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 that an advanced specification of that object 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 non demanding search.

Key words: visual-search, template, preparatory, representation, fMRI, sensory-motor.

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 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.

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 implemented 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 advance

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 neurologically 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; 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 frontal-

parietal control system (Desimone & 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 Figure 1.

2 Results

2.1 Reaction time results

Reaction time results are shown in Figure 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 Figure 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.
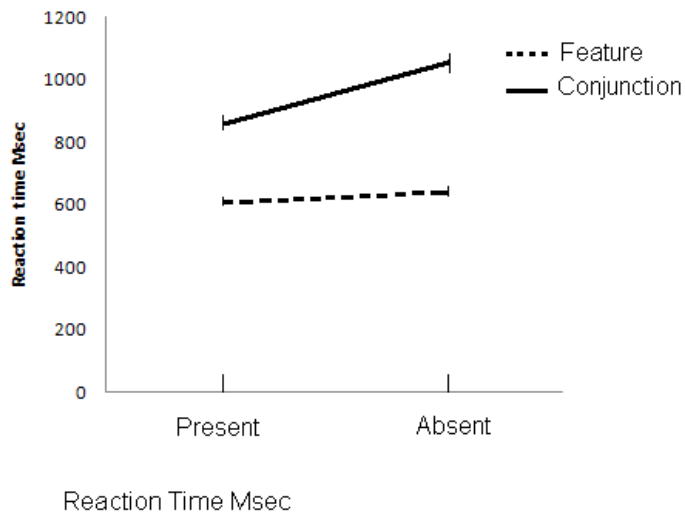
Reaction Time Msec

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

2.2 Results - fMRI (preparation)

Effects of preparation for a feature search - "Attend Prepare" (feature) versus "Watch"

(feature).

Full Talairach coordinates are given in Table 1 and Table 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 Figure 3, top row].

TABLE 1

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.

TABLE 2

Effects of preparation for a conjunction search - "Attend Prepare" (conjunction) versus

"Watch" (conjunction).

Results are shown in Table 1 and Table 2, Figure 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 Figure 3, middle row]. Finally, there were

clusters in right posterior Thalamus, bilateral ventral Striatum, bilateral anterior Lateral

Cerebellum, Midline cerebellum and Pons (Table 2).

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 GyriBA18/19, in the proximity of TOS), and

right Superior Parietal lobule BA7, in the vicinity of IPS [see Figure 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) (Figure

3, bottom and middle rows and Table 1).
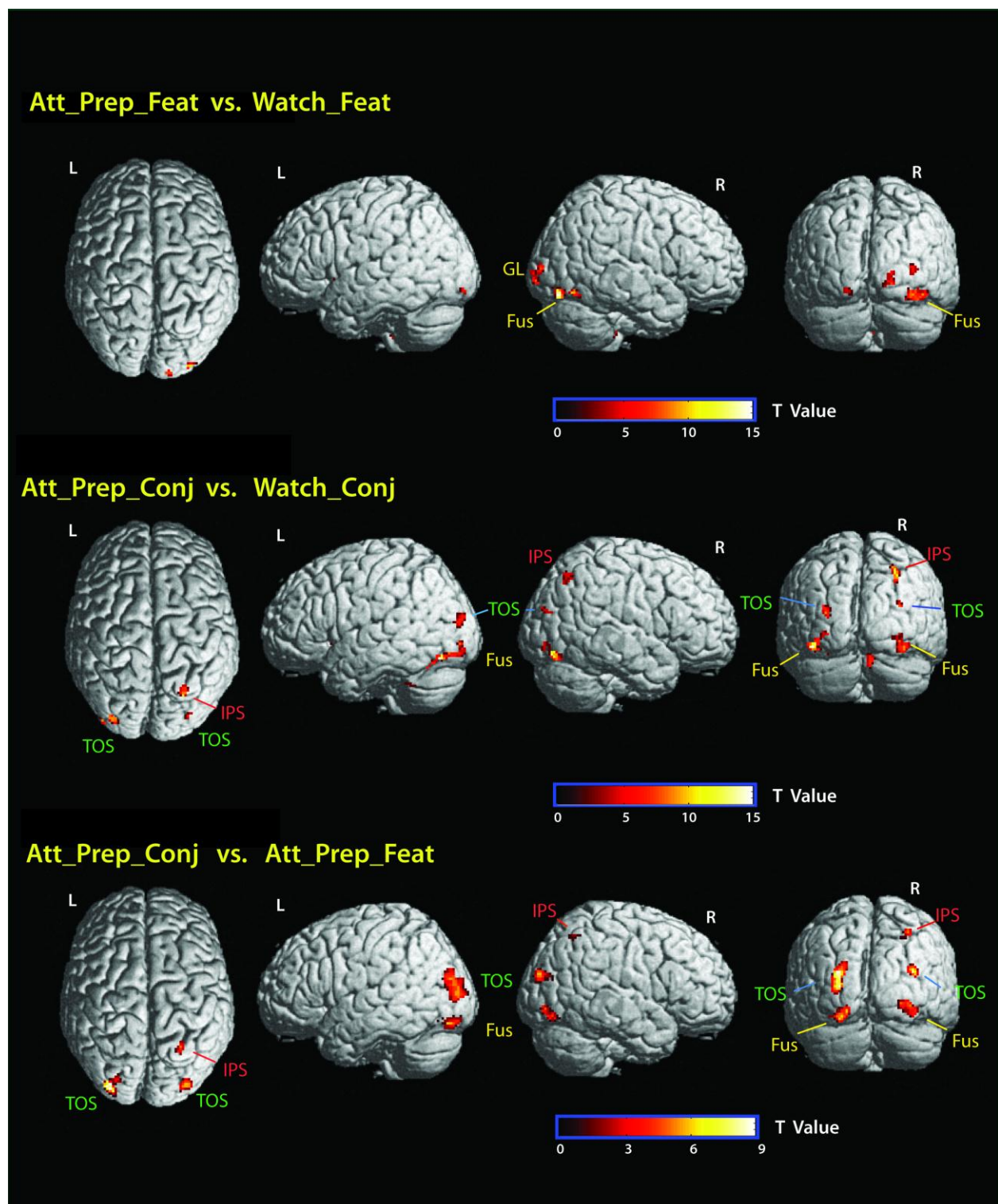
Fig 3

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.

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 (Figure 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, colour or shape maps

may be activated, when a demanding conjunction search is expected colour 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 & 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 colour 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. colour (Found &

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 second

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 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 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 colour-form conjunction search could be done would be to by inhibiting one colour

and then searching within the target colour for a unique shape (e.g. Treisman & Sato 1990).

For example when the target is a red o among red xs and blue os, the colour (blue) could be

supressed 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 distractors 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 colours 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

distractors in both colour 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 (Figure 3, 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 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 & 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 2010,). 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 colour 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 distracters 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. Cooles 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 Cooles 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 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 &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 Experimental Procedures

4.1 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

two days prior the fMRI session.

4.2 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, Shulman & Corbetta, 2001; Ollinger, Corbetta Shulman & 2001). It

involved having to decide whether a pre-defined target (a colored letter) was present or not

amongst distracters (other colored letters). Visual stimuli were viewed through a periscopic

mirror positioned about 10cm 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 Figure 1.
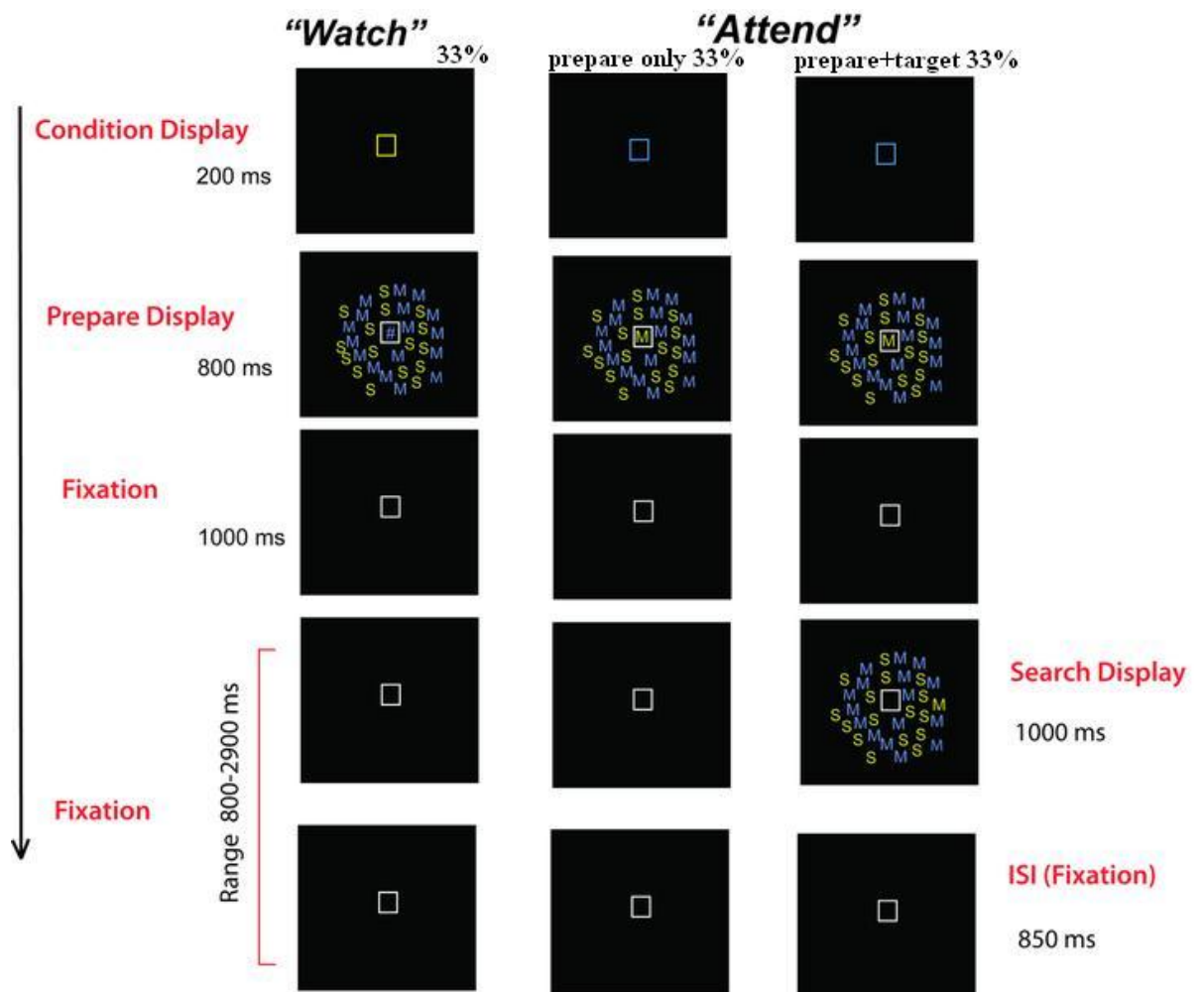
Fig 1

Sequence of screens in a trial (top to bottom) with percent of different trial types. A Conjunction search trial is illustrated. In Feature search the target shared no features with the distracters.

Trials began with the 'Condition Display' in which the outline of the centrally positioned box turned blue or yellow. The colour 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 it 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 Figure 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 distracters that could be present in the subsequent 'Search Display' (see Figure 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 distracter 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 (Figure 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 - 2,900 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 Figure 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, Corbetta & Shulman, 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 seconds.

4.3 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 mm (anteroposterior, feet–head, right–left), 3 mm slice

thickness, slice gap 1 mm, 36 axial slices.

4.4 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 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.

4.5 *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.

4.6 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. Figure 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).

5 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 sub-cortical 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.

Acknowledgments

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