



The University of  
**Nottingham**

UNITED KINGDOM · CHINA · MALAYSIA

Humphreys, Glyn W. and Allen, Harriet A. and Mavritsaki, Eirini (2009) Using biologically plausible neural models to specify the functional and neural mechanisms of visual search. *Progress in Brain Research*, 176 . pp. 135-148. ISSN 1875-7855

**Access from the University of Nottingham repository:**

<http://eprints.nottingham.ac.uk/44445/1/HumphreysAllenMavritsaki09ProgBrainRes.pdf>

**Copyright and reuse:**

The Nottingham ePrints service makes this work by researchers of the University of Nottingham available open access under the following conditions.

This article is made available under the Creative Commons Attribution Non-commercial No Derivatives licence and may be reused according to the conditions of the licence. For more details see: <http://creativecommons.org/licenses/by-nc-nd/2.5/>

**A note on versions:**

The version presented here may differ from the published version or from the version of record. If you wish to cite this item you are advised to consult the publisher's version. Please see the repository url above for details on accessing the published version and note that access may require a subscription.

For more information, please contact [eprints@nottingham.ac.uk](mailto:eprints@nottingham.ac.uk)

# Using biologically plausible neural models to specify the functional and neural mechanisms of visual search

Glyn W. Humphreys\*, Harriet A. Allen and Eirini Mavritsaki

*Behavioural Brain Sciences, School of Psychology, University of Birmingham, Birmingham B15 2TT, UK*

**Abstract:** We review research from our laboratory that attempts to pull apart the functional and neural mechanisms of visual search using converging, inter-disciplinary evidence from experimental studies with normal participants, neuropsychological studies with brain lesioned patients, functional brain imaging and computational modelling. The work suggests that search is determined by excitatory mechanisms that support the selection of target stimuli, and inhibitory mechanisms that suppress irrelevant distractors. These mechanisms operate through separable though overlapping neural circuits which can be functionally decomposed by imposing model-based analyses on brain imaging data. The chapter highlights the need for inter-disciplinary research for understanding complex cognitive processes at several levels.

**Keywords:** visual search; visual attention; computational modelling; functional brain imaging

## Introduction

The visual world presents us with a complex and dynamically changing environment where it is important to be able to select efficiently stimuli that match our current behavioural goals. Attempts to measure the efficiency of visual selection have frequently used visual search to examine which factors facilitate and which impair selection processes. Across the past 40 years, numerous studies of search have been conducted which have demonstrated that, when targets differ from distractors in terms of their basic features (their colour, shape, size and so forth), then search is relatively efficient. In such cases the time taken to find the target increases by less than 10 ms/item

as the number of distractors increases. In contrast, when targets and distractors share features, then search is much less efficient, with target detection times increasing often by 30 ms or more for each distractor present (see Wolfe, 1994). These contrasting patterns of search have often been characterised in terms of a two-stage account of visual selection (e.g. Neisser, 1967). According to this two-stage account, there is a first pre-attentive stage of visual processing which operates in parallel across the visual field and codes simple visual features. Targets that differ from distractors in their coding at this stage (having different features) can be detected in a spatially parallel manner. Targets that share features with distractors will activate overlapping representations at the pre-attentive stage and require further processing before they can be detected. This further processing is carried out at the second, attentive stage

\*Corresponding author.

1 where there is serial scrutiny of each item — often  
 3 this is conceived in terms of a serial window of  
 5 attention being shifted from item to item. Due to  
 7 this serial scrutiny, search rates increase to at least  
 9 a minimal time required to make serial shifts of  
 11 attention, and search time can be linearly related  
 13 to the number of distractors present. Two-stage  
 15 theories of this type remain highly influential. For  
 17 example, Treisman’s Feature Integration Theory (FIT; Treisman, 1998; Treisman and Gelade, 1980) maintains a distinction between feature-based pre-attentive stages and an attentional stage required to conjoin features. Wolfe’s Guided Search Theory (GST) also proposes a first stage where simple features are coded and a second stage in which the items signalled as being most different from their neighbours are serially selected (Wolfe, 1994).

19 Other accounts, however, maintain that, rather  
 21 than there being a strict dichotomy between pre-  
 23 attentive and attentive stages of vision, there is a  
 25 continuum of search efficiencies determined by  
 27 different relations between targets and distractors.  
 29 In their ‘Attentional Engagement Theory’ (AET),  
 31 Duncan and Humphreys (1989, 1992) proposed  
 33 that search efficiency was determined by the  
 35 similarity between the target and the distractors  
 37 (as above), and also by the similarity between  
 39 distractors. High target-distractor similarity hin-  
 41 ders search efficiency. High distractor similarity,  
 43 on the other hand, can facilitate search because it  
 45 enables distractors to be grouped and segmented  
 47 from the target. Thus, even when targets and  
 distractors share features search can be efficient if the distractors are homogeneous and can be grouped and rejected together (see also Humphreys et al., 1989). Duncan and Humphreys (1989, 1992) proposed that distractors were rejected together by a process of ‘spreading suppression’ when they grouped separate from targets. Quite similar ideas have subsequently been incorporated into traditional two-stage accounts in order to explain effects of distractor homogeneity. For example, FIT assumes that a process of distractor inhibition can be recruited which enables distractors to be rejected en masse through suppression of their common feature(s) (Treisman and Sato, 1990). In GST, distractor suppression operates through a process of lateral

inhibition, so that distractors with common features will tend to suppress one another.

In addition to the process of rejecting distractors, accounts such as GST assume that search is guided by top-down activation of target features. This gives known targets a competitive edge in search tasks, enabling them rather than distractors to be selected. In terms of AET, targets are given a competitive advantage due to their having a template held in working memory which has a higher resting activation value than any template for distractors (see also Bundesen, 1990, for a similar idea expressed in terms of the target having a higher ‘pertinence value’). There is clear behavioural evidence that having foreknowledge of the target makes a large difference to search, even determining whether stimuli ‘pop out’ or not. For example, large targets can be detected efficiently in the presence of small and medium-sized distractors, but medium targets are detected inefficiently amongst large and small distractors. Rather than this solely reflecting a difference in coding at the first pre-attentive stage, Hodsoll and Humphreys (2001) showed that efficient search depended on foreknowledge of the target. Having a template for the target enabled the feature differences to be used to guide search efficiently.

### Modelling search

These ideas of search being guided by top-down activation from a target template, and also by distractor suppression, can be incorporated into more formal accounts of search including both mathematical (Bundesen, 1990) and computational models (e.g. Heinke and Humphreys, 2003; Humphreys and Müller, 1993; Mavritsaki et al., 2006). One value of such models is that, by demonstrating whether a proposed architecture can generate plausible search results, they provide an existence proof that the mechanisms of search could operate in the manner proposed. For example, since linear search functions can be generated by processes operating in a spatially parallel manner, the models demonstrate that serial processing operations are not *necessarily* required. The models also provide ways of

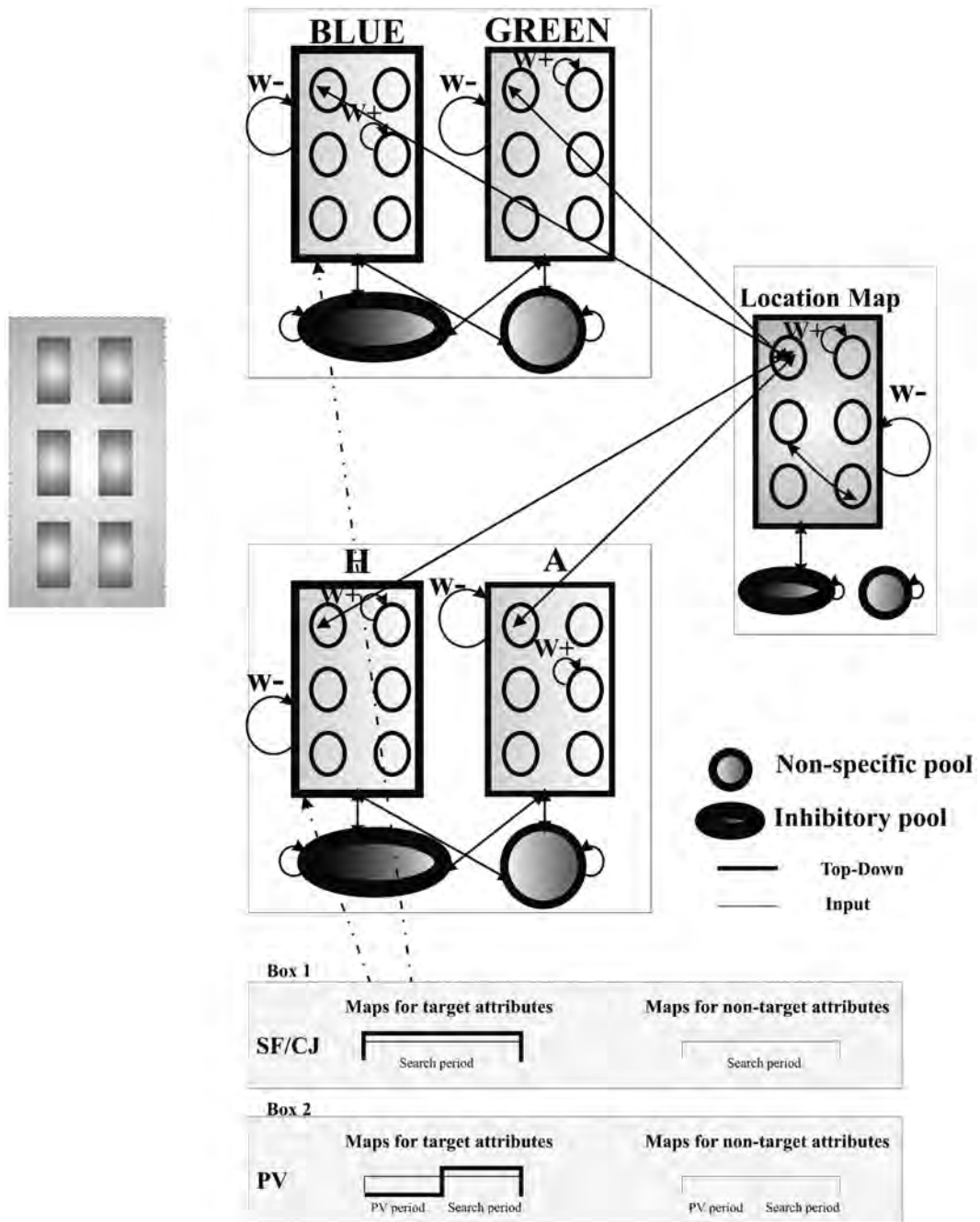
1 analysing how complex processes interact to  
 3 generate ‘whole-system’ behaviour, something  
 5 that is otherwise difficult to specify. Furthermore,  
 7 if the models can incorporate processes that  
 9 mimic real neuronal firing, then further physio-  
 11 logical constraints can be added to the constraints of  
 13 having to capture a body of psychological data, to  
 15 given a multi-level account of human perfor-  
 17 mance. This is the approach we have tried to  
 19 follow when implementing the sSoTS (spiking  
 21 Search over Time and Space) model (Mavritsaki  
 23 et al., 2006), shown in Fig. 1.

13 sSoTS incorporates processes proposed by  
 15 nearly all the major psychological accounts of  
 17 search. Within the model visual input is coded by  
 19 activating topographic maps representing simple  
 21 visual features. Within each map the units interact  
 23 through lateral inhibition, enhancing activation for  
 25 a stimulus that differs from its local neighbours.  
 27 This activation is transmitted to a ‘master map’  
 29 that sums activity for a given location within each  
 31 feature map and then feeds back this activation to  
 33 ‘sharpen’ the competition for selection at the  
 35 feature map level. In addition, top-down activation  
 37 is transmitted to the feature maps, both to increase  
 39 the activation for target features and to decrease  
 41 activity for known distractor features. This top-  
 43 down activation can give the target a competitive  
 45 edge enabling it to be selected ahead of the  
 47 distractors, with target selection determined by  
 setting a threshold for units within the master map  
 of locations. Search efficiency in the model is  
 determined by the overlap in features shared by  
 targets and distractors and by whether the  
 distractors have common or different features.  
 Search operates in a spatially parallel manner  
 across all of the items present, with efficiency  
 decreasing linearly as targets and distractors share  
 features. Activation profiles for the model are  
 shown in Fig. 2 for two ‘standard’ search cases:  
 A — where the target is defined by a difference in  
 a single feature (SF) relative to distractors (e.g.  
 target = blue H (*italic*) amongst blue As), and  
 B — target = a conjunction of features, each of  
 which is shared with a distractor (target = blue H  
 and distractors blue As and green Hs). Activation  
 in units corresponding to the location of the target  
 rise more rapidly in the single feature relative to

the conjunction case. Figure 3a shows the RTs for  
 units at the target location to reach a critical  
 threshold point (signalling a target detection  
 response) in the single feature and conjunction  
 (CJ) conditions as a function of the number of  
 distractors present. Search is more efficient  
 (increasing less with the display size) in the single  
 feature than the conjunction case. These data  
 capture the difference in search efficiency between  
 single feature and conjunction search (see Fig. 3b).  
 For illustration, data are also shown for a preview  
 condition which uses the same items as conjunc-  
 tion search but presents one set of distractors for  
 800 ms prior to the onset of the second set of  
 distractors, plus the target when present (see  
 below for further discussion).

Models such as sSoTS cannot only integrate  
 different psychological proposals but they can also  
 generate predictions about how processing may  
 operate at a neural level, given that the model is  
 based on the operation of biologically plausible  
 processing units (simulate spiking neurons). For  
 example, the feature maps may plausibly be  
 located within areas of early visual cortex which  
 respond to simple visual features. However, the  
 master map is more likely to be located within  
 posterior parietal cortex where there is evidence  
 for neurons to be coded to the locations but  
 not necessarily the features of visual stimuli  
 (Courtney et al., 1994). If units within this location  
 map are damaged, sSoTS predicts that search  
 efficiency will deteriorate, particularly for targets  
 that share features with distractors. This occurs  
 because the model is less able to ‘sharpen’ any  
 competition for selection, particularly for units on  
 the affected (‘contralesional’) side. The net result  
 is that targets on that side become difficult to  
 detect, particularly when they share features with  
 distractors. This is illustrated in the predictions for  
 both reaction times to detect the target shown in  
 Fig. 4a, and in the predicted error rates (target  
 misses), shown in Fig. 4b.

The units within the model also operate using  
 time parameters mimicking those of real neurons.  
 For example, after firing, units build up a calcium  
 parameter which reduces the future likelihood of  
 firing for a period — units enter a refractory state.  
 The emergent dynamics of activity lead to clear



43 Fig. 1. The architecture of the sSoTS model. Input into the model is fed into the feature maps and from there into the location units.  
 44 Units within maps, and at the same location across maps, operate in a mutually inhibitory way through the pools of inhibitory units.  
 45 Activity in the location maps is fed back to the earlier maps, to bias competition for selection in favour of features that differ from  
 46 their neighbours. In addition to such bottom-up biases, both excitatory and inhibitory activity can be set in a top-down manner, to  
 47 facilitate target selection. Top-down excitation and inhibition helped to bias search to favour the target.

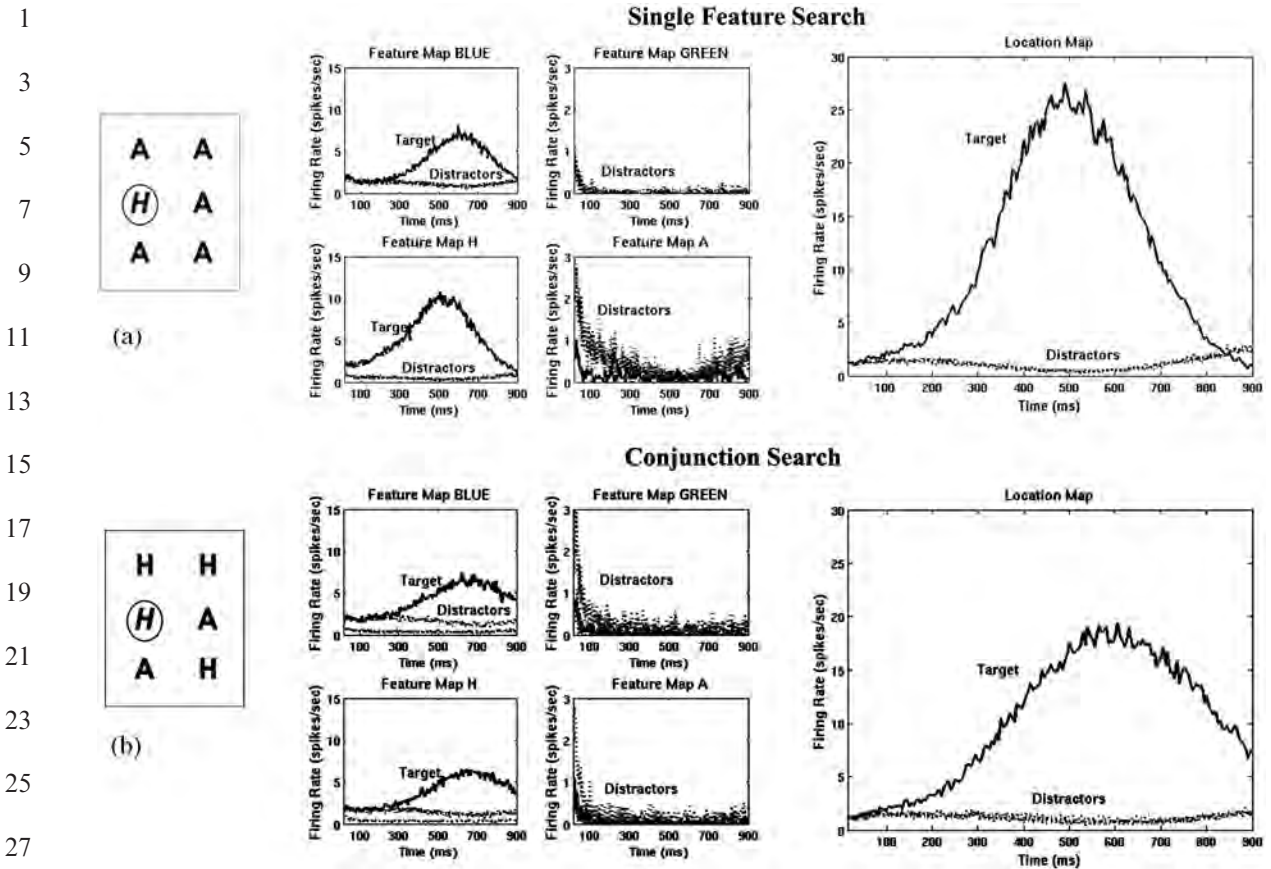


Fig. 2. (a) Activity in sSoTS plotted for four feature maps (BLUE, GREEN, H and A) and the Location map, when the target was a blue H (*italic*) and the distractors blue As. (b) Activity in the same maps for a conjunction target (blue H target, blue A and green H distractors). Activation in the Location map rises less rapidly and reaches a lower peak.

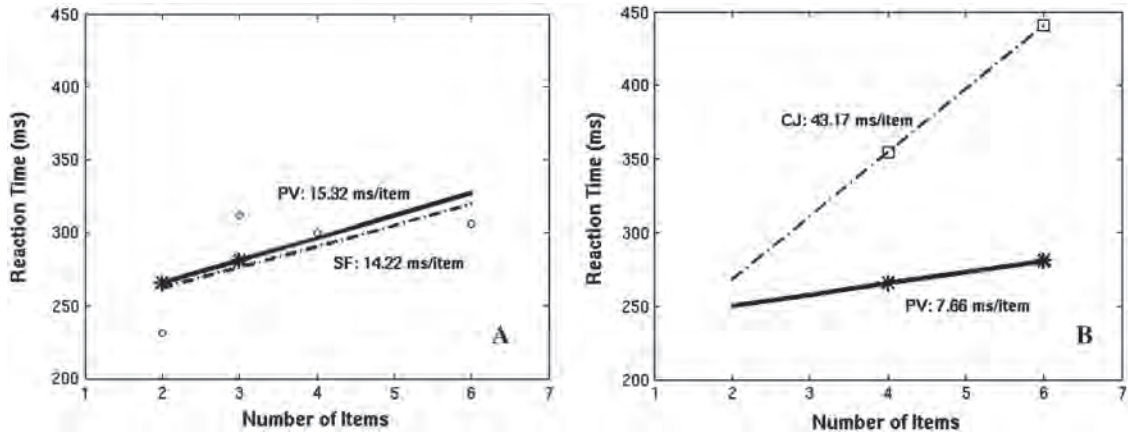
predictions being made about what might happen when the presentation of distractors is staggered over time. If there is presentation of one set of distractors prior to the other items, then activation for the initial distractors may be in a refractory state when the new items appear. Targets should be detected efficiently if they are presented at the time when distractor units are refractory, even if the distractors share their features with targets. This is illustrated in Fig. 5a.

### Visual search over time

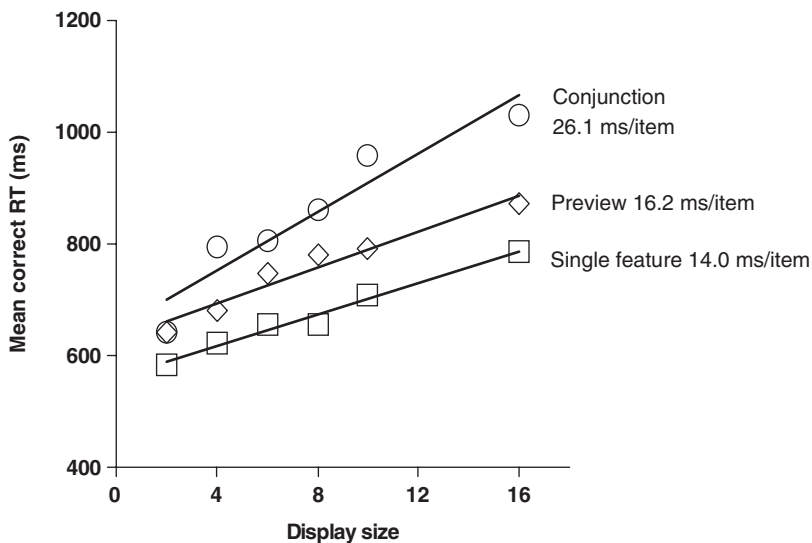
Predictions about the dynamics of visual search have been tested in studies using the 'preview'

search procedure. In this procedure the presentation of distractors is staggered over time, with one set of distractors appearing before the others and the target. This staggered presentation can facilitate target selection, as illustrated in Fig. 3b, where search is shown to be as efficient in the preview condition as in the single feature condition when only the new set of items is presented. sSoTS makes a matching prediction (Figs. 3a, b). Interestingly, and again like the model, there is a distinct time course to this effect — the first set of distractors needs to be presented up to 400 ms before the other items for search to benefit (Watson and Humphreys, 1997; Watson et al., 2003). This is a striking result because the different sets of stimuli can be temporarily segmented

## (a) Simulations



## (b) Comparable human data (from Watson, Olivers &amp; Humphreys, 2003)



**AU: 1** Fig. 3. (a) Simulations of single feature (SF), conjunction (CJ) and preview search (PV) in sSoTS. Note the steep slope on conjunction search even though the model operates in a spatially parallel manner. (b) Comparable human data (adapted from Watson et al., 2003). In human preview search, slopes for the preview condition very often match those in the single feature baseline (equivalent to when only the new search items are presented) and both are faster than the conjunction condition.

over much shorter time intervals than this — one can see that the old and new displays differ in time, but, with a short interval, it remains difficult not to be affected by the old items. This indicates that temporal segmentation alone is not sufficient to explain performance. However, the time course does match that expressed by sSoTS

(see Figs. 5a, b) — an emergent property of sSoTS's biologically plausible assumptions about the time course of the refractory state for neurons.

Other data from preview search also match other aspects of sSoTS. As we have noted, sSoTS incorporates the proposals made by psychological models that search is contingent on top-down

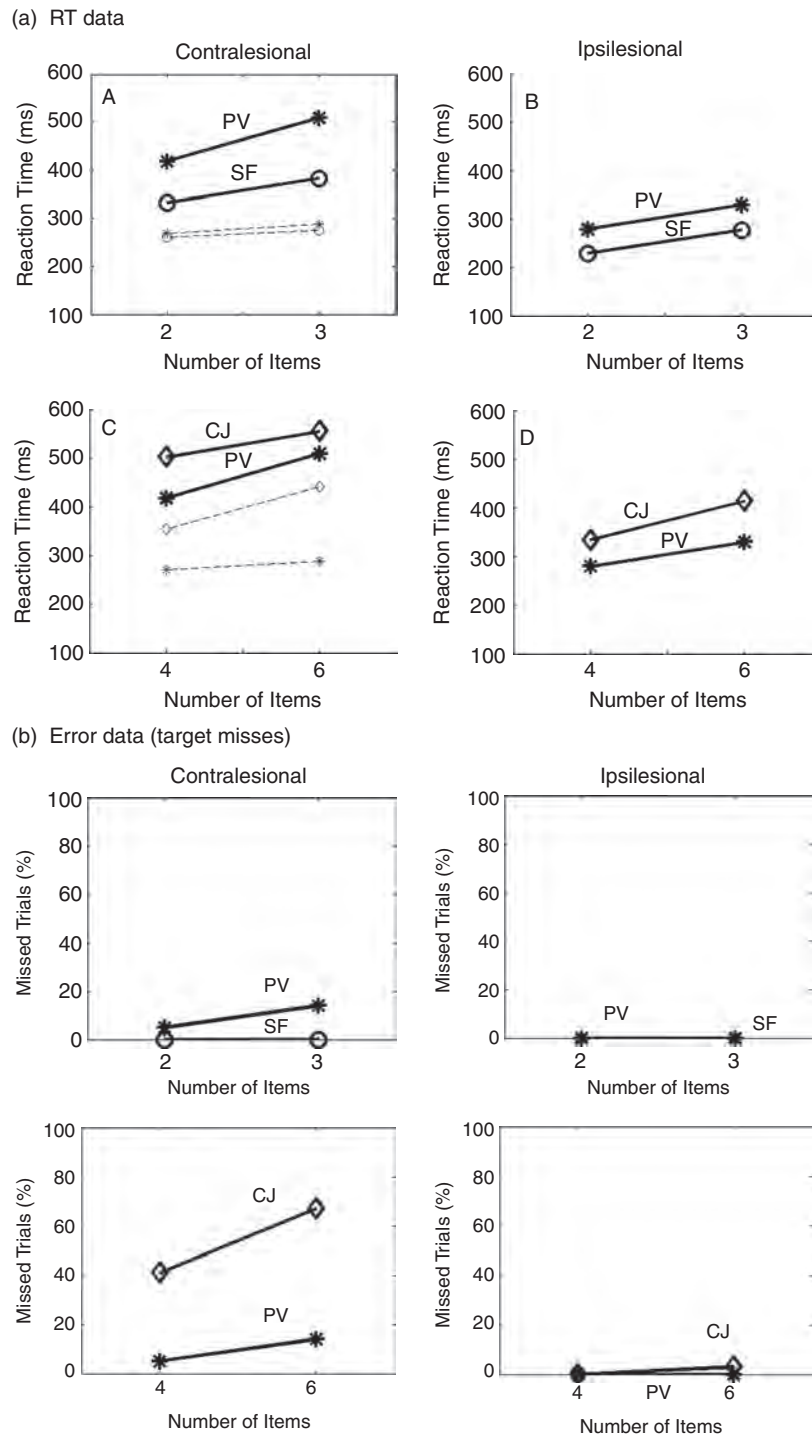
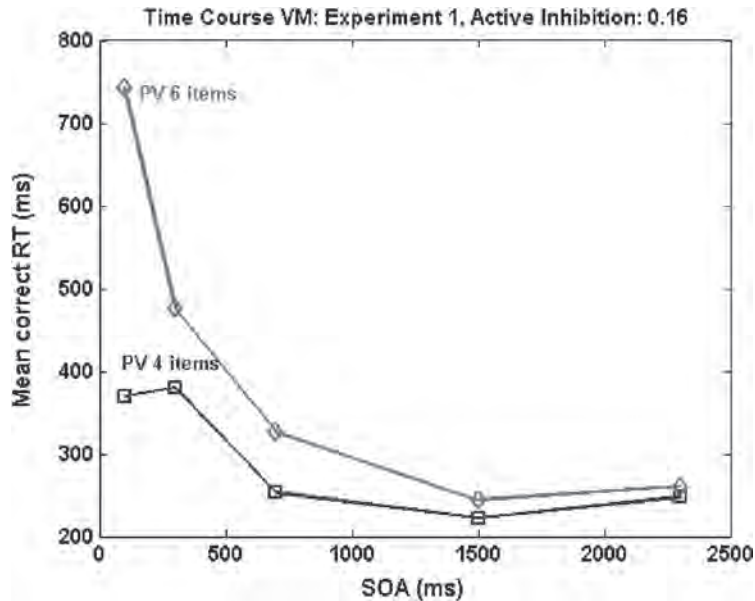


Fig. 4. Simulations of the effects of lesioning units on one side of the location map in sSoTS. (a) RT data; (b) error data (target misses). The data are shown for targets falling on the contralateral or ipsilateral side of space (side affected by lesion; side unaffected by lesion). In the top figures, the data are shown for single feature (SF) and preview search (PV) according to the number of items in the final display of the preview condition (either two or three items). In the bottom figures the data are shown for the conjunction and preview conditions, plotted against the number of items in the final display (four or six, in both preview and conjunction search). In each case the dotted lines show the results when the model was unlesioned. The results indicate that lesioning disrupts search in the conjunction and preview conditions most, for contralateral targets.



(a) Predictions from sSoTS



(b)

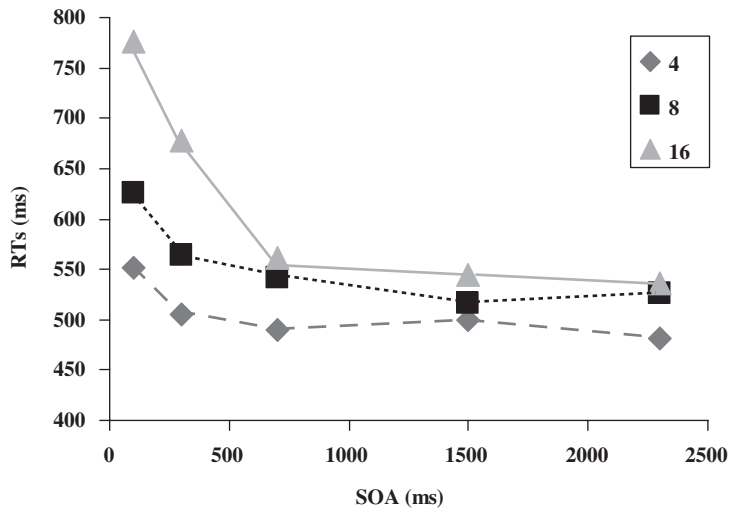


Fig. 5. (a) RTs generated by sSoTS as the duration of the preview is varied prior to the search display. (b) Data from human search as the preview duration is varied (adapted from Humphreys et al., 2004b). The model simulates the slow time course found in studies of preview search.

activation for targets and inhibitory suppression of distractors. Preview search provides good evidence for both processes operating in search. There are at least two pieces of evidence pointing to a role of inhibition. One comes from studies using probe-dot detection to measure

where attention is allocated during search. In Humphreys et al's. (2004) study participants saw a set of distractors as a preview (e.g. green horizontal lines) followed by a search display (red vertical distractors and a red horizontal target, when present). On a majority of trials participants

1 carried out the search task. On a minority of trials  
 3 they were cued to stop search and to try and  
 5 detect a small probe that could appear either  
 7 within an old distractor, a new distractor or the  
 9 background. When the preview was presented for  
 11 800 ms before the new items, search for the new  
 13 target was efficient. However, probes that fell on  
 15 old items were difficult to detect, with detection  
 17 levels in this case being lower than those found for  
 19 probes presented on the background (see also  
 21 Agter and Donk, 2005; Olivers and Humphreys,  
 23 2002; Watson and Humphreys, 1998). This is  
 25 consistent with the spatial locations of the old  
 27 items being inhibited.

15 A second piece of evidence indicating that  
 17 there is inhibition of distractors comes from work  
 19 on ‘carry-over effects’ in preview search.  
 21 Braithwaite and Humphreys (2003) and Olivers  
 23 and Humphreys (2003) presented a preview  
 25 display of distractors in one colour followed by  
 27 targets that either did or did not carry the colour  
 29 of the to-be-ignored old distractors. Targets  
 31 carrying the colour of the old distractor were  
 33 difficult to detect — strikingly, this occurred even  
 35 when the target had a singleton colour relative to  
 37 the other new items being presented, and even  
 39 when the old items were removed at the onset of  
 41 the new displays. Normally such a colour single-  
 43 ton should pop out in search. The problem in  
 45 detecting such a singleton target provides strong  
 47 evidence against the view that preview search is  
 simply based on automatic detection of the new  
 items or on the temporal segmentation of the old  
 and new displays (cf. Donk and Theeuwes, 2001;  
 Jiang et al., 2002) — if that were the case, then the  
 singleton should have popped out. This negative  
 colour carry-over effect is consistent with the  
 inhibition of the features as well as the locations  
 of the old items (cf. Humphreys et al., 2004). The  
 result also fits with the idea of spreading suppres-  
 sion, as put forward by Duncan and Humphreys  
 (1989); in this case, there is a spread of suppres-  
 sion from inhibited old distractors to new items  
 carrying the inhibited properties — the result is  
 that reaction times are slowed targets with these  
 properties. This inhibition is maintained for at  
 least some period even after the old distractors  
 have been removed.

In addition to presenting evidence for the  
 inhibition of old distractors, Braithwaite and  
 Humphreys (2003) also reported data indicating  
 effects of a positive expectancy for targets. In  
 particular, Braithwaite and Humphreys showed  
 that the negative colour carry-over effect could be  
 reduced if participants had advanced knowledge  
 of the target’s colour. These authors propose that  
 participants can independently set a top-down  
 positive expectancy for a target along with  
 adopting a negative bias against the properties  
 of irrelevant distractors. The data indicating both  
 positive and negative top-down effects in search  
 match the top-down excitatory and inhibitory  
 components operating in sSoTS.

### **The neural basis of inhibitory and excitatory biases**

When people engage in visual search a range of  
 brain areas are very often activated, most notably  
 there is a conjunction of activity in posterior  
 parietal and frontal cortices which increases as  
 search becomes more difficult (see Corbetta and  
 Shulman, 2002). However, as we have noted,  
 search involves multiple processes (positive acti-  
 vation for targets, inhibitory suppression of  
 distractors, the maintenance of target templates  
 and so forth), so it is useful to explore paradigms  
 such as preview search which can enable different  
 processes to be isolated. There have now been  
 several studies of preview search using functional  
 brain imaging, and it has been consistently found  
 that, relative to search when all the items appear  
 together, preview search is associated with  
 increased activation of several regions of posterior  
 parietal cortex (the superior parietal lobe [SPL]  
 and the precuneus; Allen et al., 2008; Humphreys  
 et al., 2004; Olivers et al., 2005; Pollmann et al.,  
 2003). This is interesting because preview search  
 can be more efficient than baseline search  
 conditions when all the items appear simulta-  
 neously, so the increased activation does not  
 simply reflect the general difficulty of search. Both  
 Allen et al. (2008) and Pollmann et al. (2003)  
 also included some ‘dummy preview’ trials where  
 only the preview appeared although participants

1 expected a search display to follow the preview  
(and so participants should engage in the same  
3 processing of the preview as on search trials). In  
both studies there was increased activation of SPL  
5 and precuneus when it was a dummy preview trial  
compared to trials which used equivalent visual  
7 displays but where the previews were unlikely to  
be ignored. This indicates that the SPL/precuneus  
9 activation is not tied to the search operation but it  
is consistent with these brain regions being linked  
11 to the inhibitory processing of distractors. The  
activation of the SPL/precuneus may reflect the  
13 operations of inhibitory neurons or some initial  
attention being paid to the old distractors in order  
15 to then inhibit them (see Humphreys et al., 2004,  
for evidence consistent with this from probe-dot  
17 procedures).

The data on functional brain imaging are  
19 supported by neuropsychological studies on selec-  
tive disorders of search in patients with brain  
21 lesions. It is well established that patients with  
damage to posterior parietal cortex (PPC) are  
23 impaired at serial search tasks (Eglin et al., 1989;  
Riddoch and Humphreys, 1987). Olivers and  
25 Humphreys (2004) found that PPC patients were  
also impaired at preview search, even though  
27 normal participants perform preview search effi-  
ciently. This again points to effects on particular  
29 processes rather there being an exaggerated  
influence of search difficulty in the patients.  
31 Humphreys et al. (2006) found that PPC patients  
impaired at preview search were nevertheless able  
33 to prioritize their attention to new onset stimuli. If  
prioritized attention to new onsets was sufficient  
35 to generate efficient preview search (Donk and  
Theeuwes, 2001), then the patients should have  
37 shown efficient preview search. In contrast to this  
the impairments indicate that additional processes  
39 (such as inhibition of the old distractors) deter-  
mine the efficiency of preview search, and these  
41 additional processes may be disrupted by PPC  
damage. Further evidence consistent with this was  
43 noted by Olivers and Humphreys (2004). They  
found that the PPC patients were particularly  
45 impaired when the new and old stimuli were  
spatially overlapping compared with when the  
47 items did not overlap and could be spatially  
segmented. These data suggest that the PPC was

critical for the segmentation and rejection of the  
old distractors, and was recruited particularly  
when spatial segmentation was difficult.

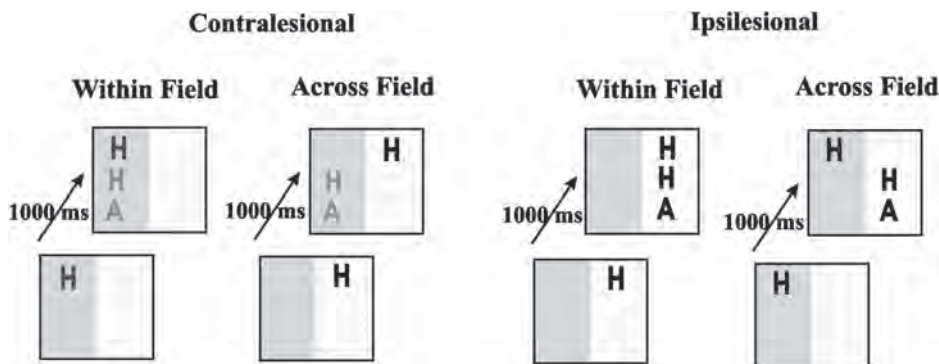
As we have noted (Fig. 4), sSoTS also predicts  
that damage to the location units within the  
model, putatively representing PPC, generates  
problems in search. Within the model this not  
only affects the detection of conjunction targets,  
but also the detection of targets in preview search.  
Humphreys et al. (2009) simulated effects of PPC  
damage by removing units from one side of the  
location map. This disrupted both conjunction and  
preview search. Similarly to the patients, the  
problems in preview search were most pro-  
nounced when the old and new items overlapped  
spatially, when temporal segmentation would  
normally augment spatial segmentation (Fig. 6).  
When lesioned, sSoTS has a reduced ability to  
implement temporal separation of new targets  
from old distractors on one side of space; this  
leads to problems in separating distractors within  
the same area of field. It is of interest that poor  
performance of the model was observed even  
when both the old and new items fell within the  
undamaged (ipsilesional) field. This is because  
poor inhibition of old ipsilesional distractors  
means that they stay as competitors for new items  
appearing in the same locations. The result is that  
target detection becomes inefficient.

These simulations of the effects of PPC damage  
provide important converging evidence linking  
specific brain regions to functional processes  
within the model.

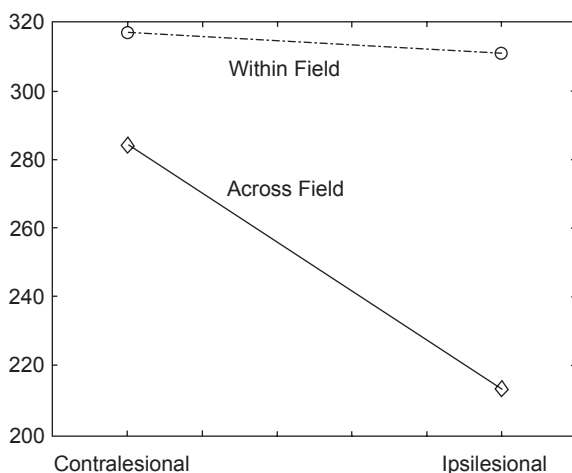
### **Modelling brain imaging data**

Another way to link the operation of an abstract  
computational model to brain function is to  
simulate data from functional imaging. Activity  
within a model such as sSoTS can be convolved  
with an assumed haemodynamic function to  
predict the BOLD response (Glover, 1999). This  
then enables us to take functional processes in the  
model, such as the operation of excitatory and  
inhibitory activity during search, and to assess  
within which brain areas the activity correlates  
with the different functional processes. We

## 1 (a) Stimulus presentation procedure



## 15 (b) Results (search RTs) from sSoTS after lesioning



33 Fig. 6. (a) The stimulus presentation procedure used to examine the effects of spatial and temporal separation in sSoTS. The initial display is the preview and this is followed by the search display. In the across field condition, the preview appears in the opposite field to the new items in the search display. In the within field condition, the new search items appear within the same field as the preview. (b) Mean RTs generated by sSoTS after unilateral lesioning of units on one side of the Location map. Targets were presented either on the contralateral (damaged units) or ipsilesional side of space (undamaged units). The data show that within field discriminations are more difficult than across field discriminations, with the detection of contralateral targets being generally worse. Comparable data from patients with PPC lesions were reported by Olivers and Humphreys (2004).

39 (Mavritsaki et al., submitted) have done this by  
 41 summing activity across different maps in sSoTS  
 43 according to whether the activity is reflecting top-  
 45 down excitation of targets or bottom-up inhibition  
 47 of distractors. The emergent results are shown in  
 Fig. 7. The figure reveals both overlapping and  
 distinct regions within PPC, and also visual  
 processing areas in occipital cortex, where activity  
 is separately correlated with the time course of

excitatory and inhibitory activity within the  
 model. This then provides a functional decom-  
 position of the network of areas that is activated  
 during search. As the functional processes of  
 target excitation and distractor inhibition will be  
 involved both in preview search and in search for  
 conjunction stimuli, it follows that damage to the  
 areas supporting the excitation and inhibition  
 processes will disrupt both types of search task.

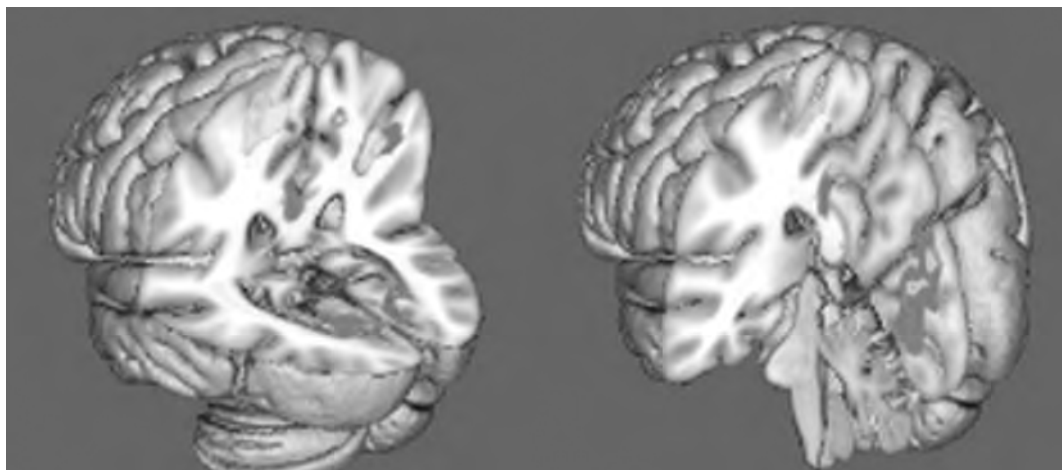


Fig. 7. Images showing brain regions where neural activity in preview search correlates with inhibitory and excitatory activity in sSoTS (when convolved with an assumed haemodynamic function). This model-based analysis pulls apart neurons within overlapping brain regions that perform functionally distinct roles in search. Areas in blue correlate with inhibitory activity in the model; areas in yellow correlate with excitatory activity.

This prediction is supported by the neuropsychological data (Olivers and Humphreys, 2004; Ridloch and Humphreys, 1987).

### The importance of multi-level analyses

We have reviewed evidence using behavioural manipulations (such as preview search), neuropsychological analyses (e.g. the effects of PPC lesions), functional brain imaging (e.g. fMRI) and computational modelling, to analyse the processes involved in visual search. Each piece of evidence has its own limitation. For example, behavioural studies reveal ‘whole-system’ behaviour, but this can make it difficult to analyse the operation of sub-component processes. Studies using functional brain imaging reveal brain areas that correlate with different processes but do not prove that these processes are necessary for a given task. Neuropsychological studies do demonstrate the necessary role of brain regions (since damage to those regions is shown to disrupt performance), but the lesion may affect more than one process which in turn makes it difficult to exactly relate an impaired function to the lesioned area. Given these limitations, it is important to use

evidence coming from each approach in order to develop an over-arching framework not subject to one limitation. In the present case, this framework can also be captured at a formal level in terms of the sSoTS model. Models such as sSoTS can help to integrate research in at least two ways. First, it can simulate effects at multiple levels (brain imaging, effects of neuropsychological deficits and effects due to emergent, whole-system behaviour), enabling us to link the different approaches and different types of data together. The weakness inherent in one approach, then, can be compensated for by the strengths of the other. For example, fMRI in normal participants may be able to localise, across the whole brain, processes involved in a given task. The necessary role of these areas would then be addressed through neuropsychological evidence. This relationship should be captured by simulating the effects of lesioning matching regions within the model. Second, the model shows how ideas expressed in different psychological models can be formally linked, enabling us to see how different models relate to one another. For example, distractor similarity influences the amounts of lateral inhibition operating in the model (cf. Duncan and Humphreys, 1989; Wolfe, 1994), while Treisman

1 and Sato's argument for feature-based inhibition  
 3 is implemented through the top-down inhibition  
 5 process in the model. Which factors are impor-  
 7 tant, under which conditions, can then be  
 9 explored. We believe this provides a working  
 11 framework through which to assess the various  
 13 factors determining search efficiency. One parti-  
 15 cularly important point, given the stab at biolog-  
 17 ical plausibility in the model, is that variations in  
 19 physiological parameters (e.g. the time course  
 21 over which neurons enter into a refractory state)  
 23 can generate psychological predictions (e.g. on the  
 25 time course of visual search); these predictions  
 27 can be tested and fed back to further inform  
 29 model development in a (virtual) cycle of model-  
 31 ling and testing. We propose that the formal  
 33 development of models such as sSoTS will play an  
 35 important part in the integration of psychological  
 37 theory and physiological data.

## Uncited reference

Humphreys et al. (2004a).

## Acknowledgement

This work was supported by grants from the  
 BBSRC, ESRC and MRC (UK).

## References

- Agter, , & Donk, M. (2005). Prioritized selection in visual search through onset capture and color inhibition: Evidence from a probe-dot detection-task. *Journal of Experimental Psychology: Human Perception and Performance*, *31*, 722–730.
- Allen, H. A., Humphreys, G. W., & Matthews, P. M. (2008). A neural marker for content specific active ignoring. *Journal of Experimental Psychology: Human Perception and Performance*, *34*, 286–297.
- Braithwaite, J. J., & Humphreys, G. W. (2003). Inhibition and anticipation in visual search: Evidence from effects of color foreknowledge on preview search. *Perception & Psychophysics*, *65*, 213–237.
- Bundesen, C. (1990). A theory of visual-attention. *Psychological Review*, *97*(4), 523–547.
- Corbetta, M., & Shulman, G. L. (2002). Control of goal directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*, 201–215.

- Courtney, S. M., Ungerleider, L. G., Keil, K., & Haxby, J. V. (1994). Object and spatial visual working memory activate separate neural systems in human cortex. *Cerebral Cortex*, *6*, 39–49.
- Donk, M., & Theeuwes, J. (2001). Visual marking beside the mark: Prioritizing selection by abrupt onsets. *Perception & Psychophysics*, *93*, 891–900.
- Duncan, J., & Humphreys, G. W. (1989). Visual search and stimulus similarity. *Psychological Review*, *96*, 433–458.
- Duncan, J., & Humphreys, G. W. (1992). Beyond the search surface: Visual search and attentional engagement. *Journal of Experimental Psychology: Human Perception and Performance*, *18*, 578–588.
- Eglin, M., Robertson, L. C., & Rafal, R. D. (1989). Visual search performance in the neglect syndrome. *Journal of Cognitive Neuroscience*, *1*, 372–385.
- Glover, G. (1999). Deconvolution of impulse response in event-related fMRI. *NeuroImage*, *9*, 416–429.
- Heinke, D., & Humphreys, G. W. (2003). Attention, spatial representation and visual neglect: Simulating emergent attentional processes in the Selective Attention for Identification Model (SAIM). *Psychological Review*, *110*, 29–87.
- Hodsoll, J., & Humphreys, G. W. (2001). Driving attention with the top down: The relative contribution of target templates to the linear separability effect in the size dimension. *Perception & Psychophysics*, *63*, 918–926.
- Humphreys, G. W., Jung-Stalman, B., & Olivers, C. N. L. (2004a). An analysis of the time course of attention in preview search. *Perception & Psychophysics*, *66*, 713–730.
- Humphreys, G. W., Kyllingsbæk, S., Watson, D. G., Olivers, C. N. L., Law, I., & Paulson, O. (2004b). Parieto-occipital areas involved in efficient filtering in search: A time course analysis of visual marking using behavioural and functional imaging procedures. *Quarterly Journal of Experimental Psychology*, *57A*, 610–635.
- Humphreys, G. W., Mavritsaki, E., Allen, H. A., Heinke, D., & Deco, G. (2009). Modelling visual search in biologically plausible neural networks: Whole-system behaviour, neuropsychological breakdown and BOLD signal activation. In D. Heinke & E. Mavritsaki (Eds.), *Computational modelling in behavioural neuroscience*. London: Psychology Press.
- Humphreys, G. W., & Müller, H. M. (1993). SEArch via Recursive Rejection (SERR): A connectionist model of visual search. *Cognitive Psychology*, *25*, 43–110.
- Humphreys, G. W., Olivers, C. N. L., & Yoon, E. Y. (2006). An onset advantage without a preview benefit: Neuropsychological evidence separating onset and preview effects in search. *Journal of Cognitive Neuroscience*, *18*, 110–120.
- Humphreys, G. W., Quinlan, P. T., & Riddoch, M. J. (1989). Grouping effects in visual search: Effects with single- and combined-feature targets. *Journal of Experimental Psychology: General*, *118*, 258–279.
- Jiang, Y., Marks, L. E., & Chun, M. M. (2002). Visual marking: Selective attention to asynchronous temporal groups. *Journal of Experimental Psychology: Human Perception and Performance*, *28*, 717–730.

- 1 Mavritsaki, E., Allen, H. A. & Humphreys, G. W. (submitted).  
 AU:6 Modelling the neural substrate of preview search. *Neuron*.
- 3 Mavritsaki, E., Heinke, D. G., Humphreys, G. W., & Deco, G.  
 (2006). A computational model of visual marking using an  
 5 interconnected network of spiking neurons: The spiking  
 Search over Time & Space model (sSoTS). *Journal of  
 Physiology (Paris)*, *100*, 110–124.
- 7 Neisser, U. (1967). *Cognitive psychology*. New York: Apple-  
 ton-Century-Crofts.
- 9 Olivers, C., & Humphreys, G. W. (2002). When visual marking  
 meets the attentional blink: More evidence for top-down  
 limited capacity inhibition. *Journal of Experimental Psychol-  
 ogy: Human Perception and Performance*, *28*, 22–42.
- 11 Olivers, C. N., & Humphreys, G. W. (2004). Spatiotemporal  
 13 segregation in visual search: Evidence from parietal lesions.  
*Journal of Experimental Psychology: Human Perception and  
 Performance*, *30*, 667–688.
- 15 Olivers, C. N. L., & Humphreys, G. W. (2003). Visual marking  
 and singleton capture: Fractionating the unitary nature of  
 17 visual selection. *Cognitive Psychology*, *47*, 1–42.
- Olivers, C. N. L., Smith, S., Matthews, P., & Humphreys, G. W.  
 (2005). Prioritizing new over old: An fMRI study of the  
 19 preview search task. *Human Brain Mapping*, *24*, 69–78.
- 21 Pollmann, S., Weidner, R., Humphreys, G. W., Olivers, C. N.  
 L., Müller, K., Lohmann, G., et al. (2003). Separating  
 23 segmentation and target detection in posterior parietal  
 cortex — An event-related fMRI study of visual marking.  
*NeuroImage*, *18*, 310–323.
- Riddoch, M. J., & Humphreys, G. W. (1987). Perceptual and  
 action systems in unilateral neglect. In M. Jeannerod (Ed.),  
*Neurophysiological and neuropsychological aspects of spatial  
 neglect*. Amsterdam: Elsevier Science.
- Treisman, A. (1998). Feature binding, attention and object  
 perception. *Philosophical Transactions of the Royal Society*,  
*353*, 1295–1306.
- Treisman, A., & Gelade, G. (1980). A feature-integration  
 theory of attention. *Cognitive Psychology*, *12*, 97–136.
- Treisman, A., & Sato, S. (1990). Conjunction search revisited.  
*Journal of Experimental Psychology: Human Perception and  
 Performance*, *16*, 459–478.
- Watson, D. G., & Humphreys, G. W. (1997). Visual marking:  
 Prioritising selection for new objects by top-down attentional  
 inhibition. *Psychological Review*, *104*, 90–122.
- Watson, D. G., & Humphreys, G. W. (1998). Visual marking of  
 moving objects: A role for top-down feature based inhibition  
 in selection. *Journal of Experimental Psychology: Human  
 Perception and Performance*, *24*, 946–962.
- Wolfe, J. M. (1994). Guided Search 2.0: A revised model  
 of visual search. *Psychonomic Bulletin and Review*, *1*,  
 202–238.
- 25  
27  
29  
31  
33  
35  
37  
39  
41  
43  
45  
47

## AUTHOR QUERY FORM

 <small>ELSEVIER</small>	<b>Book: PBR-V176</b>  <b>Chapter: 9</b>	<b>Please e-mail or fax your responses and any corrections to:</b>  <b>E-mail:</b> <b>Fax:</b>
--	--	---

Dear Author,

During the preparation of your manuscript for typesetting, some questions may have arisen. These are listed below. Please check your typeset proof carefully and mark any corrections in the margin of the proof or compile them as a separate list.

**Disk use**

Sometimes we are unable to process the electronic file of your article and/or artwork. If this is the case, we have proceeded by:

- Scanning (parts of) your article     Rekeying (parts of) your article  
 Scanning the artwork

**Bibliography**

If discrepancies were noted between the literature list and the text references, the following may apply:

- The references listed below were noted in the text but appear to be missing from your literature list. Please complete the list or remove the references from the text.**
- UNCITED REFERENCES: This section comprises references that occur in the reference list but not in the body of the text. Please position each reference in the text or delete it. Any reference not dealt with will be retained in this section.**

**Queries and/or remarks**

Location in Article	Query / remark	Response
AU:1	Has permission been obtained for Figs. 3 and 5 from publisher for copyright? If so, please provide the permission lines.	
AU:2	Please check the name of the corresponding author and provide tel. no., fax no. and email address of the corresponding author.	
AU:3	Please check as there is a discrepancy in the chapter title given in the TOC and that given in the chapter.	
AU:4	Please provide the ref. Watson et al. (2003) in the reference list.	
AU:5	Since there are two publications of Humphrey et al. (2004), as per style, we cross-refer it as '2004a' and '2004b' for tagging purposes. Please indicate by comparing with the list as either 'a' or 'b'.	
AU:6	Please provide complete details of the ref. Mavritsaki et al. (submitted).	