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Research Report

Functional brain organization of preparatory attentional control in visual search

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ABSTRACT

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

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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 separated. 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.

91 From other lines of work, reasonable expectations can be 92 formed as to the brain areas that may be involved in preparing 93 to search for a target. A short term description of currently 94 relevant visual information is often thought to be implemen-95 ted by biasing feature maps in extra-striate regions of occipital cortex (Desimone and Duncan, 1995). Consistent with this, 96 97 sustained activation over the posterior scalp has been shown 98 as people hold representations of targets for which they are 99 about to search (Carlisle et al., 2011). In the human brain, 100 feature maps for shapes and colors seem to exist in ventral 101 occipital cortex (Beauchamp et al., 1999; Corbetta et al., 1990, 1991; Shulman et al., 1999, 2003). Furthermore, it has been 102 103 demonstrated that such maps are activated when people are 104 preparing to process visual input to find a target (Chawla et al., 105 1999; Giesbrecht et al., 2003). For example, Giesbrecht et al. 106 (2003) showed increased bilateral activation in the fusiform 107 region when people are waiting to make an orientation 108 decision about a soon to be displayed colored, rectangle. It is 109 clear that in visual search some similar advanced specification 110 of the target must be formed and 'held in mind' prior to any search. The task must proceed by comparing multiple items in 111 a visual display against this representation. It seems likely 112 113 therefore that in visual search, the advanced specification of the target will also be found to be implemented here. 114

115 Importantly, as human cognition is highly flexible it seems 116 likely that the advance specification of target identity will vary with the current task demands. A target could be identical in two 117 118 search tasks, but its advanced representation is predicted to be simpler when the upcoming task is expected to be undemanding 119 120 compared to when it is expected to be demanding. For example the pre-biasing that might occur when preparing to find a red X 121 is likely to be different when the task is expected to be a 'feature' 122 123 search i.e. all distracters will be green Os, relative to when the 124 task is expected to be a 'conjunction' search i.e. distracters will 125 be green Xs and red Os. In the first, a simple representation will 126 suffice to perform the task. This could be implemented neuro-127 logically by the detection of any activation in feature maps coding other than green or O or by activation in red or diagonal 128 129 feature maps. In contrast when the distracters will be green Xs and red Os, a more elaborated representation of the target 130 including its relationship with the distracters must be formed 131 (Duncan and Humphreys, 1989). If so, it is likely that for the 132 133 identical stimulus, when preparing for such an undemanding 134 feature search there will be less neural activation than when preparing for a demanding conjunction search. This may be 135 detected as a smaller fMRI signal. 136

137 In addition to the variable activity in feature maps that might 138 be expected to be seen in occipital cortex, the 'preparing to 139 search' phase of a visual search task is likely to include other 140 regions that are involved in modulating this sensory activity. A 141 frontal-parietal control system is often proposed (e.g. Desimone 142 and Duncan, 1995; Woldorff et al., 2004) that sends bias signals to 143 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; Leonards 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 movement 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 frontalparietal 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 symbolic indication of the current target and distracter information 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

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Fig. 1 – Sequence of screens in a trial (top-bottom) with percent of different trial types. A conjunction search trial is illustrated. In feature search the target shared no features with the distracters.



Fig. 2 – Reaction time of correct responses when the target is present and when it is absent in feature search and conjunction search conditions. Vertical lines show the standard error of means.

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

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204 BOLD activity in extrastriate visual cortex, including bilateral 205 inferior occipital gyri and fusiform gyri BA19 (ventrally), and 206 more dorsally, bilateral middle occipital gyri BA18/19, in the vicinity of the transverse occipital sulcus (TOS). Additionally, 207 208 there was significant BOLD activity in right superior parietal 209 lobe (BA7), in the proximity of the intraparietal sulcus, [see Fig. 3, middle row]. Finally, there were clusters in right poster-210 211 ior thalamus, bilateral ventral striatum, bilateral anterior lat-212 eral cerebellum, midline cerebellum and pons (Table 2).

214 2.2.3. Selective effects of preparing for a feature search 215 compared to preparing for a conjunction search – "Attend 216 Prepare" (conjunction) versus "Attend Prepare" (feature) 217 Regions where BOLD activity was greater when preparing for a 218 conjunction relative to a feature search were bilateral ventral 219 occipital cortex (inferior occipital/fusiform gyri BA19), bilateral 220 dorsal occipital cortex (middle occipital gyri BA18/19, in the 221 proximity of TOS), and right superior parietal lobule BA7, in 222 the vicinity of IPS [see Fig. 3, bottom row]. Please note that 223 BOLD effects around the right intraparietal sulcus and in 224 dorsal occipital cortex coincided across the two contrasts of 225 "Attend Prepare" (conjunction) versus "Watch" (conjunction) 226 and "Attend Prepare" (conjunction) versus "Attend Prepare" 227 (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

250 Activations seen in the ventral occipital region are consistent 251 with the idea that an advance specification of the target is 252 implemented by biasing feature maps in extra-striate regions 253 of occipital cortex (Chawla et al., 1999; Desimone and 254 Duncan, 1995; Giesbrecht et al., 2003; Stokes et al., 2009). This portion of extrastriate visual cortex is similar to that which, 255 256 in previous studies, has been argued to encode both shape and color information (e.g. Beauchamp, 1999; Shulman et al., 257 2003, 1999). Significantly, preparing to search for the identical 258 259 target, but in the context of expecting it to be amongst very similar distracters rather than very different distracters 260 261 produced different results. When expecting a conjunction 262 search task, the same ventral occipital area was activated 263 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 18 s 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

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Table 1 – Talairac	h coordin	ates of oc	cipital and	parietal a	areas activ	ated durin	ng 'preparat	ion to sea	arch'.						
Conjunction prepare	Feature	e prepare vers	sus feature	watch		Conjunc	Conjunction prepare versus feature prepare								
BA	х	у	Z	cl-s	Т	х	у	Z	cl-s	Т	х	у	Z	cl-s	Т
Ventral occipital															
R IOG/GF19	31	-71	-7	126	11.6	35	-79	-9	116	14.9	25	-80	0	197	9.7
	25	-78	0		9.7	41	-68	-7		12.2	-	-	-		
	33	-84	1		9.7	33	-71	-7		9.5	-	-	-		
L IOG/GF19	-29	-62	-14	146	10.7	-	-	-			-26	-80	-9	150	6.0
	-42	-74	-9		10.5	-	-	-			-	-	-		
Dorsal occinital															
L GOm 18 (TOS)	_32	_85	16	40	10 5	_	_	_	_	_	-30	-86	13	303	67
2 0011 20 (100)	52	00	10	10	1010						-28	-79	19	000	6.2
R GOm 19 (TOS)	31	-82	23	15	9.8	-	-	-	-	-	33	-84	23	82	7.6
Occipital pole															
R GOm 18	_	_	_			35	-92	11	30	10.8	_	_	_		
L Ling 18	-	_	_			-22	-89	-5	14	10.1	_	-	-		
R Cu 17/18	-	_	_			12	-97	1	45	10.1	_	-	-		
	-	_	_			16	-100	8		9.1	-	-	-		
- · · · ·															
Parietal		60									07	5.6		70	
R LPS/ (IPS)	29	-62	40	/4	11.1	-	-	-			27	-56	45	/3	6.1
	25	-64	47		10.2										

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.

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Table 2 – Talairach co	ordinates	of sub-co	rtical area	s activate	d during '	preparatio	on to sear	ch'.										
Conjunction prepare vers	us conjunc	tion watch				Feature	e prepare ve	ersus featur	e watch	Conju	Conjunction prepare versus feature prepare							
ВА	х	у	Т	x	у	Z	cl-s	Т	x	у	Z	cl-s						
Subcortical areas																		
L Putamen/Claustrum	-25	9	6	185	13.1	-31	-6	-5	86	12.7	-	-	-	-				
	-27	2	-3		12.6	-31	-6	3		12.2	-	-	-	-				
	-29	1	3		9.8						-	-	-	-				
L Anterior Insula	-	_	-	-	-	-36	11	6	20	10.5	-	-	-	-				
R Putamen	25	8	-5	78	15.4	-	-	-	-	-	-	-	-	-				
	21	7	6	21	10.3	-	-	-	-	-	-	-	-	-				
R Thalamus	13	-15	3	61	11.6	-	-	-	-	-	-	-	-	-				
L Thalamus	-	-	-	-	-	-9	-17	5	77	12.7	-	-	-	-				
Cerebellum																		
L Ant Lat Cerebell	-33	-56	-29	30	11.0	-	-	-	-	-	-	-	-	-				
R Ant Lat Cerebell	24	-59	-25	52	10.4	31	-49	-16	50	12.5	-	-	-	-				
						21	-45	-14		9.6	_	-	_	-				

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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.

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Fig. 3 - Group activation map (15 subjects), superimposed on one subject's rendered brain during 'preparing to search'. Superior view, left lateral, right lateral and posterior views are shown. Top row, activations produced by preparing to search for a feature (Att_Prep_Feat) relative to watching the control display (Watch_Feat). Middle row, activations produced by preparing to search for a conjunction (Att_Prep_Conj) relative to watching the control display (Watch_Conj). Bottom row, preparing to search for a conjunction compared to preparing to search for a feature. Abbreviations: R, right; L, left; GL, lingual gyrus; Fus, fusiform; IPS, intraparietal sulcus; TOS, transverse occipital sulcus. Note: Top and middle row used FWE corrected contrasts. Bottom row uses FDR corrected contrasts and a different scale.

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 445 likely given the current design. Here for reasons of experimental control of visual saliency, during the preparation phase 446 447 the target is always shown surrounded by distracters and 448 when the upcoming task will be a conjunction search those 449 distracters are always very similar to the target. Furthermore, the suppression of distracters has been shown to be a highly 450 451 efficient way of biasing the perceptual system so that targets 452 'pop-out'. This is true for both feature and conjunction searches. One way in which a color-form conjunction search 453 454 could be done would be to by inhibiting one color and then 455 searching within the target color for a unique shape (e.g. Treisman and Sato, 1990). For example when the target is a 456 457 red O among red Xs and blue Os, the color (blue) could be 458 supressed and the search done on the shape dimension. In 459 this case the unique rounded shape will pop-out from the 460 straight oriented lines of the X distractors. Importantly, when this is used in one trial, it carries over to the next trial (Gever 461 462 et al., 2010), i.e. the inhibition remains active. In response to 463 the current 'prepare screen' it seems likely that inhibition is 464 developed in separating the target from distractors and main-465 tained beyond the end of the prepare phase where it actively 466 biases search during the latter part of the task. If so part of the 467 activation we see, perhaps in the transverse occipital sulci 468 may be due to active inhibition of one of the colors or shape 469 maps. Similarly, relevant dimension weighting would be 470 established during the preparation phase of 'feature' search. The features used were highly efficient 'redundantly defined 471 targets' dissimilar from the surrounding distractors in both 472 473 color and shape. Search for such targets could be speeded by the active suppression of the non-target features, 474 475 (Krummenacher et al., 2001, 2002). Neural activity reflecting 476 the development and maintenance of such suppression would be active during the 'preparation' stage. 477 478

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 Leonards 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 498 499 the context of the lack of evidence of frontal activation during 500 this part of the task. Until now it was never clear whether the 501 frontal activations that were seen in earlier visual search 502 studies reflected the representation of the target for which 503 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

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504 the Intra-parietal sulcus. This increased activation is non-505 specific, being found both in memory for visual information 506 (colors) and spatial information. In the current study atten-507 tional demands were increased by changing the task from 508 preparing to search for a feature to preparing to search for a 509 conjunction of two features. It is possible that rather than 510 sending content specific bias signals, the intra-parietal area 511 may support the ongoing activation of occipital neurons that 512 are already encoding target and distractor information. This attentional allocation might increase when a more complex 513 514 representation needs to be maintained as in the current 515 study or sustained for a longer period as in Magen et al. (2009). An alternative is that the intra-parietal area may be 516 517 primarily receiving the output from the spatially precise and 518 color and form specialized occipital neurons, perhaps as part 519 of a process of transforming the visual input into motor space 520 as suggested by Ellison et al. (2003). When participants 521 anticipate a demanding search task a more detailed representation of the target and distracters may be implemented 522 523 in these occipital regions. Their output may be what is 524 reflected in increased activation in the intra-parietal sulcus. 525

3.3. Stimulus response reassignment as target representations change

529 Concurrent activity in posterior cortex and striatum strongly 530 suggest that the advanced representation of any target in 531 visual search may be best considered as a visual-motor rather 532 than a solely visual representation. In the present study, the 533 identity of the target to which people should prepare to respond varied from trial to trial, thus the stimulus-response 534 535 representation also changed on every trial. In addition, mixed 536 amongst the 'prepare to search' trials were 'watch' trials which indicated that no response would be needed, in which case a 537 538 switch from the previous stimulus-response representation 539 would also have to be generated. This may be the processing that is being reflected as activity in the striatum. Such an 540 541 interpretation would be consistent with earlier work e.g. Cooles et al. (2004). They explicitly examined the substrate of visual 542 543 stimulus-response rule switching in the striatum and other 544 areas. Participants were cued as to whether to respond to the 545 same object as in the previous trial or to another object. 546 Significant activation in the ventral striatum was found as 547 participants switched between which of the two concrete (i.e. visually identical) objects to respond to. While in Cooles et al. 548 (2004) the analysis was restricted to areas of interest whole 549 550 brain analysis of a similar task has supported participation of the striatum while also demonstrating cerebellar involvement 551 (Bischoff-Grethe et al., 2002). They explicitly contrasted tem-552 553 plate switching and response reassignment. They report right 554 anterior-lateral cerebellum (lobule VI) activation during 555 response reassignment, similar to that seen in the current 556 results.

These studies suggests 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 distracters 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 distracters. 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 ± 7.89 years) with normal or corrected-to-normal vision. None admitted to current or past history of neurological or psychiatric conditions, learning

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564 disabilities, alcohol/substance abuse or current use of pre-565 scription medications (as ascertained through a medical 566 history checklist). One subject was discarded for not achieving sufficient proficiency in the visual search task during the 567 568 training session (see below), and a second was eliminated 569 due to technical problems during the MRI session, yielding a 570 final sample size of 15 subjects. The study was performed in 571 agreement with the regulations of the University of British 572 Columbia Behavioural Ethical Board. Participants took part in a behavioral session outside the scanner (45 min), where they 573 574 had a chance to practice the visual search task until they 575 exceeded a desired level of performance (>75% accuracy). This session took place within 2 days prior the fMRI session. 576

5.2. Task

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580 The task was designed to avoid the order invariant problem 581 and so enable the 'prepare to search' phase of a trial to be Q2 isolated from the later elements of the visual search task 582 583 (Ollinger et al., 2001). It involved having to decide whether a 584 pre-defined target (a colored letter) was present or not 585 amongst distracters (other colored letters). Visual stimuli 586 were viewed through a periscopic mirror positioned about 587 10 cm above the eyes of the participants. Throughout all trials 588 a central outline box was present in the middle of the display 589 and participants were asked to keep their eyes fixed on this 590 during a trial. The full sequence is shown in Fig. 1.

Trials began with the 'Condition Display' in which the 591 592 outline of the centrally positioned box turned blue or yellow. 593 The color instructed participants to either "Attend" to (outline of the box turning blue) or simply "Watch" (outline of the box 594 595 turning yellow) the upcoming display. This was used it to inform the participants as to whether they could simply watch 596 the display on the upcoming trial or should prepare them-597 598 selves to perform a search task. Activity during the "Watch" condition was later subtracted from activity in the "Attend" 599 600 conditions in order to control for brain activation caused by 601 simply viewing rather than actively attending to the displays.

This initial 'Condition Display' was followed after 200 ms 602 603 by the onset of a 'Prepare Display', which in the "Attend" 604 conditions ("Attend Prepare-Only" trials and "Attend Prepare 605 +Target" trials, see Fig. 1) informed the subject as to the target and type of search to prepare for on that trial. The 606 607 'Prepare Display' was comprised of the target for which participants would shortly have to search, shown inside the 608 central box, surrounded by the 31 or 32 distracters that could 609 be present in the subsequent 'Search Display' (see Fig. 1, 610 columns 2 and 3). The equivalent display in the "Watch" trials 611 612 was constructed in the same way except that the central 613 square was filled with a '#' symbol. The distracter sets were 614 matched across conditions.

The 'Prepare Display' was presented for 800 ms, and was 615 616 followed by the white central fixation box remaining on the screen for a further 1000 ms. After this in the "Watch" trials 617 and "Attend Prepare-Only" trials (Fig. 1, left and central 618 619 columns), no further stimuli were presented. The central white outline box remained on the screen and trials ended 620 following a variable interval (mean of 1850 ms, pseudo 621 622 randomly jittered with a range of 800-2900 ms). In "Attend 623 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 $210 \times 143 \times 240 \text{ mm}^3$ (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 MRIcro (Rorden C: MRIcro. http://www.mricro.com). The converted images were then analyzed using SPM5 (Wellcome Institute of Cognitive Neurol ogy, http://www.fil.ion.ucl.ac.uk/spm/) for image reorienta tion, 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.

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5.5. fMRI: within subjects

626 Event-related BOLD responses were modeled for the following trial types: "Watch" (feature), "Watch" (conjunction), 627 628 "Attend Prepare" (feature) "Attend Prepare" (conjunction) 629 "Attend Target" (feature) and "Attend Target" (conjunction) 630 by the convolution of stimulus-onset vectors for each trial 631 type with the synthetic hemodynamic response function 632 provided in SPM2. The stimulus onset vectors coincided with 'Condition Display' onset for "Watch" and "Attend Prepare" 633 634 trials and with 'Search Display' onset in "Attend Target" 635 trials. Eight nuisance regressors (six sets of realignment parameters, and the mean signal from white matter and 636 637 cerebro-spinal fluid voxels respectively) were included in the 638 model. The magnitude of the BOLD responses for each trial 639 type were calculated using the GLM implemented in SPM2.

640 To evaluate the selective effects of preparing to search for 641 a target relative to passively looking at a display, the following contrast images were specified: Prepare for a feature 642 643 search - "Attend Prepare" (feature) versus "Watch" (feature), 644 and prepare for a conjunction search - "Attend Prepare" 645 (conjunction) versus "Watch" (conjunction). To evaluate the 646 selective effects of preparing for a feature search compared to 647 preparing for a conjunction search, the contrast "Attend 648 Prepare" (feature) versus "Attend Prepare" (conjunction) was specified. 649

5.6. fMRI: between subjects

653 Contrast images for each subject were entered into two ran-654 dom effects analyses. Pair sample t-tests were set up to test the 655 null hypotheses of no difference between trial types in the 656 mean amplitude of the fitted hemodynamic response for any of these event types. We first applied the more conservative 658 FWE method for correction of multiple comparisons, t (14) 659 >8.71, p<.05, cluster-size>10. This approach yielded several 660 significant clusters for contrasts involving the lower control 661 state ("Watch" trials). However, for the higher level contrast of 662 "Attend Prepare" (feature) versus "Attend Prepare" (conjunc-663 tion) no clusters reached significance at the .05 level. We then 664 opted for selecting the more liberal FDR method for multiple 665 comparison correction, with the statistical threshold set at t 666 (14)>4.6, p<.05, cluster size>20. This approach was indeed 667 successful in yielding significant activation clusters for this 668 contrast. Fig. 3 illustrates the main results of these contrasts, 669 highlighting the common regions activated in the contrasts 670 involving "Attend Prepare" (conjunction) (middle and bottom 671 03 rows). All reported coordinates are in Talairach space, follow-672 ing conversion from Montreal Neurological Institute (MNI) 673 space, using the program mni2tal (Brett et al., 2001).

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