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Decomposing the neural mechanisms of visual search through model-based analysis of fMRI: Top-down excitation, active ignoring and the use of saliency by the right TPJ

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ABSTRACT

Despite being studied intensively over the past 30 years, the neural processes underlying visual search are not yet fully understood. In the current study we extend prior work using model-based analysis to decompose fMRI data. fMRI data on human search were assessed using activation functions predicted from the spiking Search over Time and Space model (sSoTS; Mavritsaki et al., 2006). Going beyond previous work, we show for the first time that activity in a central location map in the model, which computes the saliency of a target relative to distractors, correlated with the BOLD response in the right temporo-parietal junction (TPJ) – a key region implicated in clinical studies of unilateral neglect. This is consistent with the right TPJ responding to the relative saliency of visual stimuli. In addition, a re-analysis of search performance, with a larger participant set and a psychologically plausible response rule, showed distinct neural regions in parietal and occipital cortices linked to top-down excitation and the to active ignoring of distractors. The results indicate that excitatory and inhibitory circuits for visual selection can be separated, and that the right TPJ may be critical for responding to salient targets. The value of using a model-based approach is discussed.

Introduction

Human visual search is a complex process involving a wide range of processes including: the coding of visual features and feature differences, the grouping of visual elements, a memory template to guide attention to the target, the rejection of distractors, and a memory for previously searched locations (e.g., see Watson and Humphreys, 1997; Wolfe et al., 1989). Not surprisingly, given the complexity of the underlying processes, the functional role(s) of different brain areas involved in search is not yet fully understood. For example, while it is broadly agreed that search is controlled through a fronto-parietal attentional network that interacts with and regulates processing in earlier (occipital) regions (e.g., Corbetta and Shulman, 2002), the precise role of different parts of this network remains controversial. Corbetta and Shulman (2002), for example, have distinguished between dorsal and more ventral regions of this network, arguing that the dorsal regions are involved in endogenous control of attention in search while ventral regions respond in a more exogenous manner. Notably they propose that the right temporo-parietal junction acts as a 'circuit breaker', to detect the occurrence of unexpected but task-relevant stimuli – a process that is critical for switching attention from a currently attended location or stimulus. They link this to the clinical disorder of visual neglect, associated with damage to the inferior parietal lobe/TPJ region (Chechlacz et al., submitted for publication; Mort et al., 2003; Verdon et al., 2009). After damage to the right inferior parietal/TPJ region, neglect patients fail to orient automatically to task relevant stimuli on the contralesional side (e.g., Riddoch and Humphreys, 1983) and have problems disengaging attention from the ipsilesional side (Posner and Cohen, 1984). This is consistent with the patients failing either to detect salient signals on the contralesional side, or failing to use such signals to initiate responding.

Other work more specifically associates regions of the superior parietal lobe with the inhibitory suppression of irrelevant distractors in search (Allen et al., 2008; Humphreys et al., 2004b; Pollmann et al., 2003; Ress et al., 2000). In many cases, both inhibitory suppression and expectation-based baseline shifts may operate, making it difficult to disentangle the resultant combined activity and the combined effects on performance. For example, if an area is more active in one condition than another (e.g., in search for a conjunction target rather than a target defined by a single feature), is this due to the more active region being responsible for a particular process that differs between the conditions (e.g., the binding of visual features) or due to it more strongly regulating other areas (e.g., modulating activity in occipital areas, as attention shifts in serial search)? The problem in inference remains with neuropsychological data, when damage to an area may reflect either its functional role or its modulation of a broader network.

One way to understand complex, interactive processes is to use formal modelling, where emergent behaviour can arise from interactions between different network components. Here an understanding of the functional roles within different parts of a network can be understood either because the model was constructed to incorporate

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particular functional properties into different parts of its network in the first place, or because different functions can be identified through empirical variation in the model's parameters. There now exist several formal models of visual search. The models differ in the stress they place on the role of bottom-up guidance (e.g., Einhauser, 2007; Itti and Koch, 2001) vs. top-down control of search (Torralba et al., 2006; Wolfe, 1994), and on the role of grouping in target-distractor segmentation (e.g., Heinke and Humphreys, 2003; Humphreys and Muller, 1993). However, most assume that search derives from an interaction between bottom-up processes responding to local feature differences between visual elements, and top-down processes that set excitatory expectations for targets as well as inhibiting irrelevant distractors (e.g., Treisman, 1998). This has been modelled by feeding bottom-up and top-down input into a common selection process that competitively weights possible solutions across time as selection emerges (Hamker, 2004). In many models items are selected on the basis of activation within a central 'saliency' map that signals the location(s) of the most probable target stimuli in the field and/or that can be used to guide an action (e.g., a saccade) to that location (Bruce and Tsotso, 2009; Itti and Koch, 2001). For example Deco and Zihl (2001) incorporated both top-down and bottom-up signals into the activity simulated in maps corresponding to simple visual features (e.g., particular colours or shapes), with the saliency of each position determined through recurrent connections between each position in each feature map and the corresponding location in an over-arching location/saliency map.

The spiking Search over Time and Space (sSoTS) model (Mavritsaki et al., 2007; 2006) follows Deco and Zihl's (2001) and incorporates the above processes in a minimal architecture for search based on more realistic spiking-level neurons. sSoTS (see Fig. 1) codes visual stimuli in terms of activity within a set of feature maps, each containing neurons for a simple visual feature (e.g., a colour or shape element) at multiple

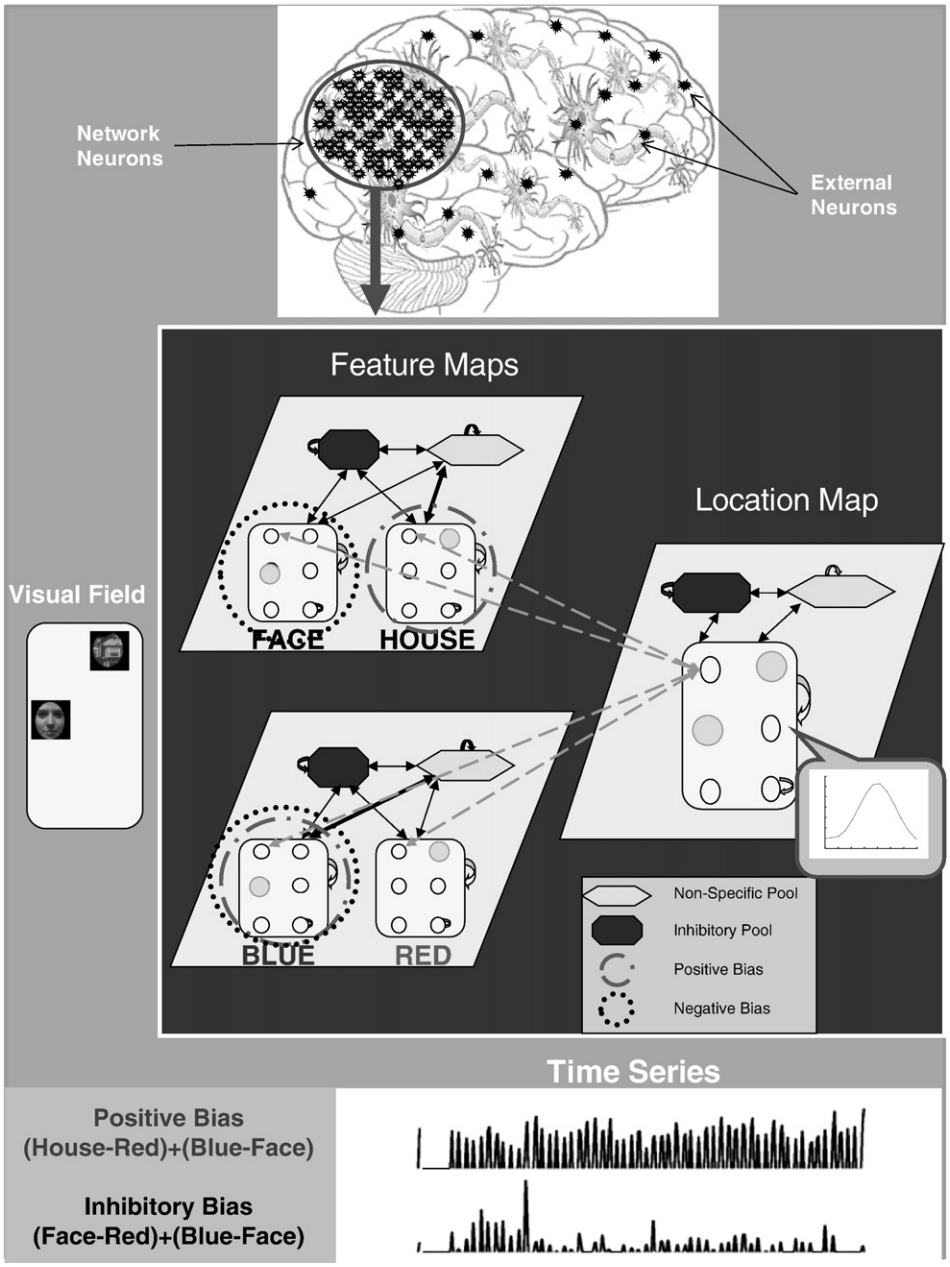

Fig. 1. The processing architecture for sSoTS. The model simulates activity within posterior neural networks that receive 'external' activation from more anterior brain regions. Within the model we simulate 4 feature maps and a location map. The inset in the location map shows the output Bold signal that can be extracted from this map.

field locations. Units at different locations compete for selection, generating lateral inhibitory behaviour. Following Deco and Zihl (2001); see also, Hamker, 2004) activity from the feature maps is sent forward to a central map of locations, where excitation at a given location is pooled to provide a signal of the saliency of that position. Activity in the location map is then fed-back to the feature maps to sharpen the competition there, enhancing winner-take-all behaviour. In addition, search is guided to a given target based on excitatory activation input into feature maps representing the target's properties, while inhibition that is applied to maps for distractor features helps to bias search against distractors. In the original simulations (Mavritsaki et al., 2006) targets were detected when units in the location map reached a set threshold, and this was taken as the point when activity would be passed-on to response systems. Using these minimal processes, sSoTS was able to simulate a range of human search data, including: (i) efficient search for targets defined by a feature difference relative to distractors, (ii) inefficient search for conjunction targets, and (iii) the emergence of efficient search over time, when conjunctions displays are temporarily segmented across the two distractor sets (cf., Watson and Humphreys, 1997; Watson et al., 2003). Given the success of sSoTS in accounting for basic spatial and temporal aspects of human search, it becomes relevant to ask where the different processes proposed by the model are incorporated in the brain. If active expectations for targets, inhibition of distractors and saliency-based signalling of probable target locations are a minimal set of processes needed to capture human search, can we identify the brain regions performing these functions?

Model-based analysis of fMRI data

Over the past 5 years, several investigators have attempted to use computational models to simulate fMRI as well as behavioural data. Here a predicted haemodynamic response (HDR) can be generated by convolving an assumed HDR function (Glover, 1999) with a given input. There are several ways that this can be done (see, Almeida and Stetter, 2002), but one approach follows from physiological studies in the monkey (Logothetis, 2008; Logothetis et al., 2001) suggesting that fMRI activity does not represent the output 'firing' of pyramidal neurons, but rather incoming activity, activity in interneurons, and recurrent excitatory and inhibitory activity. To capture this, the assumed HDR can be convolved with the total synaptic activity at given locations in a neural model (sampling the synaptic activity at set intervals). This generates a predicted HDR, which can be compared with human data. This has been done by Corchs and Deco (2002, 2004) in simulations of feature-based visual attention, and Deco et al. (2004) in simulations of working memory. In both cases, a qualitative comparison was made between the model and the observed BOLD function, contrasting performance across critical conditions (e.g., according to whether stimuli were attended or not). These studies show that fMRI data can be simulated in computational models, but the investigators did not carry out quantitative analyses to assess which brain regions were significantly correlated with activity as predicted by the model. In a preliminary study (Mavritsaki et al., 2009a) we took this additional step, where we conducted formal comparisons of the activity predicted by the sSoTS model with whole-brain activity from a study of human visual search, a method that has been also applied to reward learning (O'Doherty et al., 2007). This preliminary study showed that it was possible to extract patterns of activity linked to excitatory and inhibitory operations within the model and to link these abstracted patterns of functional responding to neural responses in specific brain regions. However, the analysis was based on a relatively small set of participants and so lacked the power to demonstrate robust functionally-related changes in brain areas. In addition, no attempt was made to link activity in localised regions of the model with that in associated brain areas. This last step is important for furthering our understanding of the functional role of brain regions, since activity in the region can then be tied to the defined role of the homolog area in the model. In the present study we use a more powerful analysis than previously, based on the full fMRI data from Allen et al. (2008). In addition, for the first time, we link activity from one functionally defined location in the model to activity patterns in specific brain regions as humans perform visual search. Finally, rather than use a set threshold function, the model's reaction times (RTs) were calculated by using an 'attention indicator' (IndA) based on Luce's choice axiom (Luce, 1959; Luce, 1977), applied at the level of the location map. The Luce index provides a more nuanced way of analysing the relative saliency of stimuli as they compete for selection, relative to the simple contrast function that was used in earlier studies (Mavritsaki et al., 2009a,b, 2007, 2006).

We examine three basic processes present in sSoTS (but also found in other models): top-down excitatory guidance of attention to targets, top-down inhibition of distractors, and identification of the target's position generated through activation of a location (saliency) map. One interesting aspect of our analysis of excitatory and inhibitory processes is that, to do this, we combined activation across different feature maps within the model in order to generate activity patterns reflecting the overall changes at a feature map level due to top-down excitation and inhibition. Note that activity within the feature maps combines excitation and inhibition so that the two factors cannot be isolated at the map level. However, combining across the maps gives us the signatures for respectively top-down excitation and inhibition. By including predicted time courses of changes in our whole-brain analyses of the BOLD activity during search, we could detect brain regions reflecting the overall, on-going excitatory and inhibitory modulation of feature maps.

This functional analysis of top-down excitation and inhibition was contrasted with the first-ever evaluation of brain areas responding to saliency differences registered in the location map in sSoTS. In this last case we introduced as a regressor into our fMRI analysis the time course of activity in the location map under contrasting search conditions. Brain regions changing in line with activity in the model's location map can be thought either to hold a saliency profile for the stimuli akin to that held in the model, or to be responding to variations in the saliency signal provided by such a map. This last development enables us to try and functionally isolate the brain region(s) that respond to saliency during human search.

Method

sSoTS model: general properties and justification

The spiking Search over Time and Space (sSoTS) model is comprised of an interconnected network of integrate-and-fire neurons. Units in the model are separated into excitatory neurons, modelled on pyramidal cells (and that comprise 80% of the neurons in the system), and inhibitory neurons, modelled on inter-neurons (comprising 20% of the neurons in the system). These proportions capture the approximate ratio of excitatory to inhibitory neurons in the cortex and have been employed in other simulations incorporating biologically plausible assumptions into neural-level models (Braitenberg and Schutz, 1991; Brunel and Wang, 2001; Deco and Rolls, 2005). In the simulations presented here, the model has 5 'maps' of the visual field: four feature maps (two representing shape and two colour) and one location (saliency) map where activity is summed from corresponding positions in the feature maps (Fig. 1). All neurons in the model receive inputs from three currents: a fast inhibitory current, mediated by GABA-like dynamics, a fast excitatory current mediated by AMPA-like dynamics and a slow inhibitory current mediated by NMDA-like dynamics (for more details for the model see Appendix A). Input into the feature maps is provided by 800 external neurons modelled using fast excitatory (AMPA-like) dynamics with Poisson noise. The external neurons are excited with a frequency of 3 Hz, if there is no stimulus at the corresponding stimulus at a given field position. However, when a

stimulus is present the firing frequency is increased to excite the neurons in the model at the corresponding position.

Within each map, the inhibitory neurons receive activation from all excitatory neurons in the layer and provide global inhibition to all the excitatory neurons present. Neurons at each location are organised into local pools with strong lateral coupling and the pools in the same feature map are interconnected with weak coupling. The feature maps are organised to simulate behavioural results on classic feature and colour-form conjunction tasks (e.g., Treisman and Gelade, 1980). The maps are divided along two feature dimensions, "shape" and "colour," and within each of these dimensions two feature values are represented. In each of these maps we simulate 6 positions in our visual field. This is the maximum possible number of positions we could simulate given our current computational power. Following Allen et al. (2008), the shapes feature correspond to "house" and "face" stimuli, and the colour features correspond to "blue" and "red." Note that we do not assume that there are topographic feature maps for all complex shape used in search. Although in this case, it is likely that there are brain regions selective for face and house stimuli (Epstein and Kanwisher, 1998; Kanwisher et al., 1997); it is also sufficient for the current simulations that the face and house stimuli differentially activate distinct topographic maps for any more primitive form elements (e.g., for curved contours, for faces compared with houses).[1]

In addition to 'within level' interactions within and across different feature maps, the maps receive output from external sources independent of the environment. These additional external sources represent top-down excitation favouring the features of targets, and top-down inhibition of the features of distractors. There is considerable behavioural and neuroimaging evidence that visual search is modulated by foreknowledge of the target. For example, 'pop out' for targets along the feature dimensions of size and orientation is contingent on participants knowing the target they are searching for Hodsoll and Humphreys (2001), and the ability to use top-down expectancies for targets may underlie some of the differences between searching for targets defined along different dimensions (e.g., Anderson et al., in press). Recent neuroimaging evidence also indicates that the visual cortex is modified by top-down expectancies for targets generated through frontal and parietal regions (Bressler et al., 2008). To capture such effects, top-down activation is given directly to all processing units in the maps representing target features. This gives target features a competitive advantage relative to the features of distractors, helping to ensure that targets rather than distractors are selected in search.

Along with top-down expectancies for targets, behavioural evidence also points to distractors being suppressed in search (e.g., Braithwaite et al., 2005; Humphreys et al., 2004a; Kim and Cave, 2001; Watson and Humphreys, 2000). For example, several investigators have combined visual search with probe detection studies, where responses to occasional probes falling at different locations are used to measure where attention is allocated (Kim and Cave, 2001; Watson and Humphreys, 2000). Probes falling on distractors can be more difficult to detect than probes falling on regions of the background, even when any low-level visual differences between these conditions are controlled for (Humphreys et al., 2004a; Kim and Cave, 2001). These effects can be found in 'standard' search tasks where all the items appear simultaneously (Kim and Cave, 2001) and they can be isolated from top-down excitatory processes in studies of so-called preview search (Watson and Humphreys, 1997). In preview search (Watson and Humphreys, 1997) one set of distractors is typically presented before adding to the same display the subsequent set of distractors plus the target (when present).[2] This enables the processes applied to (the first set of) distractors to be separated from processes applied to both targets and distractors. In probe detection studies, probes are more difficult to detect when they appear close to old distractors compared to when they fall close to new items or to empty background locations (Agter and Donk, 2005; Allen and Humphreys, 2007; Humphreys et al., 2004b), and this occurs even when probes are presented prior to the onset of the search display (Humphreys et al., 2004a). This inhibition can even spread to new items carrying the same features as the old distractors, making it difficult to detect targets (say) that have the same colour as the old distractors (Braithwaite et al., 2005; Olivers and Humphreys, 2003). This fits with the idea that whole feature maps can be suppressed, a process proposed also for search with simultaneously presented stimuli (Kim and Cave, 2001; Treisman and Sato, 1990). Interestingly, the inhibition measured using probe dot detection can be eliminated when participants receive the same display conditions but only perform probe detection. This indicates that distractor inhibition is engaged as part of the search task, and it does not simply reflect the display conditions. Evidence for inhibition also decreases when participants carry out a secondary task during the preview interval (Watson and Humphreys, 1997), suggesting that inhibition reflects a top-down (resource-dependent) bias against distractors. In sSoTS distractor suppression is captured through top-down application of inhibition to feature maps of distractors (Mavritsaki et al., 2006).

Preview search tasks also suggest that there is a relatively long time course to distractor suppression in search. For example, in order to minimise effects of old distractors on search, the old and new items need to be temporarily segmented by at least 400 ms or more (Humphreys et al., 2004a; Watson and Humphreys, 1997). This is considerably longer than the interval required to perceptually distinguish the onset of the old and new displays (Yantis and Gibson, 1994), indicating the involvement of some extra process(es). sSoTS captures the long time course of preview search through the operation of a 'frequency adaptation' mechanism that is part of the natural firing properties of thee spiking-level neurons. In neural systems, spike-frequency adaptation can be produced by several different ion channels, each one with its own characteristics. Notably, the operation of a slow [Ca2+]-activated K+ current (Madison and Nicoll, 1984) leads to the adaptation of firing over a time course of 300 ms or so, and may provide a contribution to the reduced impact of old distractors on search after more prolonged preview exposures (Humphreys et al., 2004a; Watson and Humphreys, 1997). Adaptation of the slow [Ca^{2+}]-activated K^+ current (I_{AHP}) has been modelled by Liu and Wang (2001), and their formulation is employed here. This adaptation operates as follows. The presence of an item in the visual field increases the activation of the neurons in the corresponding positions, and, as the spiking behaviour increases, so the intracellular amount of [Ca^{2+}] increases. The increase in intracellular [Ca^{2+}] leads to a decrease in the likelihood that each neuron fires, given the same input – units become refractory. As a consequence of this, the average excitation of the neurons in each of the activated pools within sSoTS decreases, so that, under conditions of preview search, there is a

[1] Given that the feature maps in the model are unlikely to reflect higher-level brain regions responding to houses and faces as individuated stimuli, this also means that activity at the feature-map level of the model is unlikely to be related directly to activity in such stimulus-specific brain regions.

[2] This staggering of the components of a search display over time distinguishes preview search from studies of potentially linked phenomena such as the distractor preview effect. Lleras and colleagues (e.g., Thomas and Lleras, 2009) have shown that responses are slowed to targets if they carry the colour of a recently rejected set of distractors (e.g., when a target present trial follows a target absent trial). However, the distractor preview effect involves an analysis of carry over effects across trials, whereas preview search examines the temporal dynamics of search over time within a single display. Empirical studies have also indicated that inhibitory effects in preview search are distinct from processes such as inhibition of return (IOR; Posner and Cohen, 1984). For example, serial search conditions that maximise IOR lead to poor inhibition of distractors in preview search (Olivers et al., 2002). Hence the inhibitory processes we are examining here should not be confused with either the distractor preview effect or with IOR.

decreased probability that old distractors will compete for selection with new targets. Preview search should consequently become more efficient than conjunction search, where the same targets and distractors are presented but at the same time (see Watson and Humphreys, 1997, for the initial evidence for this).

To examine the neural basis of human search through the lens of the sSoTS model, we used the model to predict the BOLD function in a variety of human search tasks, including search for a target defined by a single feature from distractors, search for a target defined by a conjunction of features, and search over time as well as space (preview search).

Parameter setting

The parameters for the simulations were established in 'single feature' and 'conjunction' search tasks as reported by Allen et al. (2008) (conjunction search: blue house target vs. red house and blue face distractors; feature search: blue house target vs. red house distractors). While conjunction search is typically slow and linearly related to the number of distractors, feature search is efficient and relatively immune to the number of distractors presented. Using the parameter set outlined in Appendix B, sSoTS was able to simulate these behavioural results (see Fig. 2). This replicates the results of Deco and Zihl (2001). These same parameters were then used to simulate the preview search conditions used by Allen et al. (2008); blue face distractors presented for 2 s prior to the onset of a blue house target and red house distractors. In Appendix B the parameter w^+ represents the strength of connections between the neurons in each pool, while w^- represents the strength of connections between the pools within and across each feature map. Top-down excitation is given by the parameter λ_{att}, applied to the feature maps representing the target's characteristics (i.e., the colour blue and house features). Additional to the case for conjunction and single feature search, the parameter for the I_{AHP} current was selected in order to be able to simulate preview search when there was a relatively long time period between the first set of distractors and the subsequent search display. There was also active, top-down inhibition applied to distractor features to capture the evidence for distractor suppression in search (λ_{in}). Overall the input that a pool could receive was $v_{ext} = v_{ext} + (\lambda_{in} + \lambda_{att})/N_{ext}$ (where N_{ext} = the external input provided by the search display).

The parameters for the baseline feature and conjunction search tasks were set using a mean field approximation to the spiking level model, to simplify the search of the parameter space (see Mavritsaki et al., 2007, 2006, for fuller descriptions). Reaction times (RTs) were calculated by using an 'attention indicator' (IndA) based on Luce's axiom (Luce, 1959; Luce, 1977), applied to the location map, where $\mathrm{IndA} = \frac{f_i(t)}{\sum_j f_j(t)}$ ($f_i(t)$ represents the firing rate of pool i at time t). This attention indicator represents the relative strength of activation for a signal at one location relative to the activation in other (competing) locations. If the attention indicator crossed a given threshold (set based on the average *IndA* for all conditions), then the time that the threshold was crossed was taken as the RT for the trial. If the pools that crossed the threshold at this juncture conformed to the target features, then the trial was judged as correct (a hit trial). If the pools crossing the threshold corresponded to a distractor rather than the target then the target was 'missed.' In order to avoid saturation effects due to the target activation being set high, search was run under conditions in which some errors occurred (<5%), mimicking human data.

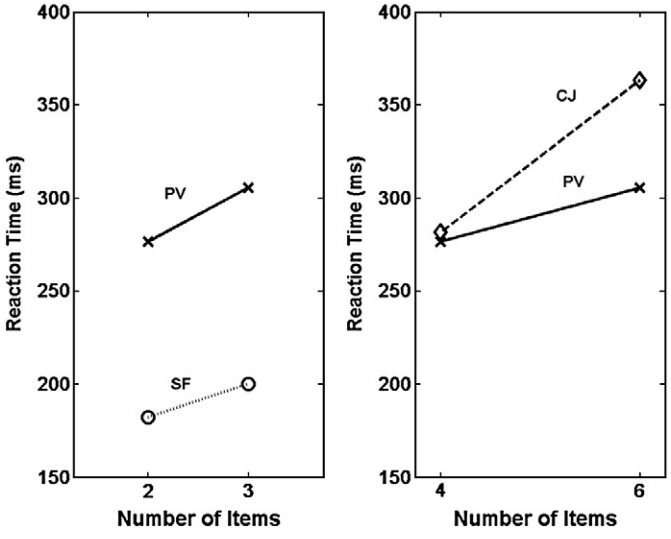

Fig. 2. The behavioural data from the model. The single feature (SF) slope is 10 ms/item, conjunction (CJ) slope is 40 ms/item and preview (PV) slope is 18 ms/item. The slopes from human data are −6, 31 and 11.5 ms/item, respectively Allen et al. (2008).

In the mean field simulations, we examined areas in parameter space where the network converged to select the target when presented (see Mavritsaki et al., 2006).This was done first for the single feature and conjunction conditions, prior to our exploring the effects of the adaptation and active inhibition parameters (influential for preview search but not for search when all the items appear simultaneously) in order to simulate successfully the search slopes for preview search (Watson and Humphreys, 1997; see Fig. 2).

Following the setting of the main parameters at the mean field level, detailed simulations were run at the spiking level only. In the spiking level simulations there is noise within the system based on a Poisson distribution of activity in the units. This generates variance across different runs of the model and enables us to analyse the data by treating each run as a separate participant, matching studies with human participants. The mean data for each model 'participant' were based on 20 simulations. Applied to model fMRI data, the different runs of the model can be taken to be homologous to the BOLD data generated by different participants.

Modelling fMRI data

To predict the BOLD (Blood Oxygen Level Dependent) response measured in fMRI studies of search, we convolved synaptic activity (Logothetis, 2008; Logothetis et al., 2001) for each unit in the model with the HDR function as proposed by Glover (Glover, 1999; see Deco et al., 2004). Our primary aim was to examine the neural regions associated with variations in the BOLD response predicted by sSoTS for (i) activity in the location map (Fig. 1); (ii) top-down activation favouring target features; and (iii) active suppression of distractors. Top-down excitation and suppression of distractors operate across all feature maps. To derive an overall measure of model-based activity reflecting these processes, we combined synaptic activity across the feature maps to extract activation changes due to each top-down process, as described below. Please note that by activation below we mean synaptic activity.

(i) The location map. To extract activity associated with the location map, the activation was pooled across the units for each location and then convolved with the HDR function. Note that activation in the location map is typically much stronger for the position where the target falls than for the other locations, and hence pooled activity for the location map tends to reflect the profile for the target, consistent with the location map serving to signal which location is the most salient. For the fMRI analysis, activation related to the model's location map on search trials was compared with a baseline when participants fixated the screen prior to search (data from Allen et al., 2008). For the data from sSoTS, we compared the HDR when search took place relative to the mean HDR to random levels of firing

in the model. Details of how the time series was extracted can be found in Appendix C.

(ii) Top-down activation. The extraction of the activation associated with top-down excitation was done as follows. Given the task of searching for a blue house target amongst blue face and red house distractors (Allen et al., 2008), there was a positive bias in sSoTS applied to maps representing blue and house. Furthermore, there was an inhibitory bias applied to maps representing the features of distractors (red and face) in the preview condition. Thus for the conjunction condition activity reflecting top-down excitation for the target was given by

(a) (Target form − Distractor form) + (Target colour − Distractor colour)
(House–Face + Blue–Red)

In preview search this formulation changed to include the active inhibition of the first set of distractors:

(b) (Map with only positive bias − Map with no bias) + (Map with positive and negative bias − Map with only negative bias)
(House–Red + Blue–Face)

To generate the predicted neural activity, the activity proposed at each time step was pooled across the units within each feature map and then combined with the activity for the same time steps in the other maps as indicated above. The activity values (combined across the feature maps) following the search displays were then used to generate a HDR function across time. This time series was used as a regressor in the analysis of fMRI data recorded by Allen et al. (2008) in their examination of single feature, conjunction and preview search. In a first analysis, the fMRI data were pooled across these three conditions to investigate search related brain regions in general, in relation to variations in top-down activation over time in sSoTS. Both the human search data and search-related activity in sSoTS were compared with their respective low-level baselines (see above). The second analysis involved a comparison between preview search and the other search conditions, given that top-down activation in the preview condition were given a 'head start' to influence search, compared with when the items appeared simultaneously. In the Allen et al. (2008) paper, separate blocks of trials were run for the preview search condition and for conditions in which the search items were presented simultaneously (combining the fMRI data for single feature and conjunction search, to maximise power). Consequently, we contrasted preview search with the combined data for the other search tasks. The brain areas whose activity pattern corresponds to the time course calculated here will reflect changes in response that mirror the involvement of top-down excitation over time.

(iii) The extraction of activity associated with top-down inhibition was performed in a similar manner. In the preview condition, active inhibition was applied to the features of the initial distractors, red and face. Hence inhibitory activity was given by

(c) (Map with only negative bias − Map with no bias) + (Map with positive and negative bias − Map with only positive bias)
(Face–Red + Blue–House)

Although active inhibition was not applied in the conjunction condition, the same formulation was applied in that condition in order to generate a baseline function, for comparison of ongoing inhibitory processes in the model under the two search conditions (preview and conjunction search). As was the case for top-down excitation, we first examined performance across all the search conditions compared to low level baselines (fixation in humans, spontaneous activity in sSoTS). Subsequently we contrasted activity in the preview condition with that in the conditions with simultaneously presented search items. The brain areas whose activity pattern corresponds to the time course calculated here will reflect changes in response that mirror the involvement of top-down inhibition over time.

fMRI data collection

The methods are as previously published (Allen et al., 2008) as part of a larger study. Participants searched for a blue house image (always present) in an array of red house and blue face images. Participants indicated with a key press whether the target item was to the left or right of fixation. All trials contained 2 displays, each lasting 2 s (plus an additional display of dots that was completely irrelevant to this analysis). In preview trials, this first display contained 4 or 8 blue faces that remained on the screen and were joined by the (4 or 8) house images in the second display. In the single feature and conjunction displays, the first display also contained blue faces, but in these trials the faces were offset before the second display. In the conjunction search condition 4 or 8 new blue faces (in new positions) were presented together with 3 or 7 red houses and the target red house. In the single feature condition no blue faces were presented in the second display. Participants performed preview search in a separate scan to single feature and conjunction search (which were combined). Within each scan the inter-trial interval was randomly jittered between 4 and 12 s. Both function scans were acquired using a quiet EPI sequence with 25, 3 mm slices (TR of 2 s, time to echo (TE) 30 ms, spin angle 79°, field of view 256×256×192 mm, matrix 64×64). Structural scans (resolution 2×2×2 mm^3 were acquired for all participants.

fMRI analysis

fMRI analysis on data from the 13 participants of Allen et al (2008) was performed using FEAT, part of fsl (www.fmrib.ox.ac.uk/fsl). The data were pre-processed as in Allen et al. (2008), including correction for head movement, within scan signal intensity normalisation, high pass temporal filtering (to remove slow wave artefacts). The predicted time courses entered as regressors for the analysis. Z (Gaussianised T/F) statistics were calculated and thresholded using clusters determined by $p<0.005$ and an extent threshold of greater than 50 voxels (see tables and figure legends for exact values).

Results

Behavioural results

The behavioural results generated by sSoTS qualitatively matched the classical findings on single feature, conjunction and preview search (Allen et al., 2008; Treisman and Gelade, 1980; Watson and Humphreys, 1997). In the single feature condition, the search slope was 10 ms/item; for the preview condition it was 18 ms/item, while it was 40 ms/item for the conjunction condition. The results are shown in Fig. 2 in relation to data on human search reported by Allen et al. (2008). There was a good qualitative match between the results for the model and for human search. For the model, there was no difference between search in the preview and single feature conditions, while preview search was more efficient than conjunction search.

Localising the location map

Activation in the location map in sSoTS was significantly related over time to activation in the right temporal-parietal junction (TPJ) (see Fig. 3). Activity in this area did not change reliably across the conditions in which there was spatial search across a set of simultaneously presented items (single feature and conjunction search) and search with temporally segmented displays (preview search). Fig. 3 presents the percentage change in BOLD activity within this area for the different search tasks. No other brain areas showed a significant co-variation in activity in relation to variation in the HDR in the location map.

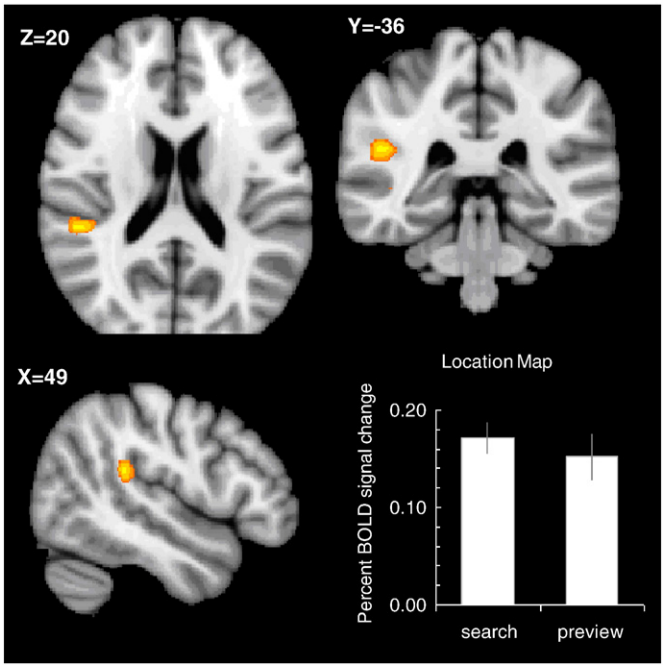

Fig. 3. Areas where activity pooled across the search conditions was associated with activity in the location map in sSoTS. The area shown is the right TPJ ($Z = 3.46$, $p < 0.005$, 717 voxels, co-ordinates of centroid: 49, −36, 20).

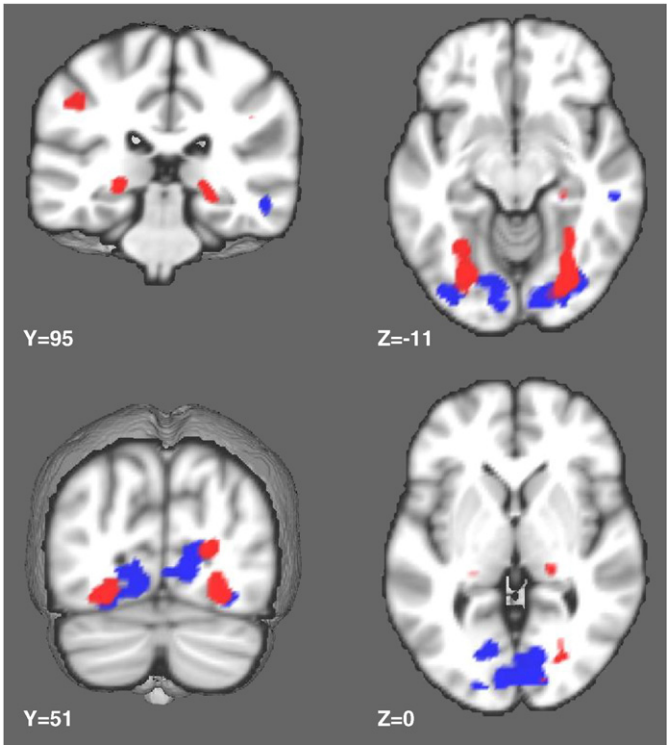

Fig. 4. Areas where activity pooled across the search conditions was associated with either with top-down excitation in sSoTS (red) or with active inhibition (blue).

Activity related to top-down excitation and inhibition

We subsequently examined whether any brain regions showed changes in activity over time that matched variation reflecting top-down excitation for targets and active (top-down) ignoring of distractors. The analyses were conducted first with the data pooled across the search tasks, and then to contrast activity in preview search relative to the conditions with simultaneously presented stimuli. The initial (overall) contrast revealed two different networks for top-down excitation and active inhibition (see Fig. 4 and Table 1). Areas that were associated with the profile of top-down excitation were found mostly in ventral cortex, including those likely to be involved in processing the house and face stimuli used in this study (para-hippocampal gyrus, fusiform and occipital face areas; Reddy and Kanwisher, 2006; Rossion et al., 2003) and also parietal regions within the left hemisphere (supra-marginal gyrus) previously associated with endogenous attention (Corbetta and Shulman, 2002). The analysis of active inhibition across the search conditions produced a reliable relationship between the predictions of the model and activity primarily in early visual cortex (occipital pole and calcarine sulcus). We note that this first analysis of active inhibition is weakened by pooling data across the search conditions, since, for the model, active inhibition plays a stronger role in preview search more than the other search conditions. The contrast between preview search and the other conditions provides a more incisive analysis of active inhibition.

The second set of analyses involved comparisons between the preview condition and the conditions with simultaneously presented items. The results are shown in Fig. 5 and Table 2. For top-down activation this again revealed regions within ventral occipital cortex where changes in related to active excitation in the preview were stronger than in the search conditions. In addition, some more dorsal regions (precuneus and superior parietal lobe) in the left hemisphere were significantly associated with the differences in active excitation across the conditions. For active suppression of distractors we found regions within parietal cortex including right angular gyrus, left supra-marginal gyrus and left superior parietal cortex, where activity in the preview condition increased relative to the other search conditions in the manner predicted by sSoTS. This result is consistent with there being more suppression of distractors in preview search than search with simultaneously presented stimuli, and with the changes in suppression over time mirroring activity activation within posterior parietal cortex.

These parietal activations, predicted by variations in active suppression in sSoTS, are close to those found previously in fMRI studies of preview search (Olivers et al., 2005; Pollmann et al., 2003). To compare the pattern of activity related to active inhibition found here with that found by Allen et al.(2008), we overlaid the results from the two studies. Fig. 6 (yellow) shows the activity relating to the preview from Allen et al (2008), using trials where only a 'dummy preview' was presented.[3] The 'dummy preview' condition provides perhaps the 'purest' measure of activity in relation to the preview in the human search data. Activity related to the active suppression of distractors in sSoTS (in blue) clearly overlays regions activated when human participants only see the preview. We would not expect active inhibition to overlay the entire preview- related activity found in human search as other non-modelled processes will be taking place in human search (e.g. expectations of for the target, temporal expectancies and response preparation etc.).

Discussion

We have presented work involving modelling, behavioural and fMRI data that aims to unveil the neural and functional processes

[3] Allen et al. (2008) embedded 'dummy preview' trials within a block of preview search trials. On the 'dummy' trials, participants expected a standard trial (both preview and search items), but only the preview appeared. Hence participants should set-up the same expectancy for search, but activation would then not be contaminated by search activity. A similar condition was also used by Pollmann et al. (2003).

Table 1
Areas that are correlated with top-down inhibition and excitation pooled across the preview and search tasks.

Cluster	Voxels	Z-max	Z-max (mm)	Location
Active inhibition related activity				
6	19,178	5.03	12 −91 9	Occipital pole, calcarine sulcus
5	355	3.24	26 −30 −7	R hippocampus
4	209	3.3	55 −31 −10	R medial temporal G
3	106	2.75	−38 −68 −20	L inferior occipital fusiform
Top-down excitation related activity				
15	5868	4.68	28 −77 −10	R occipital fusiform
14	2738	3.49	−29 −72 −12	L occipital fusiform
13	1315	3.49	−52 −23 32	L supra marginal gyrus
12	503	3.51	26 −28 −7	R parahippocampal gyrus
11	328	3.63	−23 −30 −3	L hippocampus
10	145	3.08	−33 −23 45	L precentral gyrus

Table 2
Areas that were better correlated in the preview condition than the other search conditions.

Cluster	Voxels	Z-max	Z-max (mm)	Location
Activity related to top-down excitation				
20	2894	3.78	28 −62 −9	Right occipital fusiform gyrus
19	1290	3.54	−26 −67 −10	Left occipital fusiform gyrus
18	875	4.02	−27 −89 −16	Left occipital fusiform gyrus
17	732	3.14	36 −85 −9	Right occipital fusiform gyrus
16	370	3.29	−13 −78 31	Left precuneus/cuneous border
15	349	3.21	19 −88 −15	Right occipital fusiform gyrus
14	308	3.08	−4 −92 −11	Left occipital pole
13	272	3.04	−16 −91 10	Left occipital pole
12	49	2.91	−20 −46 58	Left superior parietal lobe
Activity related to active inhibition				
4	229	3.17	47 −56 50	Right angular gyrus
3	173	3.22	−43 −51 55	Left supra marginal gyrus
2	58	3.09	−23 −57 63	Left superior parietal

involved in visual search. Using the sSoTS model we qualitatively matched behavioural data (Fig. 2). This provides an illustration that a model employing a purely parallel processing architecture is able to simulate both efficient and inefficient search, as the relations between targets and distractors varies (see also Deco and Zihl, 2001). More than this, we have shown that computational models of human search can also be used to help our interpretation of brain functions. Search tasks are complex, likely involve both excitatory guidance of search to targets and rejection of irrelevant distractors; consequently most studies of the brain regions supporting search fail to pull-apart the functional role(s) of the different brain areas typically involved. However, since the functional processes involved in search can be specified within computational models, such models may help to identify the role(s) that different brain regions play if activity within the model can be linked to brain activity. In the present study we take this step by using the sSoTS model to predict HDR functions measured in fMRI experiments, and we report correlations between the functional activity predicted by the model and BOLD activity in different brain regions.

We document three main results relating to the brain areas that correlated with (i) activity in the Location (saliency) map within the model, (ii) activity linked to the effects on the BOLD response due to top-down expectancies for targets, and (iii) activity linked to the effects on the BOLD response due to the active suppression of distractors. In the last two instances, the activity was combined across the feature maps that were the recipients of top-down excitation and inhibition, and so the profile reflects the response of the associated brain regions to changes in overall activity reflecting top-down excitation and suppression, not activity directly within feature maps.

The location (saliency) map

Our analysis showed for the first time that activity in the location (saliency) map in sSoTS (a model that investigated the visual search over time as well as space) correlated with activation over time in a region of the right TPJ (Fig. 3). As noted in the Introduction, Corbetta and Shulman (2002) argued that the right TPJ area is distinct from other sections of the fronto-parietal network controlling top-down attention, and they suggest that this region serves as a 'circuit breaker', signalling the presence of task-related stimuli in the environment where attention needs to be switched to. The role of the location map in sSoTS is not dissimilar to this idea. In sSoTS activation in the location map provides information about the likely location of a target, which can then act as an input to other response-related systems which (e.g.) programme an eye movement to that position. It is noteworthy that, in our analysis, activity correlated with

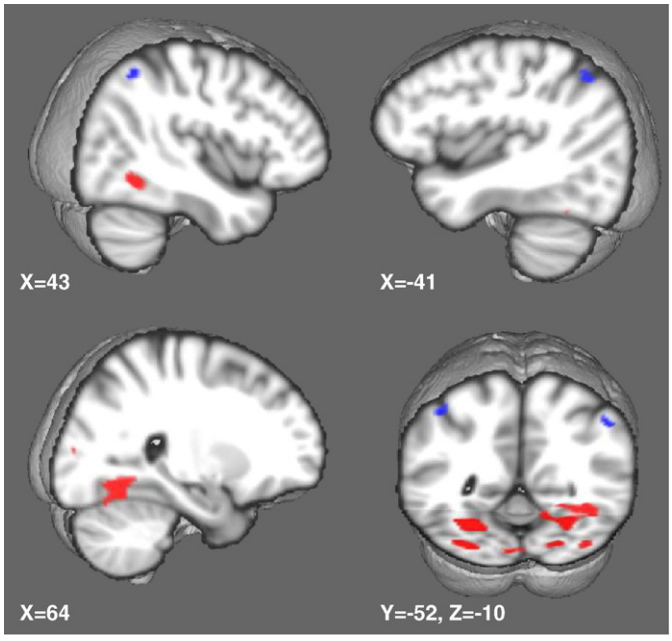

Fig. 5. Areas that showed a greater association in the preview than the other search conditions against top-down excitation (red) and active inhibition (blue) in sSoTS. Active inhibition was related to activity in parietal regions whereas top-down excitation was related mostly to activity in visual areas.

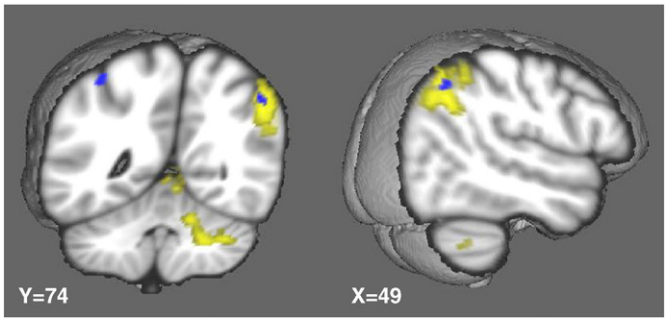

Fig. 6. Overlay of activated areas in the dummy condition of preview search from Allen et al. (2008) (yellow) and activation related to active inhibition estimated from the sSoTS model in preview search (blue).

the location map in the model was localised within the right hemisphere even though the search stimuli (including targets) were presented on both sides of space. This suggests that the neural response to stimulus saliency is based on cells with bilateral receptive fields which are activated by stimuli on the right as well as the left side of space.

One interpretation of our results is that the right TPJ literally contains a spatial map reflecting the relative saliency of stimuli in the visual field, much like the saliency map specified in many computational accounts of visual attention (Itti and Koch, 2001). However, it could also be that neurons in the right TPJ register the presence of a salient visual event from a distal saliency map, and then play a role in making the stimulus available to response systems (see Pollmann et al., 2003). Our data do not distinguish between these accounts.

On either of the above interpretations of the right TPJ it follows that lesions to this neural area should disrupt the identification of targets on the affected side of space. This is clearly reminiscent of disorders such as unilateral neglect (Vallar, 1993), with neglect patients being dominated by the saliency of items on the ipsi- rather than the contralesional side (Snow and Mattingley, 2006). There has been some recent disagreement about the neuroanatomy of visual neglect. Classically neglect has been associated with damage to posterior parietal cortex rather than more anterior regions around the TPJ (e.g. Mort et al., 2003). On the other hand, Karnath et al. (2001) argued that neglect is linked to lesions of more anterior regions including not only the TPJ but extending more anteriorly into the superior temporal lobe. In other recent studies (Chechlacz et al., submitted for publication; Verdon et al., 2009), a distinction has been drawn between different forms of neglect – in particular between neglect of spatial position in relation to the patient's body (egocentric neglect) and neglect of visual elements on one side of an object (allocentric neglect). In these studies egocentric neglect is associated with more anterior lesions including the superior temporal and inferior frontal cortices while allocentric neglect is linked to more posterior parietal-occipito-temporal damage. Interestingly, lesions to the right TPJ can be associated with both types of neglect, suggesting that the right TPJ is involved in registering targets not only in relation to a patient's body but also in relation to their position within an object.

Currently the location map in sSoTS registers stimuli in retinal coordinates, based on where elements fall in the visual field, and hence the model links more naturally to egocentric than to allocentric forms of neglect. Further work will be required to assess if a common coding system may serve both egocentric and allocentric coding in models such as sSoTS. Nevertheless, it is interesting that Mavritsaki et al. (2009b) recently reported the emergence of several characteristics of visual search in neglect patients after simulating lesioning to the location map in sSoTS (removing units from the location pools on one side of space). According to our current analysis, this would represent neglect following damage to the right TPJ region. We also note that neglect is classically associated with damage to the right rather than left hemisphere (Vallar, 1993), and this too would fit with the proposal of the response to saliency being predominantly localised within the right hemisphere.

One other point to highlight is that the current evidence for a location-based saliency response in the right TPJ contrasts with evidence from functional brain imaging which has indicated that dorsal occipital-parietal cortex is recruited when people must remember the locations of visual stimuli (e.g., Ungerleider et al., 1998). Our data suggest that the neural response to saliency in search highlights discrete regions for visual selection, but is unlikely to serve as a repository to hold the locations of stimuli in visual short-term memory.

Top-down excitation and active suppression

Along with showing activation linked to a location map, we also isolated brain regions whose activity varied with the magnitude of top-down excitation and inhibition set against the baseline level of activity when search stimuli were presented. The changes in activation reflecting top-down excitation and inhibition were derived by combining activity across feature maps; thus it reflects overall changes in activation across early representation in the model. The results here differed somewhat from our initial preliminary analysis (Mavritsaki et al., 2009a), which was conducted with fewer participants. Here we report that different networks relate to active excitation and inhibition. Regions related to active excitation for targets included visual areas shown previously to respond selectively to faces and houses (Epstein and Kanwisher, 1998; Kanwisher et al., 1997) along with more dorsal regions that form part of the proposed fronto-parietal network for visual attentional control (Corbetta and Shulman, 2002). The relations between the magnitude of top-down excitation and activity in areas of ventral cortex likely responding to houses (the parahippocampal gyrus) are expected, given that (i) activity in the model conforms to top-down activity to target features and (ii) houses were targets. The positive correlations to face regions (fusiform gyrus) were unexpected. However, it should be noted that the face stimuli carried the target colour, and hence there may be some activation of form units at the locations of face distractors brought about by colour-based activation of the location map. This would lead to some enhancement of activity in the fusiform area on trials when (e.g.) top-down activation of colour is strong. Alongside this, Humphreys et al. (2004a) found early enhancement of the detection of probes falling at the locations of previewed distractors (this was followed by later-acting inhibition). Similarly, in their fMRI study, Allen et al. (2008) reported increased activation in the fusiform gyrus when participants were set to ignore faces in previewed images. Both of these last results suggest that old items may need to be attended in order to be subsequently inhibited (see also Tsal and Makovski, 2006). Hence the increased activation of the fusiform gyrus when stimuli are inhibited may be a relic of this early attentional activity.

Irrespective of these last points, it is interesting that activity in the model used for the analysis was pooled across feature maps. Thus the activity does not represent responses in the feature maps per se, yet the regions of ventral cortex emerging in the fMRI analysis do likely correspond to target and distractor features (faces vs. houses). Apparently these feature-specific neural regions alter their activity in a manner matching variations in top-down activation summing across maps. On the other hand, the activation within more dorsal regions, associated with the fronto-parietal attention network (Corbetta and Shulman, 2002), may be abstracted from the specific features of the stimuli and relates to the 'set' for target features (e.g., a template for the target; Duncan and Humphreys, 1989), which modulates earlier visual areas.

The brain regions related to active inhibition included early visual cortex (in the contrast between all search conditions and baseline) and posterior parietal cortex (right angular, left supra-marginal and superior parietal, in the contrast between preview and the other search conditions). Given that these were all positively related to search, the results indicate that there was enhanced occipital activation when there was high suppression of distractors. At least some prior studies have discussed attentional inhibition in terms of decreases in brain activity when stimuli are ignored (e.g., Gazzaley et al., 2005; Smith et al., 2000). On the other hand, as we have noted, the suppression of previewed distractors may involve initial excitation of their representations prior to the onset of suppression (see Humphreys et al., 2004a, b). Alternatively, the enhanced activity observed when active inhibition in the model is high may reflect the recruitment of inhibitory neurons, which are involved in biasing attention against distractor stimuli. Such inhibitory effects within early visual cortex may be contingent on the 'set' to ignore old items established within posterior parietal cortex, which is most evidence in the preview condition when an early bias (prior to the search display) may be set in play. Prior research indicates that the activity is unlikely to reflect either attentional prioritisation to unoccupied regions of the display in preview search, or inhibition of return (IOR) applied to previewed locations. Allen and

Humphreys (2007), for example, contrasted preview search relative to search when all the items appeared simultaneously but attention was pre-cued to a sub-set of items (equivalent to the new items under preview conditions). There was a substantial benefit to preview search even compared with this pre-cue case. In a test of IOR, Olivers et al. (2002) had participants conduct a search through a first set of items before presenting a second set (equivalent to the preview condition) if the target was not initially present. This condition should maximise the presence of IOR to the first stimuli. In contrast to preview search, performance was very poor in this case, indicating that IOR plays little role in the effect. We conclude that the brain activity correlated with changes in active inhibition over time reflects the processes that lead to old distractors being effectively ignored in search, and that this does involve the suppression of distracting stimuli.

Finally, although we have highlighted top-down inhibitory effects in preview search, we believe it unlikely that these inhibitory processes were recruited specifically for this search procedure. Furthermore, evidence from probe dot detection studies indicates that irrelevant distractors are inhibited even in search tasks with simultaneously presented items (Kim and Cave, 2001). In studies using fMRI and a within-subjects design to look at the brain mechanisms of preview search in relation to other search tasks, Dent et al. (submitted for publication) have also shown that common areas of posterior parietal cortex are activated under conditions where one set of distractors is easily filtered (e.g., search for motion-form conjunctions). This points to common neural as well as functional mechanisms of search across the different search tasks. Nevertheless, preview search provides a convenient way to isolate and study the inhibitory suppression of distractors, since effects specific to the initial preview display can be studied separate from effects relating to search displays.

We also note that that other investigators have reported that brain regions responding selectively to houses and faces can be modulated by attention. For example, O'Craven et al. (1999) showed enhanced activation in the fusiform face area when participants attended to face relative to overlapping house stimuli. This is consistent with our evidence that feature-specific areas can be modulated top-down, by biases to or against particular stimuli (faces vs. houses).

Conclusions

We have used a model-based analysis to assess the functional roles of different brain regions in visual search. Our results suggest that the right TPJ responds to stimulus saliency, playing a key role in guiding subsequent actions to that location. In addition, separate networks of areas in parietal and occipital cortex were linked to the top-down prioritisation of target features and the active suppression of distractors. These networks, in acting together, facilitate visual search particularly under preview conditions where biases towards targets and away from distractors can be established prior to search taking place.

Acknowledgments

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

Appendix A

In this part we present more details about the model of the spiking neurons used. The sub-threshold membrane potential of the neuron is given by the equation:

$$C_m \frac{dV(t)}{dt} = -g_m(V(t)-V_L) - I_{syn}(t) + I_{AHP} \quad (1)$$

where C_m is the membrane capacitance where different values are given for excitatory $C_m$ex and inhibitory $C_m$in neurons; g_m is the membrane leak conductance where different values are also given for excitatory $g_m$ex and inhibitory $g_m$in neurons; V_L is the resting potential; I_{syn} is the synaptic current and I_{AHP} is the current term for the frequency adaptation mechanism. The values for the above parameters as well as the threshold V_{tbr} and the reset potential (McCormick et al., 1985) are given in the table in Appendix C.

The synaptic currents used are described by the following equations. The AMPA recurrent currents $I_{AMPA,rec}$:

$$I_{AMPA,rec}(t) = g_{AMPA,rec}(V(t)-V_E) \sum_{j=1}^{N_E} w_i s_j^{AMPA,rec}(t) \quad (2)$$

where V_E is the excitatory reversal potential, w_j are the synaptic weights, $g_{AMPA,rec}$ is the synaptic conductance and $s_j^{AMPA,rec}$ is the receptors fraction of open channels.

The voltage of the NMDA recurrent currents $I_{NMDA,rec}$ is dependent by the extra-cellular magnesium $[Mg^{2+}]$ concentration (Jahr and Stevens, 1990):

$$I_{NMDA,rec}(t) = \frac{g_{NMDA}(V(t)-V_E)}{1 + [Mg^{2+}] \exp(-0.062V(t)) / 3.57} \sum_{j=1}^{N_E} w_j s_j^{NMDA}(t) \quad (3)$$

where $[Mg^{2+}]$ is the concentration of magnesium, g_{NMDA} is the synaptic conductance and s_j^{NMDA} is the receptor fraction of open channels.

The voltage of the inhibitory GABA currents I_{GABA}:

$$I_{GABA} = g_{GABA}(V(t)-V_I) \sum_{j=1}^{N_I} s_j^{GABA}(t) \quad (4)$$

where g_{GABA} is the synaptic conductance and s_j^{GABA} is the receptor fraction of open channels.

The connections with the external neurons follow AMPA-like dynamics and the voltage $I_{AMPA,ext}$ follows the following equation:

$$I_{AMPA,ext}(t) = g_{AMPA,ext}(V(t)-V_E) \sum_{j=1}^{N_{ext}} s_j^{AMPA,ext}(t)) \quad (5)$$

where $g_{AMPA,ext}$ is the synaptic conductance and $s_{j=1}^{AMPA,ext}$ is the fraction of open channels. The parameters for Eqs. (2)–(5) are give in Table Appendix B. The synaptic current I_{syn} is given by the sum of the currents described above.

$$I_{syn}(t) = I_{AMPA,ext}(t) + I_{AMPA,rec}(t) + I_{NMDA,rec}(t) + I_{GABA}(t) \quad (6)$$

Furthermore, an additional current is added to the system that aims to simulate the frequency adaptation mechanism. The spike frequency adaptation mechanism used is I based on $[Ca^{2+}]$-activated $[K^+]$ hyperpolarising current I_{AHP} based on the assumption that this is the main current that produces this mechanism during the first 300 ms of adaptation (Madison and Nicoll, 1984). The I_{AHP} can be described by the equation:

$$I_{AHP}(t) = -g_{AHP}\left[Ca^{2+}\right](V(t)-V_K) \quad (7)$$

where V_K is the reversal potential of the K^+ and g_{AHP} is the synaptic conductance. The mechanism for this current can be described as the influx of a small amount of $[Ca^{2+}]$ α every time an action potential is generated, thus the intracellular level of $[Ca^{2+}]$ is increased and this

leads to further increment in I_{AHP}. The $[Ca^{2+}]$ between spikes can be described by the following equations:

$$\frac{d\left[Ca^{2+}\right]}{dt} = -\frac{\left[Ca^{2+}\right]}{\tau_{Ca}} \tag{8}$$

If $V(t) = V_{thr}$, then $[Ca^{2+}] = [Ca^{2+}] + a$, and $V = V_{reset}$

where α is the $[Ca^{2+}]$ influx and τ_{Ca} is the leaky integrator's decay constant. $[Ca^{2+}]$ concentration is initially set to 0 and the values for the rest of the parameters are given in Table Appendix B.

The fractions of open channels are given by the following equations:

$$\frac{ds_j^{AMPA,rec}(t)}{dt} = -\frac{s_j^{AMPA,rec}(t)}{\tau_{AMPA}} + \sum_k \delta\left(t - t_j^k\right) \tag{9}$$

where τ_{AMPA} is the decay time constant.

$$\frac{ds_j^{NMDA}(t)}{dt} = -\frac{s_j^{NMDA}(t)}{\tau_{NMDA,decay}} + a x_j(t)\left(1 - s_j^{NMDA}(t)\right) \tag{10}$$

$$\frac{dx_j(t)}{dt} = -\frac{x_j(t)}{\tau_{NMDA,rise}} + \sum_k \delta\left(t - t_j^k\right) \tag{11}$$

where $\tau_{NMDA,decay}$ is the decay time constant and $\tau_{NMDA,rise}$ is the rise time constant.

$$\frac{ds_j^{GABA}(t)}{dt} = -\frac{s_j^{GABA}(t)}{\tau_{GABA}} + \sum_k \delta\left(t - t_j^k\right) \tag{12}$$

where τ_{GABA} is the decay time constant.

$$\frac{ds_j^{AMPA,ext}(t)}{dt} = -\frac{s_j^{AMPA,ext}(t)}{\tau_{AMPA}} + \sum_k \delta\left(t - t_j^k\right) \tag{13}$$

The values for $\tau_{NMDA,rise}$, $\tau_{NMDA,decay}$, τ_{AMPA} (Hestrin et al., 1990; Spruston et al., 1995) and τ_{GABA} (Salin and Prince, 1996; Xiang et al., 1998) are given in Appendix B. The rise time constants for AMPA and GABA are neglected because they are very small. Furthermore, it is considered that the spikes emitted from the pre-synaptic neuron j at time t_j^k are of the form of δ-Peaks ($\delta(t)$).

Appendix B

Parameter	Values	Description
C_m excitatory	0.2 nF	Membrane capacitance for excitatory neurons
C_m inhibitory	0.5 nF	Membrane capacitance for inhibitory neurons
g_m excitatory	25 nS	Membrane leak conductance for excitatory neurons
g_m inhibitory	20 nS	Membrane leak conductance for inhibitory neurons
V_L	-70 mV	Resting membrane potential
V_E	0	Excitatory reversal potential
V_I	-70 mV	Inhibitory reversal potential
V_{thr}	-50 mV	Threshold membrane potential
V_{reset}	-55 mV	Reset membrane potential
$g_{AMPA,rec}$ excitatory	0.104 nS	AMPA recurrent synaptic conductance for excitatory neurons
$g_{AMPA,rec}$ inhibitory	0.081 nS	AMPA recurrent synaptic conductance for inhibitory neurons
g_{NMDA} excitatory	0.22 nS	NMDA recurrent synaptic conductance for excitatory neurons
g_{NMDA} inhibitory	0.258 nS	NMDA recurrent synaptic conductance for inhibitory neurons
g_{GABA} excitatory	1.287 nS	GABA recurrent synaptic conductance for excitatory neurons
g_{GABA} inhibitory	1.002 nS	GABA recurrent synaptic conductance for inhibitory neurons
$g_{AMPA,ext}$ excitatory	2.08 nS	AMPA external synaptic conductance for excitatory neurons
$g_{AMPA,ext}$ inhibitory	1.62 nS	AMPA external synaptic conductance for inhibitory neurons
g_{AHP}	7.5 nS	$[Ca^{2+}]$ dependent K^+ channel synaptic conductance
τ_{AMPA}	2 ms	Decay time constant for AMPA
$\tau_{NMDA,decay}$	100 ms	Decay time constant for NMDA
$\tau_{NMDA,rise}$	2 ms	Rise time constant for NMDA
τ_{GABA}	10 ms	Decay time constant for GABA
τ_{Ca}	500 ms	Decay constant for leaky integrator
V_K	−80 mV	Reversal potential for K^+ channel
a	0.15 μM	$[Ca^{2+}]$ influx when a spike occurs
N_E	1600 (800)	Number of excitatory neurons in each layer for the feature maps (for the location map)
N_I	400 (200)	Number of inhibitory neurons in each layer for the feature maps (for the location map)
N_{ext}	800	Number of external neurons
τ_{rp}inhibitory	1 ms	Refractory period for inhibitory neurons
τ_{rp}excitatory	2 ms	Refractory period for excitatory neurons
$[Mg^{2+}]$	1 mM	Magnesium concentration
w^+	2.2	Coupling for the pools in the feature maps
w_{i1}	1.0	Inhibition for the two feature dimension maps
w_{i2}	0.9	Inhibition for the location map
w_{i3}	1.0	Connection weight from feature maps to location map
w_{i4}	0.25	Connection weight from the location map to feature maps
λ_{in}	120 Hz	The total input that each pool receives from the external neurons to show that there is an item in the visual field.
λ_{att}	185 Hz	The total top-down that the target pools receive to signify the target's characteristics.

Appendix B (*continued*)

Appendix C

The time series was extracted from the model to match the experimental times in the fMRI data. The procedure we followed is explained in Fig. C1. In Fig. C1 we give an example for the preview condition if 5 trials were used, in reality the simulated data are based on 100 trials average. The preview condition has two different categories of display presentation, the preview search where the distractors are presented for 2 s followed by the full search display (which includes the first set of distractors) for another 2 s, so the total trial time is 4 s. In the dummy preview condition, the distractors are presented for 2 s, but there is no search display, so the total trial time is 2 s. Let us consider (as an example) that in the experiment we have the following table of display presentation and inter trials intervals (ITI) after the display presentations the total experimental time is 25 s.

As shown in Fig. C1, for each trial the average map (in this case from the location map) activation is calculated for each condition (in this case preview and dummy). Then, the average over all the trials is

Condition	ITI
Preview	3 s
Dummy	2 s
Dummy	1 s
Preview	5 s
Dummy	2 s
Preview	5 s
Dummy	

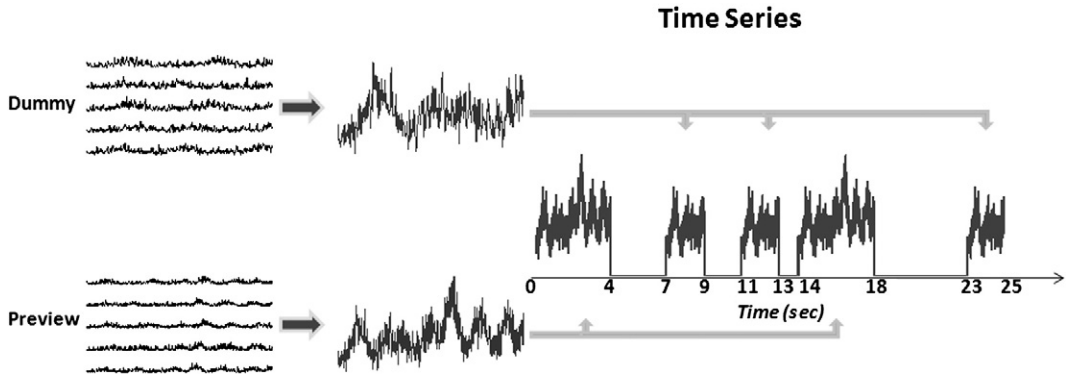

Fig. C1. Details of how the time series is extracted from the model. The average activation for each map is used for a 5 trials example. This average activation is averaged over the 5 trials and the time series that fits the experimental times is constructed.

calculated and this average is put in the correct time position to match the experimental times.

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