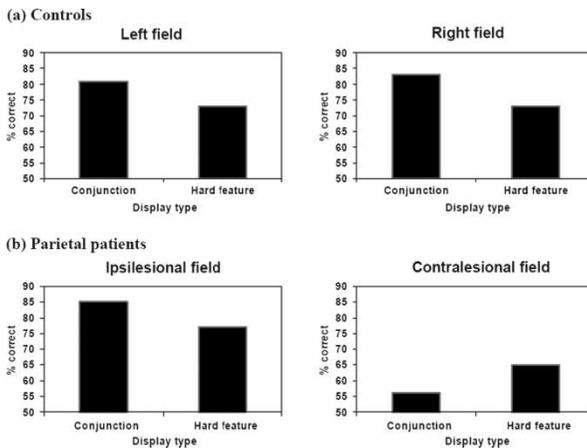**Figure 2.** The percentage correct target detections for control participants ($N=5$) and patients with unilateral parietal lesions ($N=5$). The mean duration for the control participants was 300 ms; the mean duration for the patients was 800 ms.

compared with the distractor features along each dimension; (3) effects of increased competition in selecting the feature-based target, due to the greater similarity of the feature distractors to targets. For the patients, however, quite different effects occurred on present trials according to the field where the target appeared (Figure 2b). When the target fell in the ipsilesional field, the pattern of performance followed that of the controls (better discrimination for conjunction over feature-defined targets). When the target appeared in the contralesional field performance was worse for both conditions compared with when the target fell in the ipsilesional field. However, the discrimination of contralesional conjunction targets was particularly poor, with performance now being better for the hard feature over the conjunction stimuli. The poor conjunction search was not simply due to poor colour discrimination in the contralesional field. The patients performed perfectly at discriminating the green "X" target when single items were presented in either the ipsi- or contralesional fields. This reversal of the "conjunction advantage" found with controls rules out various interpretations of the data. For example, the effects with the contralesional target cannot be attributed to general search difficulty (increased costs due to distractor similarity or to having two "templates" for feature targets), since an effect of difficulty would simply enhance the "conjunction advantage". It also cannot be attributed to patients being unable to use guided search in their contralesional field. If a guided search process was disrupted for conjunction targets then both conjunction and feature search should rely on serial search and comparison of each item relative to the memory template for the target (cf. Duncan & Humphreys, 1989). Note that guided search is typically contingent on the features of targets and distractors being relatively discriminable (Wolfe, 1994). Thus it is unlikely that any serial comparison with a memory template would be harder for such conjunctions than for difficult (low discriminability) stimuli in feature search. The conjunction search task should not become *more* difficult than the feature search task. Instead, the observed reversal of the normal pattern of performance suggests that parietal damage selectively disrupted a process necessary for conjunction but not for feature search—the most likely candidate being the binding of form and colour in the contralesional field. This is also supported by the biased false alarms generated by patients on target-absent trials. We suggest that the stable binding of form and colour properties of stimuli is modulated by the parietal lobe, and that this binding process operates as one constraint on search for targets defined by the conjunction of features from across different visual dimensions (form and colour in this case).

One account of this pattern of results is provided by FIT, which proposes that binding is contingent on a spotlight of attention (controlled through the parietal lobe) filtering out competing features in the visual field (Treisman, 1998). Parietal damage may prevent the application of the "spotlight" to the

contralesional field, so that incorrect bindings are formed. Alternatively it may be that the parietal system provides top-down feedback in a spatially parallel manner to earlier visual regions coding form and colour, stabilizing conjoint activity at common locations (cf. Humphreys et al., 2000). If the parietal lesion impairs feedback to the contralesional field, bindings may be unstable. In either case, this "binding" process is more important for detecting cross-dimension conjunctions than for detecting targets defined by a feature difference within a single dimension.

THE PREVIEW BENEFIT IN SEARCH

In the real world, visual search does not only operate across space but also across time, as we deal with new information coming into the environment and ignore old stimuli that may no longer be critical to action. Watson and Humphreys (1997) examined search across time as well as space by presenting a variation of form–colour conjunction search in which they presented one set of distractors (the preview) prior to the second set of distractors plus the target (when present) (e.g., green "H" distractors followed by blue "A" distractors + blue "H" target). Although the final display was identical to the display in a standard form–colour conjunction task, Watson and Humphreys found that there was no impact of the old items on the efficiency of search; search rates were equivalent to those obtained when just the blue items were presented (the single feature baseline condition). There was also a time course to this effect. To generate optimal performance, the old items had to have been presented at least 400 ms before the new (see also Humphreys, Kyllinsbæk, Watson, Olivers, Law, & Paulson, 2004b). There is thus a "preview benefit" in search, where only new items influence search efficiency provided old items have been in the field for some time.

Watson and Humphreys (1997) argued that at least part of the preview benefit was due to observers inhibiting a representation of the old stimuli. Evidence consistent with this inhibitory account comes from studies using probe detection procedures to examine the allocation of visual attention during search. Probes that fall at the location of old items are difficult to detect relative to probes falling on new stimuli (Olivers & Humphreys, 2002; Watson & Humphreys, 2000), and relative to probes that appear in neutral locations (Humphreys, Jung-Stalmann, & Olivers, 2004a). Other evidence suggests that there can be inhibition of the features as well as the locations of old items, so that it is difficult to detect targets that carry the same features as ignored old items (e.g., if the target has the same colour as ignored old distractors; Braithwaite & Humphreys, 2003; Olivers & Humphreys, 2002; Olivers, Humphreys, & Braithwaite, 2006 this issue). This feature-based carryover effect even modulates the detection of targets that are defined by a

salient singleton feature relative to the new distractors (Olivers & Humphreys, 2003).

Other accounts of the preview advantage have also been proposed. Jiang, Chun, and Marks (2002), for example, hold that it reflects temporal grouping and segmentation of the old and new displays, without necessarily involving inhibition of the old items. Donk and Theeuwes (2001) propose that the advantage is due purely to the capture of attention by the new onsets in the second (search) display. In many studies, these different functional accounts make similar predictions. For example, differences in probe detection at the locations of old and new items could be caused by attention being prioritized to new stimuli rather than being deprioritized away from old items. Nevertheless, differences between detection at old and neutral locations, which can occur even when probes precede the new stimuli, are less easy to explain without recourse to the notion that old locations are suppressed (Humphreys et al., 2004a).

There are now several studies of preview search that have taken a cognitive neuroscience perspective, using direct measures of brain activation during both preview and search displays. Jacobsen, Humphreys, Schröger, and Roeber (2002) measured evoked potential responses to stimuli and reported an increased and sustained negative potential that occurred prior to the search display and that was associated with participants actively ignoring the preview. This activation was most pronounced at frontal and parietal sites. Humphreys et al. (2004b) used PET to measure brain activity across blocks of search where the duration of the preview display varied. Search for the target became easier as the preview was presented for longer durations, but activity in the superior parietal lobe increased. Pollmann et al. (2003) also found increased and earlier activation in the superior parietal lobe in the preview relative to single feature and conjunction search conditions, and this was present even on "dummy" trials on which no search displays were presented after the preview. These last two studies suggest that subjects in preview search encode and possibly also inhibit a representation of the old items in the superior parietal lobes, which likely contain a spatial map of occupied areas of visual field (cf. Ungerleider & Haxby, 1994; Ungerleider & Mishkin, 1982). Pollmann et al. also found earlier and increased activation in a second site, the temporal-parietal junction (TPJ), that was associated with the ease of search rather than the presence of the preview—thus activity in the TPJ was enhanced in the single feature and the preview conditions when compared with the conjunction baseline. This TPJ activity likely reflects the allocation of attention to a salient new target, a process common to the single feature and preview search conditions.

Watson et al. (2003) note that there may be multiple factors that contribute to the preview benefit, with effects due to temporal segmentation and suppression of old items supplemented by attentional capture to new

onsets. But having new items defined by onsets may not be crucial. Donk and Theeuwes (2001) argued for the importance of new onsets because they found that old items did have an impact on search when new stimuli were isoluminant with their background (i.e., when new items were not defined by onsets). On the other hand, the locations of stimuli that are isoluminant with their background may be coded relatively coarsely, making it difficult both to inhibit old locations and to allocate attention efficiently to the locations of new stimuli. Humphreys et al. (2004a) presented search stimuli by making a colour change to the elements of a background grid. Every 16 ms, all the elements (in the search stimuli and the background grid) randomly and independently changed slightly in luminance so that, on average, the luminance was equal between the search items and the remaining contours of the grid. This way the new search items were well-defined against their background (as at any moment in time there were some random luminance differences between grid elements), without them being defined by a luminance onset (indeed some elements were defined by a luminance offset). A robust preview advantage was observed, suggesting that defining a target by its onset is not critical.

A further way to assess whether attentional capture by new onsets is necessarily a part of the preview advantage is to test whether patients who are selectively impaired in preview search can nevertheless show efficient allocation of attention to onsets. If this is the case, then efficient allocation of attention to onsets cannot be sufficient to generate the preview advantage. Olivers and Humphreys (2004) tested patients with posterior parietal damage (typically involving the inferior parietal lobe, but in some cases extending into the intraparietal sulcus). As a whole this group did not show marked neglect, but did tend to have extinction under brief stimulus presentation conditions. Olivers and Humphreys found that preview search was selectively disrupted in patients with parietal damage (especially for targets falling contralateral to their lesion—search in the preview condition could then be less efficient than in a single feature baseline and no more efficient than a conjunction search baseline). Recently we (Humphreys, Olivers, & Yoon, 2006) have built on this result by examining the performance of patients with unilateral parietal damage in paradigms where, respectively, a preview advantage and an advantage for selecting onset targets are normally observed. In both tasks, participants searched for a yellow "H" target that appeared along with a set of random letters, all also presented in yellow. In the preview study, one set of distractors was presented first for 1000 ms before the second set of distractors appeared along with the target. Display sizes of 4 old+4 new or 8 old+8 new items were used. Performance was compared with a half set baseline in which only the new items appeared (display sizes 4 and 8), or a full set baseline in which the full set of distractors appeared along with the target (display sizes 8 and 16). In

the onset-capture study, the letters were preceded by a set of premasks (for 1000 ms). Contours in the premasks were then offset to create letters, and simultaneously another letter appeared in a previously unoccupied location in the display (the onset target). The target was again a yellow "H", and the distractors were other random letters drawn in yellow. There were either 3 offset letters + 1 onset letter, or 7 offset letters + 1 onset letter. The target was equally likely to be the onset stimulus or one of the stimuli created by offsetting contours in a premask. When tested under these conditions, normal participants show an advantage in responding to a target defined by an onset relative to one defined by an offset (although the onset is then irrelevant; Yantis & Jones, 1991; Yantis & Jonides, 1984). In both the preview and the onset-capture studies, the target was always present and the participants' task was to localize it. Performance was assessed in seven patients, three with unilateral left and four with unilateral right lesions involving the parietal lobe. Example displays are shown in Figure 3.

Data from the preview search task are shown in Figure 4. The results reveal that the patients had relatively normal performance in the preview condition when the target fell in their ipsilesional visual field. Search was more efficient (i.e., there was a reduced effect of the display size) in the
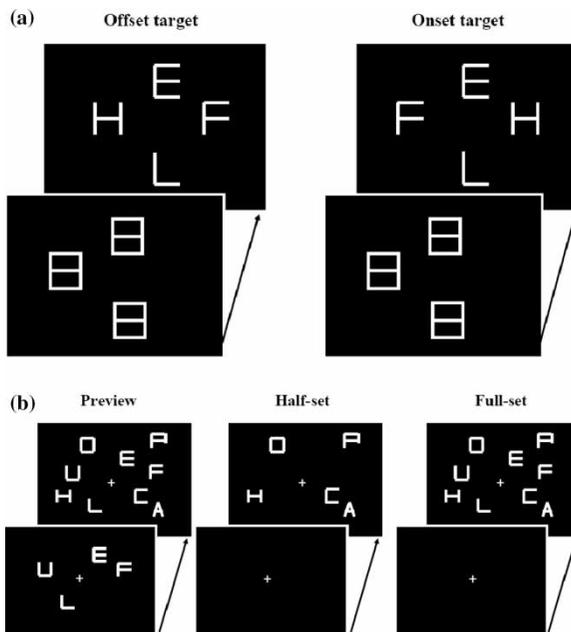

Figure 3. (a) Example displays from the offset and onset conditions; (b) example displays for the preview, half set and full set search conditions. In all cases the target is an "H".
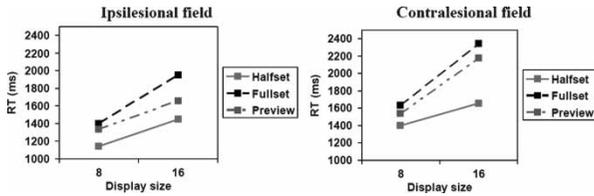
Figure 4. Visual search latencies for 7 patients with unilateral parietal damage in the half set, full set and preview search conditions, for targets falling in the ipsilesional or contralesional fields.

preview condition than in the full set baseline, and the slope of the search function was no greater in the preview condition than in the half set baseline (when only the new letters were presented). In contrast, performance was selectively poor in the preview condition when targets were presented contralateral to the lesion. With contralesional targets, there was no difference between the preview condition and the full set baseline (neither in terms of overall reaction times or in terms of the slope of the search functions), and the slope for the preview condition was reliably greater than the slope of the search function in the half set condition. Interestingly, search was slowed for both the preview and full set conditions when the target fell in the contralesional field, but there was no effect on the slope of the function in the half set baseline. This suggests that the patients remained able to attend relatively efficiently to a target in their contralesional field when it was one of a small number of new items presented in an otherwise empty display (with up to four items appearing in their contralesional and four in their ipsilesional fields). However, they were impaired when there were old items also present (in the preview condition) and when larger numbers of items were presented simultaneously (eight items in their contralesional field and eight in the ipsilesional field, in the full set baseline). The selective deficit in selecting targets in the preview condition replicates the findings of Olivers and Humphreys (2004).

The results from the onset-capture study are depicted in Figure 5. These data contrast with those from preview search. The patients showed an overall advantage for detecting onset over offset targets, and, importantly,
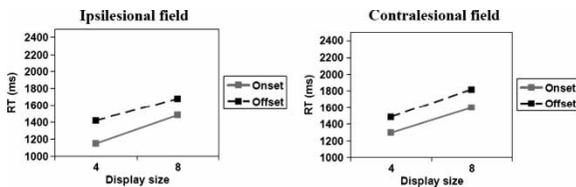

Figure 5. RTs to detect an onset or offset defined target presented in the ipsilesional or contralesional fields of patients with unilateral parietal lesions.

this did not differ for targets appearing in the contra- and ipsilesional fields (there was no interaction between field and the onset advantage). The onset advantage was apparent in the intercept rather than the slope of the search function. This may be because there was approximately equal competition for selection from the (multiple) offset distractors when the target was an onset, and from the onset+offset distractors when the target was an offset;[2] Battelli, Cavanagh, Martini, and Barton (2003) have recently reported that parietal patients have difficulty distinguishing between onsets and offset stimuli, suggesting some decreased sensitivity to onsets. Nevertheless the intercept effect does indicate that the patients could set a lower threshold for onset relative to offsets, so producing a general advantage for onset targets. If prioritized selection of onsets was sufficient to generate a preview advantage, then such a lowered threshold for responding to onset compared to offset stimuli should have led to an advantage for the preview condition over the full set baseline (and note that the old distractors remained in the field rather than offsetting, in the preview search condition, and so should have competed even less than the offset distractors in the onset condition). Also this advantage should have been equal across the fields, as the onset advantage did not interact with field. Clearly this was not the case. This in turn indicates that factors other than prioritized attention to onsets contribute to preview search, and these other factors are impaired following damage to the parietal lobe.

One possible reason for the reduced preview benefit is that parietal patients have impaired temporal segmentation (cf. Jiang et al., 2002), and so are insensitive to the staggered presentation of stimuli in preview displays. However, this fails to explain why the problem is confined to contralesional targets in the preview condition. Alternatively, there may be impaired spatial disengagement of attention from the old items falling in the patients' ipsilesional fields (cf. Posner, Walker, Friedrich, & Rafal, 1984), which selectively disrupts attentional allocation to new, contralesional, search stimuli. Olivers and Humphreys (2004) examined this last argument by orthogonally manipulating the spatial locations of old and new items in preview search, while keeping the temporal relations between the displays constant. They found that performance was worst when both the old and the new items fell in the same visual field, and that performance was improved if the old items appeared in one field and the new items in the other (even when the old items fell in the ipsilesional field and the new in the contralesional field, when poor spatial disengagement of attention from the old stimuli should have been maximized). This result indicates that the

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[2] We have also found this same pattern, of an onset advantage in terms of an intercept rather than a slope effect, in controls matched in age to the patients. It may be that competition from onsets and offsets becomes closer as participants age.

spatial as well as the temporal relations between the stimuli are important for search, but that processes concerned with the spatial segmentation of old and new items, rather than spatial disengagement of attention, are particularly problematic for the patients. The difficulty of spatial segmentation is increased when old and new items overlap compared with when they fall in the same visual field, and the posterior parietal patients had particular problems under this condition. It may be that the patients have an impaired visual-spatial working memory and so fail to maintain (and inhibit) a representation of the old items (Wojciulik, Hussain, Clarke, & Driver, 2001). Due to this failure in maintenance, old items compete for selection with the new items, with the competition being particularly strong when the items fall in the same area of field. However, we found no correlation between a measure of visual spatial working memory (the Corsi block span) and the size of the average cost in the preview condition relative to the half set baseline for contralesional targets, $r(5) = -.266$, $p > .565$. Rather than impaired visual spatial working memory *per se*, Olivers and Humphreys proposed that the parietal patients have poor spatiotemporal segmentation in vision, with parietal damage leading to a reduced ability to segment old from new items based on both their temporal and their spatial codes (particularly when the spatial codes for old and new items overlap). This spatiotemporal segmentation process may normally be enhanced by inhibition of the old items, modulated through the parietal lobe (cf. Watson & Humphreys, 1997). In any case, the neuropsychological data advance prior behavioural studies of preview search by demonstrating that prioritized attention to onsets is not sufficient to generate a preview benefit in visual search.

CONCLUSIONS

The evidence we have presented has highlighted that data from cognitive neuroscience can contribute not only to an understanding of the neural substrates of visual search, but also to an understanding of the functional mechanisms involved. We have reviewed recent neuropsychological data indicating that:

1. Patients with posterior parietal lesions can have problems with search for form–colour conjunctions that cannot be accounted for in terms of overall search difficulty or in terms of the loss of top-down guidance of search, which might take place in conjunction but not in hard feature search tasks (Humphreys & Hodsoll, 2006). This selective problem is consistent with form–colour conjunctions requiring a unique binding

process that is not required in search for low-salient targets defined within a single feature dimension.

2. Parietal patients can show an advantage in detecting targets defined by an onset over those defined by an offset, both in their contra- and their ipsilesional fields, whereas there is a selective loss of the preview benefit in search in the contralesional field (Humphreys et al., 2006). This result reveals that a maintained ability to prioritize attention to onset stimuli is not sufficient to generate the preview benefit in search, at least when other processes are impaired by the brain lesion. Other recent behavioural data reveal that a preview advantage can be observed when new stimuli are defined by a colour change rather than an onset, provided that the stimuli are well-defined relative to the background (in Humphreys et al., 2004a, but not in Donk & Theeuwes, 2001). Taken together the results indicate that prioritized attention to onsets is neither necessary (data with normal participants) nor sufficient (neuropsychological data) to produce the preview advantage. Of course this does not mean that onsets cannot contribute to preview search, and they may do so when new stimuli are defined by onsets and when other impairments do not reduce the effectiveness of onsets for selection (e.g., when there is a failure in the inhibition of old items). However, the data do show that an onset-capture account cannot provide a complete explanation of preview effects in search. The neuropsychological data, on impaired preview search, also complement evidence from electrophysiological studies (Jacobsen et al., 2002) and brain imaging (Humphreys et al., 2004b; Pollmann et al., 2003) that indicate that old items are differentially coded (and presumably deprioritized for selection) under preview search relative to baseline conditions.

As well as providing evidence on some of the functional processes that modulate search (e.g., cross-dimension binding of features, spatiotemporal prioritization, and deprioritization of selection), the data also help to reveal the role played in search by particular brain regions. For instance, the evidence on conjunction search highlights the role of the posterior parietal lobe in cross-dimension binding (Treisman, 1998). Data from brain imaging studies of preview search differentiate between the superior parietal lobe (selectively activated by previews) and the temporal-parietal junction (sensitive to the ease of search). For example, the former may hold a spatial representation of the old items, which forms the basis for their subsequent deprioritization in selection; the latter may be involved in generating a rapid orienting response to a target. Finally, the neuropsychological data on deficits in preview search (e.g., Olivers & Humphreys, 2004) suggest that parietal regions modulate the spatiotemporal segmentation of visual stimuli,

and not simply the disengagement of spatial attention or the ability to segment stimuli on the basis of temporal signals alone. One possibility is that both spatial and temporal segmentation processes are served by the selective inhibition of parietal neurons, over time, responsive to particular spatial locations.

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