Research Report

Functional brain organization of preparatory attentional control in visual search

Patrick Bourkea, Steven Brownb, Elton Nganc, Mario Liottib

aDepartment of Psychology, University of Lincoln, Brayford Pool, Lincoln LN6 7TS, United Kingdom
bDepartment of Psychology, Simon Fraser University, Burnaby, Canada
cDepartment of Psychology, University of British Columbia, Vancouver, Canada

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Looking for an object that may be present in a cluttered visual display requires an advanced specification of that object to be created and then matched against the incoming visual input. Here, fast event-related fMRI was used to identify the brain networks that are active when preparing to search for a visual target. By isolating the preparation phase of the task it has been possible to show that for an identical stimulus, different patterns of cortical activation occur depending on whether participants anticipate a ‘feature’ or a ‘conjunction’ search task. When anticipating a conjunction search task, there was more robust activation in ventral occipital areas, new activity in the transverse occipital sulci and right posterior intraparietal sulcus. In addition, preparing for either type of search activated ventral striatum and lateral cerebellum. These results suggest that when participants anticipate a demanding search task, they develop a different advanced representation of a visually identical target stimulus compared to when they anticipate a nondemanding search.

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1. Introduction

In a complex visual scene the object to which we attend is not always the most intrinsically salient e.g. the brightest or largest. Rather the things to which we attend are more often those that are relevant to our current goals and interests. For example, we can find our keys on the desk amongst the clutter or our car amongst many others in a large car park. These illustrate the general case of having something of current importance ‘in mind’ and seeking for that precise visual information in a cluttered visual world. This ability has been empirically studied with ‘Visual search’, an experimental paradigm that simulates these conditions (e.g. Treisman and Gelade, 1980). In this, participants are asked to decide whether a ‘target’ such as a specific colored letter is present or not among a display of many similar items. Despite aspects of visual search being studied for over 30 years, the cognitive neuroscience of the formation of the advanced representation of the target is poorly understood.

The global network of areas involved in visual search tasks has been well documented in functional imaging studies (e.g. Anderson et al., 2010; Donner et al., 2000; Kim et al., 2012; Leonard et al., 2000; Nobre et al., 2003). The most consistently activated areas include superior parietal cortex, intraparietal sulcus, and occipital cortex along with various parts of frontal cortex (Anderson et al., 2007). However, understanding what
aspect of visual search is performed by which part of this
network of regions remains undetermined. Specifically, the
design of these earlier studies have not allowed the ‘prepare
to search’ and the ‘search’ element of the task to be sepa-
rated. In the first, people have to develop and maintain some
adequate representation of the item to be found and in the
second they have to match incoming stimuli against this.

From other lines of work, reasonable expectations can be
formed as to the brain areas that may be involved in preparing
to search for a target. A short term description of currently
relevant visual information is often thought to be implement-
ted by biasing feature maps in extra-striate regions of occipital
cortex (Desimone and Duncan, 1995). Consistent with this,
sustained activation over the posterior scalp has been shown
as people hold representations of targets for which they are
about to search (Carlisle et al., 2011). In the human brain,
feature maps for shapes and colors seem to exist in ventral
occipital cortex (Beauchamp et al., 1999; Corbetta et al., 1990,
1991; Shulman et al., 1999, 2003). Furthermore, it has been
demonstrated that such maps are activated when people are
preparing to process visual input to find a target (Chawla et al.,
1999; Giesbrecht et al., 2003). For example, Giesbrecht et al.
(2003) showed increased bilateral activation in the fusiform
region when people are waiting to make an orientation
decision about a soon to be displayed colored, rectangle. It is
clear that in visual search some similar advanced specification
of the target must be formed and ‘held in mind’ prior to any
search. The task must proceed by comparing multiple items in
a visual display against this representation. It seems likely
therefore that in visual search, the advanced specification of
the target will also be found to be implemented here.

Importantly, as human cognition is highly flexible it seems
likely that the advanced specification of target identity will vary
with the current task demands. A target could be identical in two
search tasks, but its advanced representation is predicted to be
simpler when the upcoming task is expected to be undemanding
compared to when it is expected to be demanding. For example
the pre-biasing that might occur when preparing to find a red X
is likely to be different when the task is expected to be a ‘feature’
search i.e. all distracters will be green Os, relative to when the
task is expected to be a ‘conjunction’ search i.e. distracters will
be green Xs and red Os. In the first, a simple representation will
suffice to perform the task. This could be implemented neuro-
logically by the detection of any activation in feature maps
coding other than green or O or by activation in red or diagonal
feature maps. In contrast when the distracters will be green Xs
and red Os, a more elaborated representation of the target
including its relationship with the distracters must be formed
(Duncan and Humphreys, 1989). If so, it is likely that for the
identical stimulus, when preparing for such an undemanding
feature search there will be less neural activation than when
preparing for a demanding conjunction search. This may be
detected as a smaller fMRI signal.

In addition to the variable activity in feature maps that might
be expected to be seen in occipital cortex, the ‘preparing to
search’ phase of a visual search task is likely to include other
regions that are involved in modulating this sensory activity. A
frontal–parietal control system is often proposed (e.g. Desimone
and Duncan, 1995; Woldorff et al., 2004) that sends bias signals to
feature maps in ventral occipital cortex. Supporting evidence has
come from studies where a representation of a target location
has to be developed. In this approach a symbolic cue is given
that indicates the likely location of an upcoming target. Participants
use this advanced representation to facilitate target
detection when it occurs (Hopfinger et al., 2000; Woldorff et al.,
2004) or simply attend to that location (Kastner et al., 1999). For
example Kastner et al. (1999) asked participants to attend to one
location and count the occurrence of one of four complex
colorful images presented there. In such studies, during this
‘attended’ interval, activation is seen in both occipital cortex,
consistent with the biasing of visual spatial maps, and frontal
and parietal areas, possibly involved in biasing such maps. While
somewhat variable across studies the frontal activation typically
includes the frontal eye fields. In visual search studies frontal
and parietal activation is also often reported, however it is never
clear whether this reflects the source of the bias signal or the
attentional movements that are part of later search and match
operations. In contrast to the frontal areas that are active in
visual search which vary across studies, the parietal activation
is highly consistent. An area near the posterior portion of the
intraparietal sulcus is active (Donner et al., 2000; Leondarts et al.,
2000; Nobre et al., 2003). In addition, Shulman et al. (1999)
reported increased activation here when participants were
maintaining information during an interval, regarding move-
ment direction. Similarly, Giesbrecht et al. (2003) identified a
region that includes a similar parietal area as responsible for the
representation of task relevant information concerning colored
shapes and location. This area has also been reported to be
involved in other visual short term memory tasks (McNab and
Klingberg, 2008; Todd and Marois, 2004). It seems likely that this
area may be involved in maintaining the advanced specification
of the target during ‘prepare to search’ as part of a frontal-
parietal control system (Desimone and Duncan, 1995).

No study has explicitly isolated the network of areas that
support the development and maintenance of an advanced
representation of the target in visual search from the other
components of the task. Therefore, no study has been able to
explore whether neural activation when preparing to search
for a target, differs as a function of the anticipated demand
of the task. The present study aims to address these limitations
by separating the brain activation during the preparation
to search for a target, from the later components of a visual
search task. By isolating this time period, the changes in
neural activity that might underlie the flexible creation of
advanced specifications is investigated. This is done by
presenting participants with identical targets but in contexts
that indicate that their search will be undemanding or
demanding, i.e. a feature search or a classic conjunction
search. To minimize the interpretative processes that sym-
bolic indication of the current target and distracter informa-
tion would have produced, spatial, shape and color
information is given in a very concrete way, see Fig. 1.

2. Results

2.1. Reaction time results

Reaction time results are shown in Fig. 2. There was a main
effect of the ‘type of search’ factor with feature search being
faster than conjunction search, $F(1, 15) = 110.29, p < .001$. There was a main effect of the ‘presence of the target’ factor with ‘target present’ being faster than ‘target absent’, $F(1, 15) = 22.47, p < .001$. There was a significant interaction between the two factors, $F(1, 15) = 22.80, p < .001$. As shown in Fig. 2, there was little lengthening of reaction time when the target was absent in feature search but a substantial increase when it was absent in conjunction search. Error rates were low in feature search (1.37%) and higher in conjunction search (13.82%). Any trial with an incorrect response was excluded from the subsequent fMRI analysis.

2.2. Results – fMRI (preparation)

2.2.1. Effects of preparation for a feature search – “Attend Prepare” (feature) versus “Watch” (feature)

Full Talairach coordinates are given in Tables 1 and 2. Preparing to perform a ‘feature’ search resulted in four clusters of significant BOLD activity in extrastriate visual cortex, ventrally in right inferior occipital gyrus and fusiform gyrus BA19, more dorsally in right middle occipital gyrus BA18, and more posteriorly and medially in the left lingual gyrus and right cuneus (BA 17/18) in the occipital pole [see Fig. 3, top row].

Furthermore, there were significant clusters of BOLD activity in left ventral Striatum and adjacent anterior insula, left posterior thalamus, right anterior lateral cerebellum, and in the pons.

2.2.2. Effects of preparation for a conjunction search – “Attend Prepare” (conjunction) versus “Watch” (conjunction)

Results are shown in Tables 1 and 2, Fig. 3 middle row. Preparing to perform a conjunction search yielded significant
BOLD activity in extrastriate visual cortex, including bilateral inferior occipital gyri and fusiform gyri BA19 (ventrally), and more dorsally, bilateral middle occipital gyri BA18/19, in the vicinity of the transverse occipital sulcus (TOS). Additionally, there was significant BOLD activity in right superior parietal lobe (BA7), in the proximity of the intraparietal sulcus, [see Fig. 3, middle row]. Finally, there were clusters in right posterior thalamus, bilateral ventral striatum, bilateral anterior lateral cerebellum, midline cerebellum and pons (Table 2).

2.2.3. Selective effects of preparing for a feature search compared to preparing for a conjunction search – “Attend Prepare” (conjunction) versus “Attend Prepare” (feature)

Regions where BOLD activity was greater when preparing for a conjunction relative to a feature search were bilateral ventral occipital cortex (inferior occipital/fusiform gyri BA19), bilateral dorsal occipital cortex (middle occipital gyri BA18/19, in the vicinity of TOS), and right superior parietal lobule BA7, in the vicinity of IPS [see Fig. 3, bottom row]. Please note that BOLD effects around the right intraparietal sulcus and in dorsal occipital cortex coincided across the two contrasts of “Attend Prepare” (conjunction) versus “Watch” (conjunction) and “Attend Prepare” (conjunction) versus “Attend Prepare” (feature) (Fig. 3, bottom and middle rows and Table 1).

3. Discussion

Fast event related fMRI was used to isolate the brain networks that are active during preparing to search for a visual target from the later components of a visual search task. The results show a distinctive network activated during the preparation phase of the task. Of particular interest was the way in which the representation of a given target would vary in anticipation of a ‘feature’ relative to a ‘conjunction’ search task. In preparing for either type of search, ventral occipital areas were activated, notably to a greater extent in advance of the conjunction search. In addition, when preparing for a conjunction search, unique activity was seen in bilateral dorsal occipital cortex and in the vicinity of the right intraparietal sulcus (Fig. 3). Finally, preparing for either type of search activated ventral striatum, cerebellum, thalamus and pons.

3.1. Varying representations with anticipated task demand

Activations seen in the ventral occipital region are consistent with the idea that an advance specification of the target is implemented by biasing feature maps in extra-striate regions of occipital cortex (Chawla et al., 1999; Desimone and Duncan, 1995; Giesbrecht et al., 2003; Stokes et al., 2009). This portion of extrastriate visual cortex is similar to that which, in previous studies, has been argued to encode both shape and color information (e.g. Beauchamp, 1999; Shulman et al., 2003, 1999). Significantly, preparing to search for the identical target, but in the context of expecting it to be amongst very similar distracters rather than very different distracters produced different results. When expecting a conjunction search task, the same ventral occipital area was activated as when expecting a feature search task, but more robustly. This would be consistent with an interpretation that activity in this area reflects the formation of an advanced specification of the target and that a more extensive representation is formed when participants anticipate a more demanding visual search. For example, when an easy feature search is expected, color or shape maps may be activated, when a demanding conjunction search is expected color and shape maps or more complex representations may be activated.

Target and distracter relationships may be established outside of the dorsal occipital region followed by signals sent back to bias early processing. However, at least part of the development of the advanced representation may arise directly out of local comparisons of target and distracter items during the ‘preparation’ display. During this phase of the task the ‘target’ needs to be compared to the distracters so as to prepare for the upcoming search task. In the second part of the task similar comparisons are made in the ‘search’ display. This repeated local comparison of items is similar to the local comparison of display items that is intrinsic in the inter-trial priming procedure (Müller et al., 1995; Found and Müller, 1996; Pollmann et al., 2000). Processing on one trial alters the state of the perceptual system for the next search trial. For example, if a search is performed in the color dimension, that dimension is altered so that it is processed faster on the next trial. This type of activity is thought to produce biasing or weighting of perceptual dimensions e.g. color (Found and Müller, 1996). Similar speeding effects are found when conjunction searches are repeated (Weidner et al., 2002), driven mainly by repeating the distractors in successive trials (Kristjánsson et al., 2002; Geyer et al., 2006). We might therefore suspect that similar bottom-up biasing develops and stays active during the ‘preparation’ stage of the current task thus forming part of the preparatory set.

While, something akin to searching the display must have occurred i.e. comparison of target and distracters, this appears to have been done without overt eye movements. The fMRI data show no evidence of frontal eye field activation during this part of the task. As increased activity in this region is reported to be a consistent finding in human neuroimaging studies (McDowell et al., 2008), the lack of it is indicative of the task being done without eye-movement. While sub-threshold activations cannot be excluded, given the clear instructions, that participants were practice on doing the task without eye movement outside the scanner and reported being able to do so, it seems probable that participants were largely successfully in following the instructions to fixate the central box.

The idea of biased feature maps is consistent with a broad range of previous work it does not however fit well with the results of McMains et al., 2007. They demonstrated that there was a general increase in neural activity when preparing for a target event. However, this was non-specific e.g. in brain areas considered specialized for color processing, preparing for a color stimulus produced equal activation as preparing for a movement stimulus. This discrepancy could be understood in a number of ways. A key feature of the current study is that the target changed on every trial. This contrasts with the block design used in McMains et al. (2007) in which the same target identity is used over 18s blocks of stimuli. It may be that the constant need to establish a new target representation creates a level of activation not seen when a single representation is
### Table 1 – Talairach coordinates of occipital and parietal areas activated during ‘preparation to search’.

<table>
<thead>
<tr>
<th>BA</th>
<th>Conjunction prepare versus conjunction watch</th>
<th>Feature prepare versus feature watch</th>
<th>Conjunction prepare versus feature prepare</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>x</td>
<td>y</td>
<td>z</td>
</tr>
<tr>
<td><strong>Ventral occipital</strong></td>
<td></td>
<td></td>
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<tr>
<td>R IOG/GF19</td>
<td>31</td>
<td>−71</td>
<td>−7</td>
</tr>
<tr>
<td>25</td>
<td>−78</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>33</td>
<td>−84</td>
<td>1</td>
<td>9.7</td>
</tr>
<tr>
<td>L IOG/GF19</td>
<td>−29</td>
<td>−62</td>
<td>−14</td>
</tr>
<tr>
<td>−42</td>
<td>−74</td>
<td>−9</td>
<td>10.5</td>
</tr>
<tr>
<td><strong>Dorsal occipital</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L GOM 18 (TOS)</td>
<td>−32</td>
<td>−85</td>
<td>16</td>
</tr>
<tr>
<td>R GOM 19 (TOS)</td>
<td>31</td>
<td>−82</td>
<td>23</td>
</tr>
<tr>
<td><strong>Occipital pole</strong></td>
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<tr>
<td>R GOM 18</td>
<td>−</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>L Ling 18</td>
<td>−</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>R Cu 17/18</td>
<td>−</td>
<td>−</td>
<td>−</td>
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<tr>
<td>−</td>
<td>−</td>
<td>−</td>
<td>−</td>
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<tr>
<td><strong>Parietal</strong></td>
<td></td>
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<tr>
<td>R LPs7 (IPS)</td>
<td>29</td>
<td>−62</td>
<td>40</td>
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<tr>
<td>25</td>
<td>−64</td>
<td>47</td>
<td>10.2</td>
</tr>
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</table>

Average coordinates of 15 participants. Values are peak coordinates (mm in Talairach space). Preparation for a conjunction search and preparation for a feature search are contrasted to their passive viewing controls (left and center) and to each other (right). Areas in which peak activations occur are labeled by lobe/gyrus/sulcus and followed by a number indicating the corresponding Brodmann area. Abbreviations: R, right; L, left; IOG/GF19, inferior occipital gyrus/fusiform gyrus; GOM 18 (TOS), middle occipital gyrus (transverse occipital sulcus); Ling18, lingual gyrus; Cu17/18, Cuneus; LPs7 (IPS), superior parietal lobule (intraparietal sulcus); cl-s, cluster size.
Table 2 – Talairach coordinates of sub-cortical areas activated during ‘preparation to search’.

<table>
<thead>
<tr>
<th>BA</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>cl-s</th>
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<tbody>
<tr>
<td><strong>Conjunction prepare versus conjunction watch</strong></td>
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<tr>
<td>Subcortical areas</td>
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<td></td>
</tr>
<tr>
<td>L Putamen/Claustrum</td>
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<td>9</td>
<td>6</td>
<td>185</td>
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</tr>
<tr>
<td>-27</td>
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<td>-29</td>
<td>1</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L Anterior Insula</td>
<td>−</td>
<td>−</td>
<td></td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>R Putamen</td>
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<td>−5</td>
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<tr>
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<td>7</td>
<td>6</td>
<td>21</td>
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<tr>
<td>R Thalamus</td>
<td>13</td>
<td>−15</td>
<td>3</td>
<td>61</td>
<td>11.6</td>
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<tr>
<td>L Thalamus</td>
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<td>−</td>
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<tr>
<td>Cerebellum</td>
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<td>−29</td>
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<tr>
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<td>27</td>
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<td><strong>Feature prepare versus feature watch</strong></td>
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<tr>
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</table>

Average coordinates of 15 participants. Values are peak coordinates (mm in Talairach space). Preparation for a conjunction search and preparation for a feature search are contrasted to their passive viewing controls (left and center) and to each other (right). Areas in which peak activations occur are labeled by lobe/gyrus/sulcus and followed by a number indicating the corresponding Brodmann area. Abbreviations: R, right; L, left; Ant lat Cerebell, anterior lateral cerebellum; Vermis Cerebell, vermis cerebellum; cl-s, cluster size.
formed and held. Alternatively, the results of Giesbrecht et al., 2003 indicate that somewhat different results are to be expected when stimuli are presented centrally (as in the current study) or more peripherally (as in McMains et al. (2007)). They found that target specific preparatory activity (color or location) was seen with central presentations but this is less clearly the case with more peripheral presentations.

In addition to the ventral occipital areas, activity was observed in the vicinity of the transverse occipital sulci (TOS) when the upcoming visual search task was expected to be demanding. TOS may hence have a similar role as the ventral occipital regions in target representation. Alternatively, the transverse occipital sulci may contribute to enhanced target representation by the suppression of distracters (Wokciulik

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and Kanwisher, 1999). Such an explanation seems particularly likely given the current design. Here for reasons of experimental control of visual saliency, during the preparation phase the target is always shown surrounded by distracters and when the upcoming task will be a conjunction search those distracters are always very similar to the target. Furthermore, the suppression of distracters has been shown to be a highly efficient way of biasing the perceptual system so that targets ‘pop-out’. This is true for both feature and conjunction searches. One way in which a color-form conjunction search could be done would be to by inhibiting one color and then searching within the target color for a unique shape (e.g. Treisman and Sato, 1990). For example when the target is a red O among red Xs and blue Os, the color (blue) could be suppressed and the search done on the shape dimension. In this case the unique rounded shape will pop-out from the straight oriented lines of the X distractors. Importantly, when this is used in one trial, it carries over to the next trial (Geyer et al., 2010), i.e. the inhibition remains active. In response to the current ‘prepare screen’ it seems likely that inhibition is developed in separating the target from distracters and maintained beyond the end of the prepare phase where it actively biases search during the latter part of the task. If so part of the activation we see, perhaps in the transverse occipital sulci may be due to active inhibition of one of the colors or shape maps. Similarly, relevant dimension weighting would be established during the preparation phase of ‘feature’ search. The features used were highly efficient ‘redundantly defined targets’ dissimilar from the surrounding distracters in both color and shape. Search for such targets could be speeded by the active suppression of the non-target features, (Krummenacher et al., 2001, 2002). Neural activity reflecting the development and maintenance of such suppression would be active during the ‘preparation’ stage.

It is worth noting that while distracter displays are identical in the Attend Prepare versus ‘Watch’ analyses they are not in the comparison of the two preparation conditions. This may contribute to the more robust activations seen in the latter analysis.

3.2. The posterior brain system

In addition to the occipital activations, a single right lateralized intraparietal activation was seen when preparing to perform a ‘conjunction’ search task, consistent with a large body of literature reporting activations in foci along the length of the intraparietal sulcus in similar tasks (e.g. Donner et al., 2000; Leonard et al., 2000). The current results restrict the IPS activation during preparation to a single focus. This focus (Fig. 3 and Table 1), corresponds closely to that described by Donner et al. (2000) as AIP (anterior intraparietal) and by Leonard et al. (2000) as MIPS (medial intraparietal). It is also close to the location identified by Nobre et al. (2003) as involved in the overall demand of a search task.

Its role in preparing to search needs to be considered in the context of the lack of evidence of frontal activation during this part of the task. Until now it was never clear whether the frontal activations that were seen in earlier visual search studies reflected the representation of the target for which people were searching or some other aspect of the task. The current results provide an answer to this – at least for the concrete stimuli used here (i.e. ‘target to be searched for’ was indicated by a visually identical stimulus to the ‘target presented’). Only posterior cortex and sub-cortical brain areas are found to be active when representing the target and preparing to respond to it in an up-coming visual search display. No evidence of frontal activation was seen. While a negative result, and therefore difficult to interpret, this would be consistent with the view that the biasing of perceptual maps arises through local comparison of items in the prepare display and not through top-down control. It is possible that frontal cortex may have been engaged while learning the requirements of the task (during the instructions or the practice phase). However, for performance in the scanner the current results indicate that all aspects of the preparation to search are accomplished without frontal cortex involvement. This is consistent with a growing body of work that shows no evidence of frontal involvement in the building and maintenance of specific short-term representations of visual targets. For example Shulman et al. (1999) found no frontal activation while participants prepared to detect a specific direction of motion in a visual display. The results also dovetail with recent Event Related Potential (ERP) studies showing sustained activation over posterior scalp when people are maintaining a template of an item for which they are about to search (Carlisle et al., 2011). More broadly, it has been argued from recent neuroimaging work on visual working memory (see Postle, 2006) that frontal areas only become involved when transformation rather than memory per se, is required. While true for visual features such as motion, shape and color, an exception seems to be the advanced representation of visual stimuli at specific spatial locations. This has been robustly shown to activate frontal areas (e.g., Kastner et al., 1999; Woldorff et al., 2004) and may relate to the close connection between visual spatial attention and motor planning (Deubel and Schneider, 1996). The current results would bolster the position that apart from preparing to detect targets at a specific location, the advanced representation of target features is achieved outside of frontal cortex.

Theoretically this result is important because it is often assumed that in visual search a signal is being sent from cortical regions outside of the visual areas to bias feature maps in an appropriate and flexible way (Desimone and Duncan, 1995). However, for the concrete visual stimuli used here, the traditional assumption that frontal–parietal networks are necessarily involved in forming and maintaining a representation of a target is not supported. Given this, an alternative explanation for the role of the intra-parietal sulcus activation in preparing to search is required. While it is possible that the intra-parietal area by itself is involved in maintaining the advanced specification of the target during ‘prepare to search’ and sending bias signals to early visual cortex, this seems increasingly unlikely. Recent variants of the Todd and Marois (2004) visual short-term memory paradigm suggest that IPS activity is more related to the various attentional demands of tasks rather than any specific coding (Magen et al., 2009; Mitchell and Cusack, 2008). Magen et al. (2009) argue that attentional demands increase once the delay interval between the target memory display and the probe is lengthened so leading to an increase in activation in...
the Intra-parietal sulcus. This increased activation is non-specific, being found both in memory for visual information (colors) and spatial information. In the current study attentional demands were increased by changing the task from preparing to search for a feature to preparing to search for a conjunction of two features. It is possible that rather than sending content specific bias signals, the intra-parietal area may support the ongoing activation of occipital neurons that are already encoding target and distractor information. This attentional allocation might increase when a more complex representation needs to be maintained as in the current study or sustained for a longer period as in Magen et al. (2009). An alternative is that the intra-parietal area may be primarily receiving the output from the spatially precise and color and form specialized occipital neurons, perhaps as part of a process of transforming the visual input into motor space as suggested by Ellison et al. (2003). When participants anticipate a demanding search task a more detailed representation of the target and distractors may be implemented in these occipital regions. Their output may be what is reflected in increased activation in the intra-parietal sulcus.

3.3. Stimulus response reassignment as target representations change

Concurrent activity in posterior cortex and striatum strongly suggest that the advanced representation of any target in visual search may be best considered as a visual-motor rather than a solely visual representation. In the present study, the identity of the target to which people should prepare to respond varied from trial to trial, thus the stimulus-response representation also changed on every trial. In addition, mixed amongst the ‘prepare to search’ trials were ‘watch’ trials which indicated that no response would be needed, in which case a switch from the previous stimulus-response representation would also have to be generated. This may be the processing that is being reflected as activity in the striatum. Such an interpretation would be consistent with earlier work e.g. Coles et al. (2004). They explicitly examined the substrate of visual stimulus-response rule switching in the striatum and other areas. Participants were cued as to whether to respond to the same object as in the previous trial or to another object. Significant activation in the ventral striatum was found as participants switched between which of the two concrete (i.e. visually identical) objects to respond to. While in Coles et al. (2004) the analysis was restricted to areas of interest whole brain analysis of a similar task has supported participation of the striatum while also demonstrating cerebellar involvement (Bischoff-Grethe et al., 2002). They explicitly contrasted template switching and response reassignment. They report right anterior-lateral cerebellum (lobule VI) activation during response reassignment, similar to that seen in the current results.

These studies suggest that in the current visual search task with its concrete visual targets, a likely function of ventral striatum and right anterior-lateral cerebellum is response reassignment to a visual stimulus, which is completed during the ‘prepare to search’ phase of the task and is independent of task demand. The involvement of the striatum in maintaining a visual-motor template is plausible given that in non-human primates at least, there are substantial input-output connections from higher-order visual areas to the region around the caudate nucleus/putamen and it has been linked to both perception and memory (Levy et al., 1997; Saint-Cyr et al., 1990; Zink et al., 2003).

An alternative role for the putamen is suggested by the results of McNab and Klingberg (2007). They showed that increased activity in the left putamen was seen when participants had to actively ignore yellow colored discs rather than treating them as potential targets in a short term visual memory task. The current task also required ignoring distractors during the preparations stage and a similar function may be accomplished by the putamen here.

4. Conclusion

The current study identified a network of brain regions activated when preparing to search for a visual target embedded in a display of distractors. This was done by isolating it from the BOLD signal changes produced by the later components of the task. Target identity varied from trial to trial, requiring participants to form a new representation of the target on each trial. In addition, participants knew in advance how demanding the search was likely to be on a given trial. It was hypothesized that for an identical visual target, a simpler representation would be formed when the expected demand of the upcoming search task was low.

It was expected that this would lead to a corresponding change in neural activity. The results show a network of neural areas activated in the posterior brain and in subcortical areas when ‘preparing to search’. Importantly for the hypothesis when preparing to perform a demanding visual search task, identical targets produce new and additional neural activation in occipital and parietal areas. Future work will need to identify which attentional processes are involved in producing this pattern of result e.g. inhibition of distractors or activation of target representations, the relative involvement of the identified areas in different attentional processes and the extent of their involvement when the ‘prepare display’ is present relative to activity in the interval before the target display. Furthermore, to achieve a full understanding it will also be necessary to establish the directionality of effects and the timing of their activation during visual search. For the latter, fMRI effective connectivity analysis and methodologies with high spatiotemporal resolution (such as MEG) will be needed. These limitations notwithstanding, this is the first fast event-related fMRI study to identify neural correlates of the preparatory phase of visual search and their modulation by the anticipated demand of the visual search.

5. Experimental procedures

5.1. Participants

Seventeen participants took part in the study (8 female, one left-handed, mean age $28.2 \pm 7.89$ years) with normal or corrected-to-normal vision. None admitted to current or past history of neurological or psychiatric conditions, learning
disabilities, alcohol/substance abuse or current use of prescription medications (as ascertained through a medical history checklist). One subject was discarded for not achieving sufficient proficiency in the visual search task during the training session (see below), and a second was eliminated due to technical problems during the MRI session, yielding a final sample size of 15 subjects. The study was performed in agreement with the regulations of the University of British Columbia Behavioural Ethical Board. Participants took part in a behavioral session outside the scanner (45 min), where they had a chance to practice the visual search task until they exceeded a desired level of performance (>75% accuracy). This session took place within 2 days prior to the fMRI session.

5.2. Task

The task was designed to avoid the order invariant problem and so enable the ‘prepare to search’ phase of a trial to be isolated from the later elements of the visual search task (Ollinger et al., 2001). It involved having to decide whether a pre-defined target (a colored letter) was present or not amongst distractors (other colored letters). Visual stimuli were viewed through a periscope mirror positioned about 10 cm above the eyes of the participants. Throughout all trials a central outline box was present in the middle of the display and participants were asked to keep their eyes fixed on this during a trial. The full sequence is shown in Fig. 1.

Trials began with the ‘Condition Display’ in which the outline of the centrally positioned box turned blue or yellow. The color instructed participants to either “Attend” to (outline of the box turning blue) or simply “Watch” (outline of the box turning yellow) the upcoming display. This was used to inform the participants as to whether they could simply watch the display on the upcoming trial or should prepare themselves to perform a search task. Activity during the “Watch” condition was later subtracted from activity in the “Attend” conditions in order to control for brain activation caused by simply viewing rather than actively attending to the displays.

This initial ‘Condition Display’ was followed after 200 ms by the onset of a ‘Prepare Display’, which in the “Attend” conditions (“Attend Prepare-Only” trials and “Attend Prepare+Target” trials, see Fig. 1) informed the subject as to the target and type of search to prepare for on that trial. The “Prepare Display” was comprised of the target for which participants would shortly have to search, shown inside the central box, surrounded by the 31 or 32 distractors that could be present in the subsequent ‘Search Display’ (see Fig. 1, columns 2 and 3). The equivalent display in the “Watch” trials was constructed in the same way except that the central square was filled with a ‘#’ symbol. The distractor sets were matched across conditions.

The ‘Prepare Display’ was presented for 800 ms, and was followed by the white central fixation box remaining on the screen for a further 1000 ms. After this in the “Watch” trials and “Attend Prepare-Only” trials (Fig. 1, left and central columns), no further stimuli were presented. The central white outline box remained on the screen and trials ended following a variable interval (mean of 1850 ms, pseudo randomly jittered with a range of 800–2900 ms). In “Attend Prepare+Target” trials however, a ‘Search Display’ followed the 1000 ms fixation and participants had to decide as quickly and accurately as possible if the target was present or absent in the display of 32 letters by pressing one of two keys on a fiber optic keypad with the index fingers of either hand. In the ‘Search Display’ the central box was empty and the designated target could be either present, replacing one of the distracters that was in the ‘Prepare Display’ (target present 50%) or it could be omitted (target absent, 50%). The ‘Search Display’ was shown for 1000 ms and then replaced by a screen with just the white central box.

The target and distracter stimuli used to make the ‘Prepare Displays’ and the ‘Search Displays’, varied from trial to trial. The relationship between the target and the distracters determined whether a given visual search trial would be a feature or a conjunction search. In feature search trials, target and distracters had no feature in common (e.g. a yellow M amongst blue Ss). In conjunction search trials, as illustrated in Fig. 1, the target and distracters always shared one feature [e.g. a yellow M, amongst yellow Ss (same color) and blue Ms (same shape)]. Equal numbers of feature and conjunction visual search trials were included. The same ‘Prepare Displays’ used in “Attend Prepare+Target” trials were used in the “Attend Prepare-Only” trials and in “Watch” control trials (but with the central target replaced by a ‘#’). To enable the isolation of the BOLD signal produced during the prepare phase from that produced by the target search phase, one third of trials were “Watch” trials, one third were “Attend Prepare-Only” and one third were “Attend Prepare+Target” (see, Ollinger et al., 2001).

There were 3 runs of 196 trials. After every run, feedback was given in the form of mean reaction time and the number of their errors shown in the center of the screen for 30 s.

5.3. Image acquisition

Echo-planar images were collected on a Philips Gyroscan Intera 3.0-T scanner, equipped with a 6-channel SENSE coil. Conventional spin-echo T1-weighted sagittal localizers were used to view head position and to graphically prescribe the functional image volumes. Functional image volumes sensitive to the blood oxygen-level dependent (BOLD) contrast signal were collected with a gradient echo sequence (TR/TE 2000/30 ms, 90° flip angle, field of view 210 × 143 × 240 mm³ (anteroposterior, feet–head, right–left), 3 mm slice thickness, slice gap 1 mm, 36 axial slices).

5.4. Image processing

PAR/REC format data from the 3T Philips system were converted to Analyze format using MRicr0 (Rorden C: MRicr0. http://www.mricro.com). The converted images were then analyzed using SPM5 (Wellcome Institute of Cognitive Neurology, http://www.fil.ion.ucl.ac.uk/spm/) for image reorientation, realignment, normalization into Montreal Neurological Institute space, and smoothing with a Gaussian kernel (8 mm full width at half maximum) to compensate for inter-subject anatomical differences and optimize the signal to noise ratio.
5.5 fMRI: within subjects

Event-related BOLD responses were modeled for the following trial types: “Watch” (feature), “Watch” (conjunction), “Attend Prepare” (feature) “Attend Prepare” (conjunction), “Attend Target” (feature) and “Attend Target” (conjunction) by the convolution of stimulus-onset vectors for each trial type with the synthetic hemodynamic response function provided in SPM2. The stimulus onset vectors coincided with ‘Condition Display’ onset for “Watch and “Attend Prepare” trials and with ‘Search Display’ onset in “Attend Target” trials. Eight nuisance regressors (six sets of realignment parameters, and the mean signal from white matter and cerebro-spinal fluid voxels respectively) were included in the model. The magnitude of the BOLD responses for each trial type were calculated using the GLM implemented in SPM2.

To evaluate the selective effects of preparing to search for a target relative to passively looking at a display, the following contrast images were specified: Prepare for a feature search – “Attend Prepare” (feature) versus “Watch” (feature), and prepare for a conjunction search – “Attend Prepare” (conjunction) versus “Watch” (conjunction). To evaluate the selective effects of preparing for a feature search compared to preparing for a conjunction search, the contrast “Attend Prepare” (feature) versus “Attend Prepare” (conjunction) was specified.

5.6 fMRI: between subjects

Contrast images for each subject were entered into two random effects analyses. Pair sample t-tests were set up to test the null hypotheses of no difference between trial types in the mean amplitude of the fitted hemodynamic response for any of these event types. We first applied the more conservative FWE method for correction of multiple comparisons, \( t(14) > 8.71, p < .05, \) cluster-size > 10. This approach yielded several significant clusters for contrasts involving the lower control state (“Watch” trials). However, for the higher level contrast of “Attend Prepare” (feature) versus “Attend Prepare” (conjunction) no clusters reached significance at the .05 level. We then opted for selecting the more liberal FDR method for multiple comparison correction, with the statistical threshold set at \( t(14) > 4.6, p < .05, \) cluster size > 20. This approach was indeed successful in yielding significant activation clusters for this contrast. Fig. 3 illustrates the main results of these contrasts, highlighting the common regions activated in the contrasts involving “Attend Prepare” (conjunction) (middle and bottom rows). All reported coordinates are in Talairach space, following conversion from Montreal Neurological Institute (MNI) space, using the program mni2tal (Brett et al., 2001).

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