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The neural correlates of attention orienting in visuospatial working memory for detecting feature and conjunction changes

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ABSTRACT

The neural mechanisms of attentional orienting in visuospatial working memory for change detection were investigated. A spatial cue was provided with the onset time manipulated to allow more effective top-down control with an early cue than with a late cue. The change type was also manipulated so that accurate detection depended on color or the binding of color and location. The results showed that both the frontal and parietal regions subserved the change detection task without cueing. When data were collapsed over the two change types, early cueing increased activation in the right inferior frontal gyrus (IFG) and middle frontal gyrus (MFG) while late cueing increased activation in the right inferior parietal lobule (IPL) and temporoparietal junction (TPJ) as compared with the no-cue condition. The cue onset time led to different levels of enhancement in the frontal and posterior cortices related to top-down control and stimulus-driven orienting. For feature detection, early cueing increased activation in the right MFG and late cueing increased activation in the bilateral precuneus (PCu), right TPJ, and right cuneus. The neural correlates of conjunction detection involved the right PCu and cerebellum without cueing, were associated with the anterior MFG, left IFG, and the left STG with early cueing, and involved the right MFG, left IFG, and right IPL with late cueing. The left IFG was correlated with memory retrieval of the cued representation for conjunction detection, and the right posterior PCu was associated with maintenance and memory retrieval among competing stimuli.

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1. Introduction

Detecting changes in the visual environment is important for daily functioning. For example, a change in a traffic signal dictates the next appropriate behavior when driving. Yet, people often fail to detect such changes even when the change is quite large. This failure can be attributed largely to the limitations of attention (see [Rensink, 2002](#) for a review).

However, the cognitive functions of attention in change detection are still open to debate ([Allen et al., 2006](#); [Wheeler and Treisman, 2002](#); [Yeh et al., 2005](#)). The investigation of the brain regions that subserve change detection may provide evidence critical to resolve the debate.

Change detection involves multiple cognitive processes: encoding two stimulus arrays, maintaining one stimulus array in working memory, retrieving memory representations, and

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comparing the test stimuli with the retrieved memory representations for a decision. Attention should be engaged in each process, and one of its critical functions may be to prioritize information transfer (e.g., [Duncan and Humphreys, 1989](#); [Schmidt et al., 2002](#)) to visuospatial working memory for further processing. Yet, most imaging studies have focused on the neural correlates of change detection ([Beck et al., 2001, 2006](#); [Pessoa and Ungerleider, 2004](#)) or the neural correlates that subserve the encoding, search, and the response phases ([Huettel et al., 2001](#)). Few have addressed the impact of attention prioritization on the neural activation for change detection.

Nobre and colleagues ([Griffin and Nobre, 2003](#); [Nobre et al., 2004](#)) investigated attention orienting to memory representations. They presented a spatial cue either before (pre-cue) or after (retro-cue) a stimulus array. Memory recognition was based on color information. They found greater activation in a distributed fronto-parietal network for the retro-cue than the pre-cue condition ([Nobre et al., 2004](#)). Given that spatial cueing engages both the bottom-up stimulus-driven process and the top-down control in neural activation ([Hopfinger et al., 2000](#); [Hopfinger and Ries, 2005](#)), it is likely that the frontal and parietal regions subserve different functions in the task context of change detection.

[Yeh et al. \(2005\)](#) integrated the cueing paradigm with the change detection paradigm in a behavioral study to investigate the role of attention in prioritization of information transfer into visuospatial working memory for change detection. Following [Wheeler and Treisman's \(2002\)](#) manipulation of change type, they likewise manipulated whether the detection task could be performed based on color features (feature-change condition) or on the binding of color and location (conjunction-change condition). Replicating [Wheeler and Treisman's \(2002\)](#) findings, they found lower accuracy in conjunction detection than in feature detection when multiple test stimuli were presented in the test display. Moreover, they found that an early cue in the delay period improved detection performance no matter whether the detection task required feature binding or not. In contrast, a late cue that occurred shortly before the test display deteriorated detection performance regardless of change type. They argued that the decision was more difficult in the conjunction-change condition than in the feature-change condition and that attention prioritizes information processing (referred to as the prioritization-decision hypothesis). Recent behavioral studies also suggest that features of an object are automatically bound ([Allen et al., 2006](#); [Treisman and Zhang, in press](#)). That is, binding per se may not require additional attention resources.

The purpose of this study is to reveal how neural mechanisms subserve attentional prioritization for change detection. The behavioral data ([Yeh et al., 2005](#)) showed that cueing can both benefit and cost performance depending upon the cue onset time. It is likely that early cueing allows effective top-down control of prioritization to benefit performance. In contrast, late cueing could disrupt ongoing maintenance in visuospatial working memory. With a short delay after the cue onset, the test display could again disrupt the ongoing selection process. Processing of the uncued stimuli could interfere with the processing of the cued stimulus. That is, the relative involvement of top-down control and stimulus-driven atten-

tion orienting may underlie the benefit and cost due to cueing. The results from functional magnetic resonance imaging (fMRI) can verify this hypothesis by revealing the relative level of neural activation in the frontal and parietal regions.

With the involvement of multiple cognitive processes in change detection, top-down control should be engaged to regulate these processes. A fronto-parietal network should underlie the cognitive functions as [Pessoa and Ungerleider \(2004\)](#) showed with an orientation change detection task. The onset of a spatial cue engages both the bottom-up stimulus-driven process and the top-down control in neural activation ([Hopfinger et al., 2000](#); [Hopfinger and Ries, 2005](#)). The involvement of the two types of attention orienting should be observed regardless of the cue onset time when the spatial cue provides useful information. The question is whether the cue onset time influences the relative dominance of the two types of attention orienting in neural activation.

Although cueing reduces the memory and decision load to one item, it should increase the neural activation related to top-down control for prioritizing and regulating processes. Given that top-down control operates for a longer duration with an early cue to effect prioritization, neural activation in the regions related to the top-down control should be significantly higher in the early-cue condition in contrast to the no-cue control condition. According to the prioritization-decision hypothesis, a late cue that operates for a short duration results in ineffective top-down control. As a result, the increase by late cueing in regions related to the top-down control may not be significant in contrast to the no-cue control condition. The relative level of activation in the regions related to top-down control should be ranked from the no-cue control, to late cueing, to the early cueing condition.

Stimulus-driven attention orienting should also operate in the three conditions. In the no-cue control condition, stimulus-driven orienting occurs when the initial stimulus array is shown. It occurs again when the test display is shown as stimulus onset captures attention ([Cole et al., 2003](#); [Peterson et al., 2002](#)). Attention, without cueing, also needs to shift between the current percept and the memory representation before a decision can be made. Spatial cueing should also capture attention to activate stimulus-driven orienting to the cue. However, an early cue could guide the top-down control so that attention can effectively focus on the cued representation in the delay period and process the cued stimulus at the test phase with high priority to lower the amount of shifting between the percept and the memory representation. On the other hand, the amount of time available for the top-down control to guide attention is short with a late cue. The onset of the test display may disrupt the top-down control and reflexively shift attention between the current percepts and memory representations of multiple stimuli. Activation in the regions related to stimulus-driven attention orienting should be higher with late cueing than with early cueing or no-cue control.

In summary, both the top-down control and stimulus-driven processes should be involved in the no-cue control, early cueing, and the late cueing conditions. According to the prioritization-decision hypothesis, the cue onset time should influence the relative level of neural activation in the frontal and parietal regions in contrast to the no-cue control

condition. In contrast to the no-cue control, early cueing is expected to increase activation in the frontal regions because of effective top-down control over a longer duration. In contrast to the no-cue control, late cueing is expected to increase activation in the parietal regions because stronger stimulus-driven orienting arises from the less effective top-down control.

With cueing engaging the top-down control, the prioritization-decision hypothesis postulates that top-down control involves the retrieval of the memory representation at the cued location in the initial stimulus array. Yet, it is unclear whether retrieval is necessary when the decision is easy. It is likely that an easy decision is based on the perceptual signals from the feature dimension given that new features replace old ones in the feature-change condition. In the conjunction-change condition, the decision is difficult because all the features remain identical at the global level (Yeh et al., 2005) or because each bound representation is vulnerable (Allen et al., 2006). As a result, accurate conjunction detection requires the retrieval of detailed information that contains individual items at each location. Thus, cueing may engage memory retrieval only for conjunction detection. We investigated how cue onset time influences the neural correlates of detecting feature and conjunction changes.

2. Results

2.1. Behavioral results

Table 1 shows the accuracy and the mean reaction time (RT) in each condition. We conducted a 2 (change type: color/conjunction) $\times$ 3 (cue type: no cue/early/late) repeated measures analysis of variance (ANOVA) to investigate the cueing effect on change detection. The results showed a significant main effect of cue type on RT [$F(2,18)=28.86$, $p<.0001$]. The Tukey post hoc test showed a significantly ($p<.01$) faster RT with early cueing (563.82 ms) and a significantly ($p<.01$) slower RT with late cueing (656.86 ms) in comparison to the no-cue control condition (605.70 ms). No other effects reached significance in RT.

The analysis of accuracy data showed a significant main effect of change type [$F(1,9)=17.76$, $p<.005$] and of cue type [$F(2,18)=19.05$, $p<.0005$]. The accuracy data replicated previous findings that conjunction detection is less accurate than feature detection (88% vs. 95%). An early cue significantly ($p<.01$) improved accuracy (95%) and the late cue significantly ($p<.05$) deteriorated accuracy (89%) in contrast to the no-cue condition (92%). There was a trend ($p<.1$) that an early cue improved accuracy in conjunction detection to a greater extent

Table 1 – Mean accuracy (% correct) and reaction time (RT in ms) in each condition

		No cue	Early cue	Late cue
Color change	Accuracy	95.7 $\pm$ 2.5	97.0 $\pm$ 2.2	93.6 $\pm$ 4.7
	RT	601.15 $\pm$ 46.56	561.70 $\pm$ 54.87	650.29 $\pm$ 54.29
Conjunction change	Accuracy	87.3 $\pm$ 5.1	92.9 $\pm$ 5.6	83.5 $\pm$ 7.3
	RT	610.25 $\pm$ 49.95	565.95 $\pm$ 58.17	663.44 $\pm$ 53.78

Fig. 1 – Areas of significant activation in contrast to the no-cue control condition associated with (a) early cueing and (b) late cueing. The results of each ROI analysis are shown in c; MFG: middle frontal gyrus, IPL: inferior parietal lobule, TPJ: temporoparietal junction.

than it benefited feature detection, perhaps because of a ceiling effect in detecting color changes without a spatial cue.

2.2. fMRI results

2.2.1. The main effect of the early cueing effect

In contrast to the no-cue control condition, greater activation was observed in two frontal regions of the right hemisphere in the early-cue condition (Fig. 1a, Table 2) when data were collapsed over feature and conjunction detection blocks. The two regions were the inferior frontal gyrus (IFG, Brodmann area (BA) 9/46, 46, 9) and the middle frontal gyrus (MFG, BAs 46/9, 46, 6, 9, 8).

2.2.2. The main effect of the late cueing effect

With data were collapsed over feature and conjunction detection blocks, greater activation was observed in the right posterior precuneus (PCu, BA 7) in the late-cue condition in contrast to the no-cue control condition (Fig. 1b, Table 2). Greater activation was also observed in the right inferior parietal lobule (IPL, BA 40) and the right temporoparietal junction (TPJ, BA 39). The whole brain analysis did not show any significant difference between the early- and late-cue conditions.

Table 2 – Brain areas and their Talairach coordinates in which significantly activated clusters were detected for the early cueing and late cueing effects

Brain regions		Early-cue minus no-cue condition					Late-cue minus no-cue condition			
	BA	x	y	z	t		x	y	z	t
Middle frontal gyrus	R 46/9	48	23	26	7.17					
	9	42	10	36	5.48					
	6	38	5	55	5.82					
	8	40	35	39	4.64					
Inferior frontal gyrus	R 9/46	46	13	27	7.35					
	46	51	26	15	6.77					
	9	57	7	27	5.6					
Precuneus	R 7						4	–67	49	6.40
Inferior parietal lobule	R 40						51	–49	39	6.13
Temporoparietal junction	R 39						48	–51	19	5.34

Note. BA: Brodmann area, t: t-value, L: left hemisphere, R: right hemisphere.

2.2.3. Regions of interest (ROI) results

In contrast to the no-cue control condition, the results from the whole brain analysis did not show a significant difference in the parietal regions for the early-cue condition and no significant difference in the frontal regions was observed in the late-cue condition. Given that the random effects analysis is strict (Göbel et al., 2004), the null results may have arisen from the use of only 10 participants. To better reveal the relative level of neural activation in the frontal and parietal regions among the three cueing conditions, we conducted an ROI analysis. As change detection requires regulation of multiple cognitive processes, the task should engage the frontal and parietal regions. The cue onset time should influence the relative dominance of frontal and parietal activation.

The ROI results showed a pattern of relative enhancement as expected (see Fig. 1c). The results from the paired t-test analyses showed that activation was significantly greater with early cueing than the no-cue control condition in the right MFG [$t(9)=3.70$, $p<.01$] and TPJ [$t(9)=3.33$, $p<.01$]. In contrast to the no-cue control, late cueing significantly increased activation in the right IPL [$t(9)=4.43$, $p<.005$] and the TPJ [$t(9)=3.68$, $p<.01$].

Table 3 – Brain areas and their Talairach coordinates in which significantly activated clusters were observed for feature detection

Brain regions		Early-cue minus no-cue condition					Late-cue minus no-cue condition			
	BA	x	y	z	t		x	y	z	t
Middle frontal gyrus	R 9	48	15	29	6.86					
	6	44	4	50	5.81					
Precuneus	R 7						10	–70	42	7.24
	L 7						–8	–72	37	6.56
Temporoparietal junction	R 39						48	–50	15	5.34
Cuneus	R 17						20	–68	7	5.17

Fig. 2 – Areas of significant activation associated with color detection under (a) early cueing and (b) late cueing in contrast to the no-cue control.

The difference in the right IPL was marginally significant [$t(9)=2.09$, $p<.07$] between the early- and late-cue conditions.

The results from the ROI analysis show that change detection without cueing involves the right MFG, IPL, and TPJ. The results converging from the whole brain analysis and the ROI analysis show that cueing increases activation in both cortices. Early cueing significantly increased activation in the right IFG, MFG, and TPJ when contrasted to the no-cue control. Late cueing significantly increased activation in the right IPL and TPJ in contrast to the control. The contrast between early and late cueing reveals a marginally significant difference in the right IPL.

2.2.4. Cueing effects on feature detection

In contrast to the no-cue control, the results showed greater activation in the right MFG (BAs 9 and 6) under early cueing. With late cueing, greater activation was observed in the bilateral PCu (BA 7), the right TPJ (BA 39), and the right cuneus (Cu, BA 17). Table 3 and Fig. 2 show the results.

2.2.5. Detecting conjunction changes

We examined the neural correlates of conjunction detection in contrast to feature detection (see Table 4 and Fig. 3). Greater activation was observed with a small cluster in the right PCu (BA 7) and the right cerebellum in the absence of spatial cueing. With early cueing, greater activation was observed in the anterior MFG (BA 46/10), left inferior frontal gyrus (IFG, BA 45), and the left STG (BA 22). With late cueing, greater activation was observed in the right MFG (BA 9), left IFG (BA 45), and the right IPL (BA 40).

3. Discussion

Cueing, which engages both top-down control and stimulus-driven orienting, indeed increased neural activation in the frontal and parietal regions in contrast to the no-cue control condition for change detection. As the prioritization-decision hypothesis predicted, an early cue engaged more activation in

Table 4 – Brain areas and their Talairach coordinates in which significantly activated clusters were observed for conjunction detection

Brain regions			No cueing					Early cueing				Late cueing			
		BA	x	y	z	t		x	y	z	t	x	y	z	t
Middle frontal gyrus	R	46/10						38	43	9	5.68				
		9										44	26	25	5.47
Inferior frontal gyrus	L	45						–48	21	3	5.62	–48	34	2	6.62
Precuneus	R	7	6	–68	46	5.62									
Inferior parietal lobule	R	40										51	–34	46	6.05
Superior temporal gyrus	L	22						–51	–8	–1	5.29				
Cerebellum	R		26	–66	–34	5.87									

the right MFG and IFG related to the top-down control and a late cue engaged greater activation in the right IPL and TPJ related to stimulus-driven orienting in contrast to the no-cue control.

When the decision was easy with feature detection, an early cue prioritized information transfer and maintenance in working memory. With effective top-down control and a high signal-to-noise ratio in the decision process based on the presence of two new colors, memory retrieval may not be necessary. Activation increased only in the right MFG in contrast to no-cue control. A late cue that occurred shortly before the test display disrupted the maintenance of multiple stimuli and shifted attention to the cued location. Memory retrieval of all the stimulus representations was engaged to identify which one was positioned at the cued location while the test stimuli were processed. In comparison with the no-cue control, a late cue increased activation in the right Cu related to feature processing and in the bilateral PCu associated with maintenance and retrieval of multiple stimuli.

Conjunction detection was more difficult than feature detection. When spatial cueing was not provided, maintenance and retrieval of all the stimulus representations at their respective locations in the initial display were important because all the colors remained the same in the test display. The right PCu and cerebellum showed greater activation. Given a difficult decision, an early cue prioritizes information processing through planning and sequencing the transfer, maintenance, retrieval, and decision processes. Planning was associated with the right MFG, sequencing was related to the left STG, and memory retrieval of the cued stimulus was linked to the left IFG. Late cueing instigated both top-down control and stimulus-driven orienting. Stimulus-driven orienting was related to the right IPL. Top-down regulation was associated with the right MFG, and memory retrieval of the cued representation was associated with the left IFG.

3.1. Top-down control and stimulus-driven attention orienting in change detection

Multiple stimuli must be encoded, maintained, and retrieved for comparison in a change detection task. Without spatial cueing, the top-down control would be required to regulate multiple cognitive processes over multiple stimuli. As expected, activation in the right MFG was observed. The right MFG has been linked to on-line organization of spatial working memory (see Goldman-Rakic, 1998) and higher-order executive processes including the manipulation of stimulus representations in spatial working memory (Glahn et al., 2002), the monitoring of an earlier selection in preparation for the next response (Petrides, 1998), selection to bias control over posterior regions (Curtis and D'Esposito, 2003; Rowe and Passingham, 2001), strategic organization of processes (Rypma and D'Esposito, 2003), and executive coordination (see Collette and Van der Linden, 2002 for a review). On-line organization and executive processes are all related to top-down attention control.

Change detection also requires stimulus-driven attention orienting. This bottom-up attention orienting may occur at the onset of the initial stimulus array and at the onset of the test stimulus array. Stimulus onset captures attention (Cole et al., 2003; Peterson et al., 2002) and the onset of the test display also shifts attention orienting between memory representations and current percepts. Thus, activation in the right IPL and TPJ was observed in the no-cue control condition. The capturing effects initiated by stimulus presentation are similar to various orienting processes investigated in the

Fig. 3 – Areas of significant activation associated with conjunction detection in contrast to color detection under (a) no-cue, (b) early cueing, and (c) late cueing conditions.

previous studies that also found greater activation in these two neural substrates.

The right IPL is associated with a shift of attention between spatial locations indicated by the presence of a predefined stimulus (Yantis et al., 2002). The finding of greater activation in the right IPL rather than in the SPL is consistent with Pessoa and Ungerleider's (2004) results. Pessoa and Ungerleider (2004) found greater activation in bilateral IPS for change detection when the attentional state was controlled. They suggested that the IPS subserves reactive attention in change detection. Stimulus-driven processes engage reactive attention. Greater activation in the IPS was observed during the visual search period for detecting a change in natural scenes (Huettel et al., 2001). Visual search requires stimulus-driven orienting. Nobre et al. (2004) also found greater activation in the IPS in the retro-cue condition in contrast to the pre-cue condition. The right IPL/IPS may support stimulus-driven attention orienting among multiple memory representations in the delay or among multiple test stimuli in change detection at the test. The right TPJ is also related to stimulus-driven attentional capture (Serences et al., 2005), directing attention to salient events (Astafiev et al., 2006), and stimulus-driven orienting to behaviorally relevant stimuli (Kincade et al., 2005).

Cueing, regardless of the onset time, increased neural activation in the right MFG which is related to the top-down control. However, the relative level of enhancement differed as a function of cue onset time. An early cue allowed a longer duration of top-down control during which executive processes could be performed for prioritization. In contrast to the no-cue control, early cueing significantly increased activation in the right IFG and MFG as revealed by the whole brain analysis. Late cueing increased activation in the region related to top-down control, but the enhancement was not significant even when individual variation in the location and magnitude of response was considered in the ROI analysis. These results should be replicated with a larger sample.

Both early and late cueing also increased activation in the right TPJ, which are associated with stimulus-driven attention orienting. Nevertheless, the increase in the right IPL was significant only with late cueing in contrast to the no-cue control condition. Moreover, the signal change in the IPL was marginally larger with late cueing than with early cueing in the ROI results. Stimulus-driven orienting appears to be stronger with late cueing than with early cueing as predicted by the prioritization-decision hypothesis. Although the early and late cues involved activation in the same regions, the relative level of activation enhancement differed.

3.2. Cueing effects on feature detection

The overall cueing effects on neural activation were based on the data from both feature-change and conjunction-change conditions. When the decision was easy in feature detection, prioritized transfer and maintenance of the cued color were sufficient to make the decision with early cueing. Maintenance in visuospatial working memory was correlated with activation in the right MFG (BAs 6 and 9) as these two areas are systematically activated by a large range of working memory tasks (see Wagner and Smith, 2003).

In the late-cue blocks, participants could not predict which stimulus would be cued and may have initially adopted a non-selective strategy to hold all the stimuli in memory (Gegenfurtner and Sperling, 1993). When the late cue occurred to disrupt maintenance, attention shifted to the cued location while all the stimuli were retrieved for identifying the cued representation in memory. The process may have still been ongoing when the test display was shown shortly after the late cue. Visual processing hence was engaged for perceptual analysis of the test display while memory retrieval continued. As a result, activation increased in the right TPJ associated with stimulus-driven orienting, in the right Cu related to perceptual analysis, and in bilateral posterior PCu linked to voluntary control of attention and memory retrieval.

Voluntary control of attention and memory retrieval is required in studies that investigate control of attention with predefined digits indicating whether participants should shift or hold attention (Shomstein and Yantis, 2006) because participants must recall the instruction related to the digit for the control of attention. The two processes are also involved in shifting attention in visual search and memory search (Makino et al., 2004), in the retrieval of episodic memory (Lundstrom et al., 2005; see Cavanna and Trimble, 2006 for a review), in the retrieval of spatial information from visual working memory (Mohr et al., 2006), in the recognition phase for both working memory and long-term memory tasks (Ranganath et al., 2003), and in the retrieval of a word from working memory (Cabeza et al., 2002; Koch et al., 2006). Activation in the posterior PCu is correlated with these tasks.

The results suggested that early cueing activated executive control processes for prioritization even when the decision was easy with feature changes. Late cueing appears to activate stimulus-driven visual processing and also maintenance and retrieval of multiple stimuli for easy decision. These neural activation patterns suggest that maintenance and retrieval of multiple stimuli may not occur when the decision is easy under effective top-down control with early cueing.

3.3. Detecting conjunction changes

As all the initial colors remain in the test display, the task of conjunction detection was more difficult than feature detection. Accurate detection requires maintenance and retrieval of precise color-location bindings in the stimulus display. The task demand on attention and memory retrieval was higher in conjunction detection than in feature detection. Activation in the right posterior PCu and cerebellum increased when contrasting the conjunction-detection blocks with the feature-detection blocks without spatial cueing. The association of the right cerebellum with attentional demand and memory retrieval is consistent with results from previous studies. Activation in the right cerebellum is sensitive to the level of task difficulty in a visual attention task (Tomasi et al., 2004). Activation in the right cerebellum has been shown to be involved in covert reorienting (Lepsien and Pollmann, 2002), attention to specific features (Allen et al., 1997), and processing of an infrequent visual target (Huettel et al., 2004). The right cerebellum is also sensitive to the load effect in retention and retrieval of a memory search task (Habeck et al., 2005) and to the load effect in retrieval (Cairo et al., 2004).

Taken together, the demand on attention and memory retrieval is relatively greater for conjunction detection in contrast to feature detection in the absence of spatial cueing. The results are consistent with the postulation that conjunction detection is more difficult than feature detection (Yeh et al., 2005) or that conjunction representations are vulnerable (Allen et al., 2006). The demand for retrieval of episodic information is hence larger than the demand imposed by feature detection.

When a spatial cue was presented in the delay period and also at test for a difficult decision, the cued representation was retrieved for comparison and decision. The retrieval process was associated with greater activation in the left IFG for conjunction detection regardless of the cue onset time. The retrieval and comparison based on a specific item are required in memory tasks especially when detailed information must be retrieved and compared. Thus, activation in the left IFG has been associated with many long-term memory tasks such as accurate judgment of recognition success when failing to recall (Kikyo and Miyashita, 2004), correct recognition of faces (Leube et al., 2003), and recall production (Cabeza et al., 2003). The IFG region with enhanced activation in our study is in the vicinity of the regions that relate to the retrieval of source memory based on episodic information (Dobbins et al., 2002; Dobbins and Wagner, 2005). The left IFG was also associated with tasks that involved retrieval from working memory such as matching two dot matrices that were successively presented with a delay of 4 s (Suchan et al., 2002) or recognition of a probe 7.4 s after three consecutive presentations of non-natural objects (Bledowski et al., 2006). This finding highlights that an episodic trace of the cued stimulus was retrieved for conjunction detection.

The locus of the MFG engaged by cueing for conjunction detection differed as a function of cue onset time. Although both early and late cueing engage top-down control regulation, the control process differs as function of cue onset time when the decision is difficult. With a short period for the late cue to effect selection and prioritization, planning and sequencing of processing are unlikely. As a result, late cueing increased activation in the right BA 9 of the MFG that has been associated with manipulation in working memory. Planning and sequencing are more likely to occur with an early cue to prioritize information transfer, maintenance, retrieval, and comparison for top-down regulation. Activation increased in the anterior portion at the border with the BA 10 area of the MFG. This finding is consistent with the results of previous studies in which coordination of two or more processes is required. In a review, Fletcher and Henson (2001) highlighted the function of the anterior frontal region (BAs 8 and 10) in coordinating and monitoring self-generated information such as processes or goals. Ramnani and Owen (2004) suggested that the frontal pole (BA 10) is related to the integration of the outcomes of two or more separate cognitive operations in achieving a behavioral goal. Indeed, the outcome of two separate cognitive operations must be integrated in planning to utilize the early spatial cue and benefit performance. The first operation is the processing of the early cue, and the second operation is to retrieve what is at the cued location in the initial stimulus array. Both outcomes are self-generated information related to the behavioral goal.

In addition to the common regions in the left IFG and right MFG, early and late cueing increased activation in different posterior regions for conjunction detection. The late cueing increased activation in the right IPL related to stimulus-driven attention orienting. In contrast, early cueing can prioritize information processing through planning and sequencing. It is likely that the left BA 22 of STG/STS is related to the sequencing. Sequencing is required in tasks that demand reasoning as reasoning often involves step-by-step mental hypothesis testing. Thus, greater activation in the left BA 22 as a part of a network has been associated with syllogism reasoning (Goel et al., 1998), analogical reasoning (Luo et al., 2003), and goal attribution (Schultz et al., 2004).

The results suggested that cueing engaged retrieval of episodic information and top-down control for conjunction detection. Early cueing engaged top-down control in coordinating and regulative reasoning of internal information related to the behavioral goal. Late cueing activated manipulation in working memory and engaged more stimulus-driven orienting for conjunction detection in contrast to feature detection.

3.4. Two types of memory retrieval: an unresolved issue

We postulated that maintenance and retrieval of multiple stimuli are required in conjunction detection without cueing and also in feature detection with late cueing. Activation in the right posterior PCu was associated with change detection in these two contexts. We also postulated that the cued representation was retrieved for comparison when a spatial cue was presented for the difficult decision in conjunction detection. Activation in the left IFG increased in this context regardless of the cue onset time.

Activation in both the posterior PCu and the left IFG is associated with retrieval of episodic memory in the paradigms that investigate long-term memory. The results obtained from this study highlight two questions that need to be addressed in future research: the continuity of retrieval processes recruited in working memory and long-term memory, and the possible functional dissociation between the posterior PCu and IFG in memory retrieval. Several studies have investigated the first issue. Using a working memory paradigm with an immediate test, Mitchell et al. (2004) found that source judgment of the format (picture or word) and location (on the right or left of the screen) was associated with the left prefrontal cortex (PFC) including the MFG and IFG as observed in previous long-term memory studies. This finding supports the continuity of the evaluative process with the left PFC recruited when the task requires retrieval and monitoring of specific features (Mitchell et al., 2004). Similar findings can be observed for episodic retrieval of words and recognition of a test word based on working memory (Cabeza et al., 2002). Commonalities and differences are also found among different memory tasks. Activation in the left PCu and the right fronto-polar cortex was associated with working memory tasks and cued recall of words (Nyberg et al., 2002). Activation in bilateral PCu increased during the recognition phase of both a working memory and a long-term memory task (Ranganath et al., 2003). The similarity in neural mechanisms suggests that working memory and

episodic-memory retrieval share a processing component (Koch et al., 2006).

To our knowledge, no prior study has specifically addressed the second issue of possible functional dissociation between the IFG and posterior PCu in memory retrieval. We postulated that the demand of maintenance and retrieval of multiple stimuli increases activation in the posterior PCu and the demand of retrieving the cued representation increases activation in the IFG in our study. As retrieval of the cued representation requires retrieval and monitoring of a specific item, the finding is consistent with the suggestion that the left PFC is likely to be recruited when the task requires retrieval and monitoring of specific features (Mitchell et al., 2004). The delayed-matching-sample task used in Suchan et al.'s (2002) study also required retrieval of detailed information because the second dot matrix was either identical to the first matrix or differed by one dot. The finding of the left IFG in a study of working memory retrieval (Bledowski et al., 2006) also provides support for the retrieval of a specific stimulus. In this study, load was manipulated so that either one non-natural object or three consecutive objects were presented for later recognition. During working memory retrieval, greater activation was observed in the left IFG when contrasting the load three versus the load one conditions.

The results of previous studies on working memory do not fully support our postulation that the posterior PCu is associated with the maintenance and retrieval of multiple stimuli in working memory. Consistent with our postulation are the studies that use multiple items in a working memory task and found enhanced activation in the posterior PCu, such as presenting four words (Cabeza et al., 2002), four pairs of consonants (Koch et al., 2006), or two rotated half circles for

computing the intermediate angle (Mohr et al., 2006). The 2-back task and the random number generation task also require maintenance and retrieval of multiple stimuli. Greater activation in the PCu was observed for both tasks (Nyberg et al., 2002). Yet, activation in the posterior PCu also increased in face recognition when only one face was required to be maintained during a delay period of 7 s (Ranganath et al., 2003). Given that face recognition may require fine discrimination, the posterior PCu may be related to memory retrieval when inter-item interference is strong and voluntary attention is demanded. Inter-item interference is strong with the maintenance and retrieval of multiple stimuli. Future research may verify this hypothesis as research that reveals the possible roles of attention in memory should be of importance (see Wagner et al., 2005 for a review).

4. Experimental procedures

4.1. Participants

Ten right-handed volunteers (half female) aged 21 to 25 (mean age = 23.5 ± 1.27 years) were recruited from Chang Gung University. All participants were healthy and without any neurological or psychiatric history. Informed written consent was obtained from all participants prior to the study, the nature of which was fully explained.

4.2. Stimuli and task

Fig. 4 shows an example of stimulus arrays. Stimulus arrays were composed of four colored squares randomly selected from a set of six colors: red, green, blue, yellow, cyan, and

Fig. 4 – An example of (a) an early cue in the color-change condition, (b) a late cue in the conjunction-change condition, and (c) an example of condition counterbalance in a quartile. There were four quartiles in each run.

magenta. Each stimulus extended approximately $0.52^\circ \times 0.52^\circ$ and was positioned randomly in one of the eight possible peripheral locations of an invisible 3×3 matrix that extended approximately $6.2^\circ \times 6.2^\circ$. An initial stimulus array was first presented, and a second display of the stimulus array was presented after a retention interval. The participants' task was to detect whether there was any change between the two arrays. In the feature-change condition, two new colors that were not used in the initial array replaced the old ones. In the conjunction-change condition, two stimuli switched position so that correct detection required accurate binding of color and location. The two changed items were randomly selected from the four stimuli on each trial. There were two changes in the feature-change and in the conjunction-change conditions. A gray background was used throughout the whole experiment.

When a spatial cue was presented during the retention interval, a white line pointed to the upper left corner of a stimulus location and remained on screen until the participant responded. When the two arrays were identical in the no-change trials, this cued position was randomly selected from the four stimulus locations. In the change trials, the cued position was randomly selected from the two locations where changes would occur. Participants were told that the spatial cue indicated the location a change would occur in the change trials and were encouraged to use the cue. With the cue, participants could simply judge whether there was any change in the cued test item from the stimulus at that location in the initial display. Although two stimuli of a test array differed from the initial array in a change trial (two new colors or two stimuli switched position), the cueing effects with one spatial cue were similar to the effects with two cues (Yeh et al., 2005). Fig. 3a shows an example of a feature-change condition with an early cue; Fig. 3b shows an example of a conjunction-change condition with a late cue.

4.3. Design and procedure

To replicate the behavioral experiments in Wheeler and Treisman's (2002) and Yeh et al.'s (2005) studies, a blocked design was adopted. In a blocked design, the type of change is constant with either feature changes or conjunction changes. In the feature-change block, the change trials always consisted of test displays with two new colors replacing the old ones. In the conjunction-change block, the change trials always consisted of switching two objects in the stimulus arrays. In each block, half of the trials were no-change trials and the other half consisted of change trials. Change and no-change trials were randomly mixed in each block. Ten practice trials were conducted for each condition prior to scanning, and participants could easily identify the cueing time and change type in each block. With this knowledge, they could adjust the attentional set according to the task demand in each block.

The experiment consisted of two runs in which the whole brain was scanned. The cue onset time was manipulated between runs. Half of the participants performed the early-cue run first before performing the late-cue run; the order was reversed for the other half. There were 16 blocks in each run, divided into four quartiles. Within each quartile, there were

four blocks from the 2 (presence or absence of cue) $\times$ 2 (change type) design. A Latin-square design was used to counter-balance the order of the four blocks in each quartile. Each condition in a block consisted of ten trials, with random presentation of five trials with changes and five trials without change.

In the two blocks where a spatial cue was presented, the cue always pointed to the location a change would occur in the change trials and to a random object in the no-change trials. This manipulation of cueing had been shown to affect detection performance (Yeh et al., 2005). To separate conditions and allow participants to rest, participants viewed a fixation cross for 6 s after completing each block. Fig. 3c shows the schematic diagram of a quartile.

Each trial began with a 900 ms fixation cross (see Fig. 3) positioned in the center of the screen. An initial display of four colored squares was presented for 180 ms. Following a retention interval of 900 ms, a test display of four colored squares appeared for 1020 ms during which participants judged whether there was any change in the test array as compared to the initial stimulus array. Participants pressed the left button of a response box with the index finger of their right hand for a yes response and pressed the right button with the middle finger of their right hand for a no response.

The spatial cue in the early-cue block was presented 200 ms after the offset of the initial stimulus display. Thus, participants had 700 ms to rehearse and maintain the cued representation before the test display was shown. The spatial cue was presented 800 ms after the offset of the initial stimulus display in the late-cue run. As a result, participants had only 100 ms to process the cue and to initiate the selection process before the test display was presented. Participants were instructed to respond as accurately and as quickly as possible.

4.4. fMRI scanning and imaging data processing

The experiment was run on a 1.5-T Magnetom Vision MRI scanner (Siemens, Erlangen, Germany) at the Chang Gung Memorial Hospital. The stimuli were visually presented on a goggle display system (Resonance Technology Inc., CA, USA). Both eyes were corrected to normal visual acuity with lenses during the experiments. The participant's head was restrained in a molded plastic facial mask to reduce motion during the scan. A single-shot T2*-weighted gradient echo echo-planar imaging (EPI) sequence (TR=3000 ms, TE=60 ms, flip angle=90°) was used for BOLD imaging. Twenty-four slices were acquired with a slice thickness of 5 mm to cover the whole brain (matrix size=64 $\times$ 64, and in-plane resolution=3 mm $\times$ 3 mm). During each run, 192 images per slice were obtained with a total time of 576 s. The anatomical MRI was acquired using a T1-weighted, 3D gradient-echo pulse sequence, which provided images of high resolution (1 mm $\times$ 1 mm $\times$ 1 mm) for the entire brain.

The fMRI data were analyzed using the SPM99 software (Wellcome Department of Cognitive Neurology, London, UK) in MATLAB 6.0 (MathWorks, Inc., Natick, MA, USA). The first two scans of EPI series were excluded from further processing to minimize the transit effects of hemodynamic responses, and the remaining functional images were corrected for each

participant's motion with sinc interpolation. The realigned images were then normalized into the standard SPM/MNI template and thus transformed into a standard stereotaxic space and resampled with a resolution of $2 \times 2 \times 2$ mm³. A Gaussian filter of 10-mm full width at half maximum (FWHM) was then applied to smooth the data spatially, to accommodate for anatomical variability across subjects, as well as to satisfy the assumptions of Gaussian field theory (Worsley et al., 1996). The box-car function convolved with the canonical hemodynamic response function was used to identify significant activated voxels. The data were then high-pass filtered with a cut-off period of 144 s to remove low frequency drifts in the BOLD signals.

The subject-level statistical analyses were performed using the general linear model for blocked designs. Linear contrasts of interest were constructed to obtain subject-specific estimates of cueing-related activity for the following main effects: (1) the overall cueing effect minus the no-cue condition, (2) the early-cue condition minus the no-cue condition, (3) the late-cue condition minus the no-cue condition. In addition, linear contrasts were also constructed in the whole brain analysis to examine the neural correlates associated with change detection for the following comparisons: (1) feature detection with early cueing minus feature detection without cueing, (2) feature detection with late cueing minus feature detection without cueing, (3) conjunction detection minus feature detection without cueing, (4) conjunction detection minus feature detection in the early-cue run, and (5) conjunction detection minus feature detection in the late-cue run. These estimates for contrasts were then entered into a standard SPM second-level analysis with subject treated as a random effect using a one-sample *t*-test. The expected mean difference value for the *t*-tests was set to zero. A voxelwise intensity threshold ($p < .001$) and a spatial extent threshold (cluster size greater than 27 voxels) were combined to control for multiple comparisons (Forman et al., 1995; Poline et al., 1997). All significant activated areas were transformed into Talairach space (Talairach and Tournoux, 1988). Anatomical labels (lobes and gyri) and the Brodmann area (BA) of the local maxima of the activated clusters were determined using a 3D electronic brain atlas (Lancaster et al., 1997).

Because the random effect analysis is a strict and conservative test (e.g., Göbel et al., 2004), ROI analyses were then conducted using the Russell Poldrack's SPM ROI Toolbox (<http://sourceforge.net/projects/spm-toolbox>) to investigate the relative level of neural activation among the no-cue control, early cueing, and the late cueing condition. On the basis of the cueing-related activation areas derived from the overall data collapsed from the early and late cueing blocks, the right MFG ($x=40, y=15, z=31$), IPL ($x=51, y=-49, z=39$), and TPJ ($x=51, y=-46, z=18$) were functionally determined as ROIs. We defined the size of each ROI as a sphere with the center at the peak of activation with a radius of 10 mm. For each participant, the adjusted raw data of the ROI were extracted for all task conditions using the SPM ROI toolbox. The mean BOLD signal changes of the early-cue, late-cue, and no-cue conditions were then computed for each participant in paired *t*-test analyses to evaluate the statistical significance of the difference in each ROI.

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