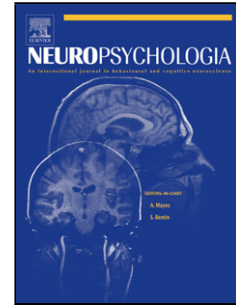


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Encoding strategy accounts for individual differences in change detection measures of VSTM.

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Abstract

Visual short-term memory (VSTM) capacity is often assessed using change detection tasks, and individual differences in performance have been shown to predict cognitive aptitudes across a range of domains in children and adults. We recently showed that intelligence correlates with an attentional component necessary for change detection rather than with memory capacity per se (Cusack, Lehmann, Veldsman, & Mitchell, 2009). It remained unclear, however, whether different attentional strategies during change detection have most impact during the encoding or maintenance of information. Here we present recent findings from our laboratory supporting the hypothesis that attentional selection during encoding dominates individual differences in change detection measures of visual short-term memory.

In a first study, we unpredictably varied whether short-term memory was probed using change detection or whole report, encouraging participants to adopt the same encoding strategy throughout the tasks. Change detection performance of lower-IQ individuals improved. In a second study, we found that deficits in top-down attentional selectivity can be alleviated in participants with low change detection performance by providing helpful grouping information during encoding. Finally, a meta-analysis of neuroimaging data from 112 participants performing a variety of VSTM tasks showed that performance correlates with activity in several parietal and frontal regions during the encoding but not the maintenance phase. Taken together, these results support the notion that encoding strategy and not short-term memory capacity itself largely determines individual differences in visual change detection performance.

Keywords

visual short-term memory; memory capacity; individual differences; selective attention; IQ

1. Introduction

Individual differences in visual short-term memory have been a popular topic in both behavioural and neuroimaging research. One reason for this is the link between visual short-term memory (VSTM) capacity and intelligence. Numerous studies have shown that the two are highly related (e.g. Kyllonen, & Christal, 1990) but not identical (Ackerman, Beier, & Boyle, 2005; Conway, Kane, & Engle, 2003). However, it is less clear what factors cause individuals to differ in their performance in VSTM tasks and measures of intelligence.

Two distinct paradigms are often used to measure VSTM. In both, an encoding display containing the items to be memorized is followed by a maintenance delay. The paradigms differ in how memory is then assessed. In change detection (CD), a probe is presented and participants are asked to decide whether it is the same or different from the corresponding stimulus during encoding. In report tasks, participants have to report the stimuli they remember – if the items are letters for instance, by saying them or typing them in. Report tasks in which only a subset of items has to be remembered, are referred to as “partial report” (PR), while tasks in which all items have to be remembered are known as “whole report” (WR) tasks. In a recent study, we found that the relationship between VSTM performance and intelligence was dependent largely on whether individuals were assessed using CD or WR (Cusack, Lehmann, Veldsman, & Mitchell, 2009). WR performance increased with load, peaking at a set-size of 4 and staying constant as set-size increased further. CD estimates of the number of items in memory also peaked at set-size 4, but thereafter showed a marked dip as load increased. Importantly, IQ correlated with the size of this dip but not with VSTM capacity (as measured by $K = N*(H-FA)$, where N = number of items in set, H = proportion of hits, FA = proportion of false alarms; Cowan 2001). This indicates that an additional cognitive process during change detection underlies the relationship between intelligence and VSTM capacity.

Numerous researchers (e.g. Heitz, Redick, Hambrick, Kane, Conway, & Engle, 2006; Jarrold, & Towse, 2006; Kane, & Engle, 2002) have suggested that selective attention is the driving factor that determines VSTM capacity as well as performance in cognitively demanding tasks such as assessments of IQ. Engle (2002) for instance argues that working memory is a manifestation of attentional capabilities, which in turn correlate with intelligence. We therefore suggested that lower-IQ participants adopted suboptimal attentional selection during the encoding phase of the CD task, attempting to encode everything instead of selecting a manageable subset of items,

thus making the memory representations more fragile. Importantly, WR assessments of VSTM appear to foster a more selective encoding strategy such that differences between low and high performing participants are diminished.

The first two studies presented in this paper provide further support for this hypothesis by showing that individual differences in encoding strategy dominate CD measures of VSTM and can be alleviated by encouraging more selection during encoding. It remained unclear, however, whether this impact of attentional selection only determines which items are encoded or also has an impact on how individuals maintain this information in short-term memory. We, therefore, drew upon results from five different neuroimaging studies conducted in our laboratory to investigate the link between VSTM capacity as measured by CD and activity in regions of the brain that are commonly activated by short-term memory and cognitively demanding tasks.

From previous neuroimaging studies, it is clear that the brain networks activated by attention and short-term memory are very similar (Awh, & Jonides, 2001; LaBar, Gitelman, Parrish, & Mesulam, 1999; Mayer, Bittner, Nikolic, Bledowski, Goebel, & Linden, 2007). Duncan and Owen (2000) for instance have shown that some regions are activated by cognitively demanding tasks irrespective of the precise nature of the task. Posterior parietal cortex is one of the regions that reliably reflects the amount of information held in short-term memory (Todd, & Marois, 2004, 2005) but how far this activation is purely memory-specific is hard to disentangle. In attentional and perceptual tasks drawing upon similar stimuli to those often used in change detection tasks, Mitchell and Cusack (2008) showed that posterior parietal cortex responded in the same load dependent manner as during memory tasks. Additionally, numerous studies have found correlations between the ability to control attention and short-term memory capacity (e.g. Awh, & Jonides, 2001; Kane, Bleckley, Conway, & Engle, 2001; Bleckley, Durso, Crutchfield, Engle, & Khanna, 2003). In a neuroimaging study, Linden et al. (2003) showed that limits in attention seemed to be the constraining factor for short-term memory capacity, but how and when attention influenced memory performance remained unclear. Kane and Engle (2002) argue that memory capacity is determined by demands on executive attention during the maintenance of information in the face of potential interference. Similarly, Curtis and D'Esposito (2003) suggest that activity of dorsolateral prefrontal cortex (DLPFC) during the maintenance phase of memory tasks reflects top-down direction of attention to control rehearsal of information in memory. On the other hand, Vogel, McCollough and Machizawa (2005) suggest that differences in VSTM capacity relate to efficiency of attentional selection during encoding, with high capacity

individuals being better at selecting the relevant information to remember. This has also been endorsed by McNab and Klingberg (2008) and Edin and colleagues (Edin, Klingberg, Johansson, McNab, Tegner, & Compte, 2009) whose findings suggest attentional selection acts as a gatekeeper to short-term memory by selecting only the most relevant items during encoding (also see Awh, Vogel, & Oh, 2006). They showed that the middle frontal gyrus, globus pallidus and basal ganglia serve attentional control functions that regulate which information is passed on for storage in short-term memory. Individual differences in VSTM capacity, thus, seem to arise from different abilities to filter relevant information in these frontal and subcortical regions before they are maintained in short-term memory by parietal cortex.

In this paper we present two new behavioural experiments to probe the link between attentional processes at encoding and performance on change detection and whole report tasks. We then examine individual differences across a set of neuroimaging experiments from our laboratory that have allowed separate modelling of neural activity during encoding and maintenance. Specifically, we test for a relationship between change detection performance and magnitude of activity in different regions of interest (ROIs) in the two task phases. Our results confirm the hypothesis that individual differences in VSTM capacity as measured by change detection tasks are related to different attentional strategies used during encoding, with lower-IQ participants adopting a suboptimal strategy of trying to encode all stimuli even when the information presented clearly exceeds their capacity limits.

2. Experiments

< Table 1 about here >

2.1 Behavioural experiments

2.1.1 Blocked vs. intermixed probes

In the first experiment we tested the hypothesis that attentional selection during encoding influences change detection measures of VSTM capacity. Cusack et al. (2009) found that CD

measures of VSTM were contaminated by some cognitive process that depressed performance at higher set-sizes, so that fewer items were remembered when eight were presented than when just four were presented. Measuring VSTM using WR gave an estimate that was higher and less variable, particularly for larger set-sizes. No evidence was found for a relationship between non-verbal IQ and this estimate of VSTM capacity. Instead IQ was correlated with an additional factor that contaminated change detection estimates.

An issue that was not fully resolved is what process was disrupted during change detection. One possibility (favoured in Cusack et al., 2009) is that change detection encourages a maladaptive strategy *at encoding* of trying to remember everything, particularly in lower-IQ individuals. However, another possibility that must be considered is that the presentation of the *probe* in change detection could disrupt memory recall. To explain the pattern of results in that paper, probe interference would have to be more severe at higher set-sizes. It might be, for example, that when a greater number of items are presented, the memory traces created for each item are weaker, and hence more easily disrupted by the subsequent probe display.

The aim of the current experiment was to investigate this issue, by identifying the portion of a change detection task that suffers at higher set-sizes, particularly in those with lower IQ: is it the way items are encoded, or the nature of the probe? To do this, we repeated the comparison between CD and WR, but in two different contexts. In one, as in Cusack et al. (2009), we presented CD and WR in two different blocks. This allowed for adaptation of encoding strategy. In a second pair of blocks, which were identical to each other, we randomly intermixed the CD and WR trials. In this case, there could be no difference in encoding strategy, as the volunteer did not discover until the probe phase of each trial what response task was required. Any residual difference between the two trial types when they were intermixed had to be due to effects at probe. Additional effects between blocked and intermixed trials had to be due to strategic differences, presumably at encoding.

Method

Since Cusack et al. (2009) found substantial differences between WR and CD performance in a lower-IQ group only, 16 participants (13 female, 22-61 years old, $M = 53$, $SD = 12.0$) with low non-verbal intelligence ($M = 30.1$, $SD = 2.7$, as estimated using Cattell's Culture Fair Test), were selected from a previous larger study ($N = 61$, 21-64 years old, $M = 47$, $SD = 12.97$, grouped into a high and low IQ group by median-split) to directly assess whether performance could be

improved in these participants. Mean age in this sample was high as participants were recruited during the summer and not from the typical student population. Each participant completed four blocks. In one of the four blocks, all of the trials were CD; in another block, they were all WR; and in two of the blocks, equal numbers of WR and CD trials were randomly intermixed. As in Cusack et al. (2009), the WR and CD procedures were closely matched. Identical encoding displays were presented, with set-sizes of 2, 3, 4, 6 or 8 letters, followed by a 1200ms maintenance period. The encoding displays were presented for 183ms, the screen background was mid-grey, letters were randomly chosen from the set ABDEFGHJKMNQRTY, and their colour (black or white) was randomized. Letters were presented in upper case Arial with height $\sim 3.8^\circ$ visual angle at a location randomised within a rectangle $\sim 28^\circ$ by 37° visual angle centred at the middle of the screen, subject to the constraint that the centres of two letters could not be closer than $\sim 6.7^\circ$. In the WR task, after the delay period a box appeared and participants were asked to type all the letters they remembered using a standard keyboard and then press "Enter". The next trial did not commence until a response had been made. In the CD task, a probe display was presented that comprised a single letter at the location of one of the letters in the encoding display (chosen at random), and participants were asked to press one of two buttons to indicate whether the probe letter had been present anywhere during encoding, irrespective of location. There was a 50% chance that it had been present. As for the WR task, a response could be made at any point after the onset of the probe display and the next trial began right after the response had been made. The button mapping was counterbalanced across participants. Five of the participants, performed longer sessions comprising 960 trials in total (96 trials/set size/task) and the remaining 11 participants completed 480 trials in total (48 trials/set size/task). Blocks and trial types within each block were fully randomised. Approval for the experiment was given by the Cambridge Psychological Research Ethics Committee.

Analysis

The number of items remembered at each set-size was estimated for each procedure, correcting for guessing. To calculate the number of letters remembered in the CD tasks, a double-high-threshold model was used, which assumes that K_{CD} items were remembered perfectly and the remainder were guessed ($K_{CD} = N \cdot (H - FA)$ where N = number of items in set, H = proportion of hits, FA = proportion of false alarms; Cowan 2001). To calculate the number of letters remembered in the WR trials, the number of letters correctly reported was counted and from this subtracted an estimate of the guessing rate. This used the conservative assumption that the participants had learnt the subset of 15 letters that could appear in the stimuli (hence

possibly overestimating the guessing rate and slightly underestimating capacity): $K_{WR} = C - E \cdot N / (15 - N)$ where E = number of letters reported that were not in the display, C = correctly reported letters. The data were submitted to a three-way repeated measures ANOVA, with factors context (blocked, intermixed), task (WR, CD) and set-size (5 levels) to investigate the effect of intermixing probes on performance K . This was followed by post-hoc analysis of the significant effects of interest.

Results

Figure 1 shows the estimates of the number of items remembered (K) as a function of set-size for the two tasks (WR, CD) in the two different contexts (blocked, intermixed).

All main effects were significant with people performing significantly worse in blocked vs. mixed trials ($F(1, 15) = 13.142, p < .005$) and in CD vs. WR tasks ($F(1, 15) = 29.893, p < .001$). Furthermore, the main effect of set-size was significant ($F(4, 60) = 26.008, p < .001$) but this was expected given that K is dependent on the set-size. Additionally, the interaction between context and task ($F(1, 15) = 12.546, p < .005$) and the three-way interaction between context, task and set-size were significant ($F(4, 60) = 3.432, p < .05$).

Importantly, subsequent post-hoc analyses¹ revealed that our results replicated Cusack et al. (2009). When presented in separate blocks, performance for CD (as measured by K) was much worse than for WR (WR vs. CD, $t(15) = 5.771, p < .001$ across set-sizes; individual set-sizes 3,4,6,8, $p < .01$). Furthermore, there was a distinct drop-off in the number of items remembered in CD at higher set-sizes (CD set-size 4 vs. 8, $t(15) = 2.376, p < .05$; 4 vs. 6, $t(15) = 2.106, p = .052$).

Furthermore, intermixing CD with WR actually improved performance in the CD task (CD-Mix vs. CD, $t(15) = 3.711, p < .005$ across set sizes; individual set sizes: 3, 6, $p < .05$; 8, $p = .051$). In the absence of strategic adjustments, it might be expected that the requirement for task switching on a trial-to-trial basis would make performance worse, and so the reverse effect is impressive. This is consistent with a more selective strategy on CD trials as a result of a context in which WR must sometimes be performed. There was only a little cost to WR when mixed with CD (WR vs. WR-Mix, $t(15) = 1.375, p = 0.19$ across set sizes; individual set-size 8, $p < .005$).

¹ Paired samples t-tests, two-tailed significance values reported

< Figure 1 about here >

Lastly, mixing trials did not abolish all of the difference between WR and CD (WR-Mix vs. – CD-Mix, $t(15) = 2.846$, $p < 0.05$ across set-sized; individual set-sizes 3 & 4, $p < 0.05$). This suggests that even when encoding strategies are matched across WR and CD, there remains some effect of the probe method. This might be due to an interference effect of the probe display on memory in CD. Alternatively, it might be some artefact associated more specifically with the response production.

Discussion

These results concur with our previous finding, and show that how items are encoded has a strong influence on how well people perform in a change detection task. In agreement with Vogel, McCollough and Machizawa (2005) and McNab and Klingberg (2008), we have previously hypothesized that the efficiency of attentional selection, namely whether an individual tries to encode all stimuli at once or selects a few, determines change detection performance and is related to intelligence. We have explored this by unpredictably probing participants either using WR or CD, but we can also obtain converging evidence by instructing participants to encode only a subset of the presented stimuli. In the next experiment we therefore used a partial report task and provided bottom-up grouping cues to manipulate the difficulty of attentional selection.

2.1.2 Manipulating the difficulty of attentional selection in PR

We previously found that whole report tasks provided a less variable estimate of VSTM capacity than change detection and hypothesized that this was because of differences in attentional selection. In order to test whether individuals differ in the attentional strategy they use during CD but not WR, we needed to compare performance in these two tasks to performance in a third task that directly manipulated attentional selection. A common way to control and measure attentional selection in this context is to use a partial report (PR) task (e.g. Bundesen, Pedersen, & Larsen, 1984; Duncan, Bundesen, Chavda, Olson, Humphreys, & Shibuya, 1999; Peers et al., 2005; Sperling, 1960). To this end, we asked participants to remember only some of the items in the display (target letters defined by case) while ignoring simultaneously

presented distracters (letters of the opposite case). This imposed an explicit requirement for selection and should, therefore, be impacted by individual differences in attention. Additionally, we manipulated selection difficulty by providing salient bottom-up grouping cues, which were either congruent (helpful grouping) or incongruent (unhelpful grouping) with the top-down task instructions (see Table 1, second row).

Bottom-up grouping of stimuli presented during a VSTM task will bias attentional selection towards encoding the items that are grouped together (Woodman, Vecera, & Luck, 2003). In particular for individuals who do not naturally draw upon a selective attentional strategy to encode information into short-term memory, helpful bottom-up grouping should, thus, improve performance considerably. According to our hypothesis, the CD but not the WR measure is contaminated by variability in selection efficiency. We were, therefore, interested in how bottom-up grouping affected the PR performance of participants with high and low VSTM capacity as assessed by the CD vs. the WR task. Importantly, we could make different predictions for the effect of grouping depending on whether we split participants based on their performance in the WR or CD task. If attentional selection dominates CD but not WR measures of VSTM, any effect of manipulating selection difficulty should be larger for participants performing badly in the CD task than for participants performing badly in the WR task. Specifically, we predict that participants with a low CD estimate of VSTM capacity will benefit most from clear guidance as to which items they have to encode.

Method

Sixteen participants were tested, of whom 11 were female. Ages ranged between 20 and 58 years with a mean of 36.3 ($SD = 15.0$). Participants were chosen on the basis of a previous experiment, which screened people using the change detection task described below. Two groups of eight participants whose VSTM capacity was low and high, respectively were selected from the entire group ($N = 80$, separated into high and low capacity by a median-split). The two groups did not differ in their mean age ($t(14) = 1.78$, $p = .097$; low: $M = 42.5$, $SD = 15.4$, 23-58 years, 6 female; high: $M = 30.0$, $SD = 12.5$, 20-57 years, 5 female) or gender distribution.

During the change detection task, participants were shown a variable (1, 2, 3, 4, 6, or 8) number of coloured discs for 150ms. After a 1200ms memory interval, one of the original discs was probed. It either remained unchanged or was replaced by a different colour (chosen randomly) in 50% of trials. Participants completed 12 trials per condition, resulting in 72 trials in total, with

order randomized and counterbalanced with Change/No Change trials. The colour and position of the probed item was selected at random on each trial. The colour change detection task was flanked by a verbal short-term memory test on two spoken digits, to minimise verbal recoding of the colours (Luck, & Vogel, 1997). The probe remained on the screen until the response was made (first for the colour and then for the number response) and the next trial started after a 500ms ITI. Given the small number of trials, rather than estimating VSTM capacity as the maximum K (Cowan, 2001) across all set-sizes, we estimated K at each set-size and then averaged across all set-sizes to get mean K . Note that this estimate is affected by both true capacity and the performance decrease at higher set sizes (Cusack et al., 2009).

In the WR task, we presented participants with briefly displayed arrays of letters (either white or black) for 183ms. The configuration and parameters of the stimulus display were identical to those described in the experiment above (2.1.1). Participants were asked to attend selectively to letters of either lower or upper case only (“targets”) and to report the letters they had seen by typing them on a keyboard immediately after the stimulus display had disappeared. Response was self-paced and the next trial started immediately after a response had been made. Letters were chosen randomly with the constraint that they could not be repeated in the same trial. Three different types of arrays were presented: two arrays displaying either 3 target letters (WR, low load; 3T), or 6 target letters (WR, high load; 6T) alone or an array presenting 3 target letters together with 3 distracters of the opposite letter case (PR; 3T3D). In addition, we modulated the presentation of the letters in the different conditions, such that two groups were formed by their coherent motion and colour. The effect of interest was in the partial report trials, where the grouping could be either “helpful” (by grouping the targets and distracters separately) or “unhelpful” (by grouping 2 targets/distracters with 1 distracter/target). We estimated VSTM capacity using the K_{WR} measure as described in the experiment above (2.1.1). Participants completed five blocks. In each block 18 trials per condition (3T, 6T, 3T3D (none), 3T3D (helpful), 3T3D (unhelpful)) were presented in random order, yielding a total of 90 trials per condition. Approval for the experiment was given by the Cambridge Psychological Research Ethics Committee.

Results

We expected that bottom-up grouping should affect individuals performing badly in the CD and WR task to different extents. We therefore correlated memory capacity (K_{CD} and K_{WR}) with the effect of grouping, as measured by the difference between K in the helpful and unhelpful PR

conditions. This revealed a strong negative correlation of K_{CD} with grouping (Spearman: $\rho = -.811$, $p < .001$). It is notable that the extent to which bottom-up grouping affects performance explains more than half (66%) of the variance in K_{CD} , suggesting that this measure of capacity is dominated by attentional factors. In contrast, the correlation between K_{WR} and grouping was not significant (Spearman: $\rho = -.300$, n.s.), explaining only a fraction (9%) of the variance. The difference between the correlations was significant ($Z = 2.09$, $p < .05$), using a two-tailed Fisher's r-to-z transform. In the following analysis, we separated participants according to their performance in the CD and WR tasks to more thoroughly analyse the effect of bottom-up grouping on their performance.

Attentional selection in low and high K_{CD} groups

Using a repeated-measures, mixed-effects ANOVA with between-subjects factor capacity (low, high) and within-subjects factor grouping type (helpful, unhelpful), we analysed how performance in partial report (PR) trials was improved or depressed when grouping was helpful or unhelpful relative to the no-grouping condition.

The repeated-measures ANOVA revealed a significant effect of capacity ($F(1, 14) = 9.899$, $p < .01$) and grouping type ($F(1, 14) = 144.176$, $p < .001$). In addition, there was an interaction between capacity and grouping type ($F(1, 14) = 27.660$, $p < .001$). We subsequently analysed the individual conditions in order to find out how performance varied across the two subgroups. First, the effect of helpful and unhelpful grouping was compared within each subgroup of participants. Not surprisingly, helpful grouping led to better performance compared to unhelpful grouping for both low K_{CD} ($t(7) = 9.606$, $p < .001$) and high K_{CD} ($t(7) = 7.695$, $p < .001$) participants. Interestingly, the increase in performance in the helpful grouping condition was much larger for low K_{CD} participants than for high K_{CD} participants ($t(14) = 5.861$, $p < .001$; see Figure 2). This greater improvement for low K_{CD} participants after encouraging the use of a more selective strategy suggests that it is the encoding strategy normally used that differs between low and high K_{CD} participants, with high K_{CD} participants automatically adopting a more selective strategy.

< Figure 2 about here >

Attentional selection in low and high K_{WR} groups

We also divided participants according to their VSTM capacity during the WR task (K_{WR}) and conducted the same analyses as described above for the division by K_{CD} . Again, the low and high K_{WR} groups did not differ in age ($t(14) = 1.65, p = .121$; low: $M = 42.1, SD = 15.8$, 20-57 years, 6 female; high: $M = 30.4, SD = 12.5$, 22-40 years, 5 female) or gender distribution. Additionally, this division was independent from the division into low and high K_{CD} groups with 6 low/high K_{CD} participants being in the opposite K_{WR} group. Since Cusack et al. (2009) showed that WR estimates of capacity were less variable than CD estimates (likely due to the nature of the probe in WR tasks encouraging more selection, even for low-K participants), we expected a smaller difference between the improvement in performance in the PR trials when splitting participants by K_{WR} . The repeated-measures ANOVA showed a main effect of grouping type ($F(1, 14) = 60.821, p < .001$), but no effect of capacity ($F < 1$) or their interaction ($F(1, 14) = 3.575, n.s.$), thus confirming our prediction.

Target Selectivity

We also ran the same ANOVA as above on the proportion of distracters reported during the probe phase of the PR trials. This allowed us to directly investigate target selectivity in the two groups of participants. We again found a significant main effect of the between-subjects factor CD capacity (low or high, $F(1, 14) = 7.627, p < .05$) and the within-subjects factor grouping type (helpful or unhelpful, $F(1, 14) = 21.030, p < .001$), as well as an interaction between these two factors ($F(1, 14) = 13.843, p < .005$). Helpful grouping decreased distracter intrusions relative to the number of distracters reported in the unhelpful grouping condition for the low K_{CD} ($t(7) = 4.435, p < .005$), but not high K_{CD} ($t(7) = 1.234, n.s.$) participants. This again suggests a relationship between K_{CD} and the ability to select relevant and suppress irrelevant information, and supports the notion that the difference between low K_{CD} and high K_{CD} participants is one of attentional selection and not memory capacity per se. In contrast, for WR, an ANOVA on the distracter intrusions showed only a main effect of grouping type ($F(1, 14) = 10.760, p < .005$), while the main effect of group ($F < 1$), and the interaction ($F < 1$) were again not significant.

Discussion

The data show that participants with low capacity as assessed by change detection suffer from poor attentional selection during the encoding phase. When attentional selection was aided by helpful bottom-up grouping of the relevant stimuli, low- K_{CD} participants significantly improved in performance on the PR task. This effect was present in terms of both the number of items in

memory and the number of distracter items reported, a direct measure of mis-selection. Importantly, the relationship between attentional selection and improvement in performance was only seen when grouping participants by performance in the CD task, but not the WR task. Together, these results support the idea that what differs between participants and determines performance in CD tasks is the encoding strategy naturally used. More specifically, individuals with high capacity measures in CD are able to adopt a selective encoding strategy and filter out irrelevant items using top-down executive resources, whereas those with low capacity measures show suboptimal selection and are, hence, greatly helped by bottom up grouping cues.

2.1.3 Behavioural Experiments - Summary

The two behavioural experiments presented here, along with Cusack et al. (2009), provide converging evidence that change detection measurements of VSTM capacity are affected by attentional processes during encoding. The first experiment manipulated the type of response probe presented, by intermixing whole report and change detection probes. This intermixing alleviates the depression in performance seen at higher set sizes during pure change detection, suggesting that encoding strategy in the form of suboptimal attentional selection is responsible for decreased performance in change detection paradigms. The second experiment manipulated the grouping of items in a partial report task and showed that the magnitude of the effect of grouping is negatively related to capacity in change detection but not whole report. This suggests that change detection estimates are related to the attentional strategy used by the participant at encoding. The data, therefore, support our hypothesis that individuals with lower non-verbal IQ (study 1) or with measures of low capacity in change detection tasks (study 2) normally adopt an attentional strategy that aims at encoding all items in a display without prioritizing at high set-sizes, when not all items can be remembered.

2.2 Meta-analysis of Imaging Experiments

Introduction

While the behavioural results discussed above (2.1) suggest that attentional strategies during encoding influence estimates of short-term memory capacity, it remains unclear whether the strategy used while encoding information into memory also has an impact on how the items are

retained in memory during the maintenance phase of a change detection task. Different studies have focused separately on whether attentional selection is relevant during encoding (Awh, Vogel, & Oh, 2006; McNab, & Klingberg, 2008) or maintenance (Curtis, & D'Esposito, 2003; Kane, & Engle, 2002). It is possible that individuals using more efficient attentional selection during encoding also show differences in how they maintain this information in short-term memory. On the other hand, it could be hypothesized that while encoding strategy might differ between individuals, how the encoded items are maintained in memory does not vary, indicating that attentional selection only has an impact during encoding. Neuroimaging allows us to directly differentiate activation during the different phases of short-term memory, making it possible to investigate whether people differ in the way they encode and maintain information and how this is related to their capacity.

We therefore conducted a meta-analysis to assess whether estimates of VSTM capacity were related to activation during the encoding and maintenance phase of five VSTM tasks (see studies 3-7 in Table 1) that we have recently conducted. We focused on regions of interest (ROIs) commonly activated in short-term memory and cognitively demanding tasks (Table 2). The stimuli used differed across the experiments allowing some generalization of results.

Methods

Five diverse VSTM studies with a total of 112 participants were included in the meta-analysis. Participants had to perform a change detection task in four of these studies and a 2-Alternative-Forced-Choice task in the fifth. Table 1 provides an overview of the experimental designs and stimuli used in the different studies. Importantly, the experiments shared many common experimental design characteristics. They all included a clearly defined encoding, maintenance and probe phase that could be modelled separately to distinguish activity due to these different stages of the VSTM task.

Experiments

All subjects in all experiments reported normal or corrected-to-normal visual acuity, normal colour vision, and no history of psychological or neurological impairment. All gave informed consent and were paid for taking part. Ethical approval was given by the Cambridge Psychology Research Ethics Committee (CPREC) or the Local Research Ethics Committee (LREC) for each study. In all experiments, stimuli were presented using Visual Basic .NET except for Experiment 7, which used Matlab (<http://www.themathworks.com>) and the Psychtoolbox (Brainard, 1997).

The experiments were carried out over a time period of approximately 26 months (with on average 6.37 months between the start of individual experiments, $SD = 2.87$) and participants were recruited from a large volunteer panel.

In the first neuroimaging study (Experiment 3; Mitchell, unpublished PhD thesis), stimuli were abstract silhouettes and after a first encoding and maintenance period participants were presented with a retrocue intended to reduce the initial load. This retrocue was followed by another maintenance period before the probes were presented. A General Linear Model was fit to the data with regressors for the each of the task phases (across load conditions). Only beta values corresponding to the first encoding period were included in the meta-analysis in order not to confound the encoding processes with reactions and altered processing due to the cue. Betas and estimates of memory capacity were averaged across the two maintenance phases. Fifteen participants were tested (8 female, 19-43 years old, $M = 28.5$, $SD = 8.3$).

In Experiment 4, participants were presented with three or six dots and had to mentally manipulate them to form the outline of a shape. After a variable maintenance period, they performed a 2AFC task to identify this shape. A General Linear Model was fit to the data with regressors for the each of the task phases and load conditions. Beta values as well as the estimate of memory capacity during the encoding and maintenance period were averaged across load conditions. Seventeen participants were tested (10 female, 19-40 years old, $M = 22.1$, $SD = 5.6$).

Experiments 5 and 6 investigated retinotopic representations during short-term memory. Participants had to attend to two of four sectors. The sectors were colour-coded and participants were instructed before the start of the experiment which colour they had to pay attention to. Each of the sectors contained gratings (see Table 1 for an example of the stimuli) whose pattern continuously changed during the encoding phase. Participants had to maintain the final configuration in short-term memory for a variable time period. The two experiments only differed in how the sectors were oriented and how the probe was presented (two vs. one sectors, respectively). Seventeen participants were tested in Experiment 5 (8 female, 22-40 years old, $M = 25.6$, $SD = 4.5$). Fourteen of the participants were scanned a second time with scanning sessions at least two weeks apart and were treated as separate participants in the analysis².

² Univariate analysis had shown that it did not make a difference whether sessions of the participants scanned twice were combined or not.

Twenty-six participants were tested in Experiment 6 (16 female, 19-35 years old, $M = 26.2$, $SD = 4.6$).

The last study (Experiment 7) investigated the effect of familiarity on change detection performance. Participants had to remember either one or two abstract gray-scale shapes during a variable maintenance period. Two of the 26 shapes were presented very frequently and were, thus, very familiar to the participants. For the meta-analysis, beta values were averaged across conditions (number of high frequency items in the encoding display) and set-size for the encoding and maintenance phase. Twenty-three participants were tested (15 female, 18-38 years old, $M = 25.7$, $SD = 5.4$).

Imaging Methods & Analysis

All data were acquired on a Siemens Tim Trio 3 Tesla scanner using a 12 channel head coil. An MPRAGE sequence acquired a whole brain T1-weighted structural image, at 1mm^3 resolution. The functional data was acquired with echo-planar imaging (EPI) sequences. All the EPI sequences shared similar parameters ($TR = 2$ s, $TE = 30\text{ms}$, flip angle = 78° , 32 slices of matrix 64×64 with a 25% gap, voxel size $3 \times 3 \times 3.75\text{mm}^3$) in all but the two retinotopy experiments (5 and 6 in Table 1; $TR = 2.150$ s, voxel size $2.42 \times 2.42 \times 3\text{mm}^3$).

Data were pre-processed using SPM5 (Wellcome Department of Imaging Neuroscience, London, UK; <http://www.fil.ion.ucl.ac.uk/spm>) following a standard procedure. The EPI data were corrected for head motion and slice timing, co-registered to the structural (using a mutual information algorithm) and affine normalised to the Montreal Neurological Institute (MNI) template brain. The resulting images were spatially smoothed with a 10-14mm full-width half-maximum Gaussian kernel and temporally filtered to reduce signal drift using a high-pass, 128s cut-off. Each voxel in these EPI images was fitted with a general linear model composed of a set of regressors specific to each experiment, which were convolved with the canonical haemodynamic response function (HRF). Importantly, in all of these experiments we varied the duration of the maintenance and either the inter-trial-interval (ITI) or encoding epochs (within the range of 1–17.4s; except for Experiment 7 in which ITI and encoding were constant). Jittering with variable intervals (some of them long) has been shown repeatedly to achieve separation of sequential events in event-related designs (e.g. Rowe and Passingham (2001), using a delay period jitter of 8.5-17.5s or Sakai and Passingham (2003), using a jitter of 4-12s) and allowed us

to separately model the encoding, maintenance and response epochs. All experiments additionally included regressors to model out residual movement artefacts.

In order to assess whether Blood-Oxygenation-Level-Dependent (BOLD) activity was dependent on an individual's performance in VSTM tasks we conducted a region of interest analysis using the same ROIs for the five different studies. Seven ROIs were chosen based on indications from the previous studies discussed above (also see Cusack, Mitchell, & Duncan, 2008) that these regions are reliably activated during short-term memory tasks (four intraparietal sulcus regions: superior IPS, inferior IPS, "Silver" IPS, MD-IPS; an inferior frontal sulcus (MD-IFS) and a lateral occipital cortex (LOC) region; see Figure 3 and Table 2 for an overview). Additionally we included one region (Middle Frontal Gyrus (MFG)) that has been implicated in controlling attention during short-term memory tasks (McNab, & Klingberg, 2008). All ROIs were defined as spheres of 10mm radius around the peak activity reported in the respective studies (see Table 2), using marsbar (Brett, Anton, Valabregue, & Poline, 1997).

< Figure 3 about here >

< Table 2 about here >

For each study, task phase and ROI, mean beta values for the relevant GLM regressors were extracted from the original SPM analysis. Only the encoding and maintenance period were taken into account, averaging across set sizes and conditions within the individual experiments. Memory capacity was estimated for the 112 participants using Cowan's (2001) formula ($K=N*(H-F)$ and $K=N*(2*PC-1)$ for the 2AFC task; where N =number of items in the encoding display, H =proportion of hits, FA =proportion of false alarms, PC =percent correct). Mean signal strength (mean beta values for the relevant regressors) and K values were standardised within each study to account for stimulus differences and were correlated using Pearson's correlation.

Results

Individual univariate analyses showed that the regions involved during encoding and maintenance (vs. baseline) of these different tasks substantially overlap (see Figure 4). Importantly, many of the regions commonly involved in short-term memory showed significant activity during the encoding and maintenance phase of all five studies.

< Figure 4 about here >

Across the 112 participants, with inter-study differences removed by standardisation of the BOLD and K estimates, memory capacity positively correlated with encoding activity in superior IPS ($r = .300, p < .005^3$), MD-IPS ($r = .286, p < .005$), Silver IPS ($r = .218, p < .05$), MD-IFS ($r = .286, p < .005$), LOC ($r = .279, p < .005$) and Middle Frontal Gyrus ($r = .197, p < .05$) while maintenance activity did not show significant correlations with K in any of these regions (see Figure 5). In order to test whether the lack of significant correlations during maintenance was due to a higher degree of noise or reflected actual differences in slope, we compared the difference between the significant encoding and the maintenance correlations using an adaptation of the Williams-Hotelling test (Meng, Rosenthal, & Rubin, 1992). Specifically, if the slopes were not significantly different this would imply that the lack of significant correlations during maintenance is simply due to higher variability in the data during this task phase. Slopes were significantly different for all of the ROIs that showed significant correlations with capacity during encoding but not maintenance (sup. IPS: $Z = 1.93, p < .05$; MD-IPS: $Z = 2.73, p < .005$; Silver IPS: $Z = 3.47, p < .001$; MD-IFS: $Z = 2.68, p < .005$; LOC: $Z = 4.10, p < .001$; MFG: $Z = 4.24, p < .001$) indicating that the absence of correlations with performance during the maintenance period was not due to noise.

< Figure 5 about here >

These results suggest that differences in BOLD activation during the encoding of items into short-term memory are associated with how well individuals perform in the task. This is in agreement with the results of the behavioural studies discussed earlier and points towards a strong influence of encoding strategy on estimates of short-term memory capacity. Additionally, the finding that activity in superior IPS but not inferior IPS correlates with performance shows a parallel with Xu and Chun's (2009) differentiation between "object individuation" in inferior IPS and "object identification" in superior IPS. According to their findings, "object individuation" is fixed to about four items and is independent of encoding demands and complexity while "object identification" is thought to be flexible and dependent on the demands of the task. This difference in flexibility is also supported by recent data examining the functional connectivity of

³ Significance values reported here are uncorrected. Except for Silver IPS and MFG all ROIs survive Bonferroni correction for multiple comparisons at $\alpha=0.05$.

these regions across a broad range of tasks. While the inferior IPS shows consistent strong connectivity with perceptual regions (the LOC), the superior IPS sometimes connects strongly with perceptual regions and sometimes with frontal regions (Cusack, Sundermann, & Owen, submitted). It seems reasonable to assume that attentional selection determines how many of the items reach the “object identification” stage. The results are, furthermore, in accordance with McNab and Klingberg’s (2008) finding that activity in the middle frontal gyrus predicts short-term memory capacity and acts as a control to filter irrelevant items from being encoded and passed on to be stored in parietal regions.

3. Discussion

Individual differences in short-term memory capacity have been subject to psychological research for decades and have often been assessed using change detection tasks. Here we have shown that the attentional strategy used during the encoding phase of the task strongly influences change detection performance. This builds upon Cusack et al.’s (2009) finding that individual differences in intelligence do not correlate with memory capacity itself, but rather with an additional cognitive process during change detection. It has been assumed for a number of years that attentional selection and short-term memory are strongly related mechanisms (e.g. Awh, Vogel, & Oh, 2006). It was unclear, however, when attentional control takes effect in a short-term memory task, during encoding (Awh, Vogel, & Oh, 2006; McNab, & Klingberg, 2008), maintenance (Kane, & Engle, 2002; Curtis, & D’Esposito, 2003) or both. We have addressed this question in two behavioural experiments and by conducting a meta-analysis of five imaging studies recently carried out in our laboratory.

Our results indicate that individuals differ in the strategy they adopt during the encoding phase of change detection tasks, with low performing participants not selecting a subset of items but instead trying to encode everything, even when the presented information clearly exceeds capacity, and performance consequently suffers. This is in accordance with suggestions that information is filtered for relevancy before entering short-term memory (Awh, Vogel, & Oh, 2006; McNab, & Klingberg, 2008) and that individuals differ in their attentional ability to separate relevant from irrelevant items. Drawing upon the finding that short-term memory capacity increases during childhood, Cowan, Morey, AuBuchon, Zwilling and Gilchrist (2009) conducted a change detection study with children (7-8 and 12-13 years old) and adults and showed that

attentional efficiency of seven-year-olds was equal to that of the older children and adults for low set-sizes. Compared to the older children and adults, however, attentional efficiency significantly dropped for higher set-sizes. Cowan et al. (2009) concluded that young children show a similar attentional ability to filter out irrelevant information as adults as long as set-size does not exceed four items. This result parallels our observation of lower-IQ individuals showing a significant drop in performance at higher set-sizes. It is possible that young children, like lower-IQ individuals, use a maladaptive strategy to encode information into short-term memory that they learn to adjust when growing older.

A question that remains is which aspect of the tasks encourages particular attentional strategies. In WR, individuals choose which items to report, but in CD, a single item is probed at random. If in CD the participant encodes only a subset of the sample (the most effective strategy at high set-sizes) then there will be a proportion of trials when one of the other items is probed, and nothing will be known about it. If this is found discouraging, it might encourage broader but shallower encoding. This would lead to different predictions by different VSTM models. If a broader attentional set leads to partial encoding of many items, then a model of memory with a limited number of slots (e.g., Zhang, & Luck, 2008) would straightforwardly predict a loss of information. In contrast, a model in which memory resources can be divided between an arbitrary number of items (e.g., Bays, & Husain, 2008), would not necessarily predict worse performance as a result of shallower encoding of a greater number of items.

A related question is how much control individuals have in choosing their attentional strategy: Is strategy consciously chosen; does the nature of the task encourage the unconscious and automatic selection of a particular strategy; or is poorer performance a sign of poorer strategic control? Kane, Brown, McVay, Silvia, Myin-Germeys and Kwapil (2007) found that individuals with low memory capacity reported mind-wandering during difficult tasks considerably more often than better performing participants. By using a partial report paradigm that imposed the need for selection, we could show that those individuals performing badly in CD significantly improved in the presence of helpful bottom-up cues to selection. Individuals who do not naturally use a selective encoding strategy can thus be encouraged to do so, in turn improving their performance considerably. It is also possible that the difference between lower- and higher- IQ individuals lies in the ability to switch attentional strategies when noticing that they are not performing well in a task.

An issue not examined in the current study is the effect of the time available for encoding (cf. Bays, Catalao, & Husain, 2009; Eng, Chen, & Jiang, 2006). It might be, for example, that it takes time to apply effective selection, and that in some people this process is more rapid than in others. ERP studies of VSTM show sustained activity during the maintenance period that relates to capacity (Vogel, & Machizawa, 2004). It is possible that this partly reflects ongoing encoding of the information, especially since encoding time as well as the delay period in these experiments is short (100ms and 900ms, respectively in Vogel, & Machizawa, 2004). Future experiments could investigate whether encoding time interacts with the effects we have described.

It is intriguing that individual differences were associated with brain activity during encoding, and not maintenance. It might be that individuals' memory capacity is similar, but that how well relevant information is selected to be encoded into short-term memory varies (Vogel, McCollough, & Machizawa, 2005). Alternatively, some individuals may be more able to "compress" – encode items efficiently – and so fit more into the same underlying memory capacity (cf. Orbán, Fiser, Aslin, & Lengyel, 2008). This hypothesis makes the counter-intuitive prediction that when capacity limits have not been reached, individuals with lower capacity would show more activity during maintenance, due to less efficient compression. At higher load, activity would be similar across participants. Hence, the difference between lower and higher load would be greater in higher-capacity individuals. This is the pattern reported in the literature (Linden et al., 2003; Todd, & Marois, 2005; Vogel, & Machizawa, 2004; Vogel, McCollough & Machizawa, 2005), although it is usually attributed to greater activity for high load rather than less activity for low load. We are not aware of studies that have searched for the measure that would discriminate these possibilities.

Of course, there could also be circumstances in which activity during maintenance would track memory performance. For example, experiments 4-7 did not impose strong requirements for attentional selection during the maintenance period; if information had needed to be maintained in the face of distracting stimuli, then activity during this task phase may have also correlated with individual differences in performance (Clapp, Rubens, & Gazzaley, 2009; Olesen, Macoveanu, Tegner, & Klingberg, 2007; Sakai, Rowe, & Passingham, 2002).

Despite the predominant effects of encoding strategy, our first behavioural study also showed that the way in which memory was probed had a residual effect even when participants were

encouraged to adopt the same encoding strategy throughout the experiment. It is, therefore, reasonable to assume that change detection tasks are vulnerable to interference by characteristics of the probe (Makovski, Sussma, & Jiang, 2008). For instance, it has been shown that configural information is encoded in VSTM, such that when the context is disrupted during the probe, memory performance decreases. Presenting all remembered items in the probe display improves performance relative to showing a single cued item or disrupting the characteristics of the un-cued probes (Jiang, Olson and Chun, 2000; Vidal, Gauchou, Tallon-Baudry and O'Regan, 2005). Such effects have greater impact at higher set sizes (Woodman, Vecera, & Luck, 2003), suggesting that bottom-up grouping has little effect below capacity. This is in accordance with the drop off we saw in our change detection task, which only came into effect at set sizes above capacity. Interestingly, bottom-up grouping of remembered items differentially alters brain activity in distinct parietal brain areas responsible for VSTM maintenance (Xu, & Chun, 2007), one of these being the superior IPS region correlating with performance in our meta-analysis.

Overall, our current results replicated and extended our earlier study showing that individual differences in alternative measures of short-term memory – change detection and whole-report – are influenced by distinct cognitive components, in particular, attentional selection during encoding. Intermixing change detection and whole report probes during a VSTM task improved participants performance on change detection without affecting whole report, suggesting that the attentional set used during encoding affects measures of change detection. In a partial report task, the helpful effect of bottom-up grouping during encoding selectively aided performance of participants with a low change detection estimate of VSTM capacity, indicating that change detection measures of VSTM are dominated by individual differences in attentional selectivity during encoding. Performance in whole report tasks, on the other hand, is much less affected by encoding strategy. Furthermore, individual differences in VSTM capacity correlated with BOLD signal during encoding but not maintenance. Taken together, these results support the hypothesis that variations in performance as assessed by change detection tasks are primarily determined by differences in encoding strategy and it is this attentional component that correlates with measures of IQ, not short-term memory capacity itself.

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Figure Captions

Figure 1: Performance in the four different conditions of Study 1. When participants do not know whether they will be probed using WR or CD (VSTM-CD-Mix, VSTM-WR-Mix) performance significantly improves in the CD condition (red-dashed line) only.

Figure 2: Results of the partial report task. The y-scales display the effect of helpful and unhelpful grouping relative to no grouping, in terms of estimated number of targets held in memory (K_{PR}) and number of distracters reported. The leftmost column shows results when participants are grouped into high and low K_{CD} subgroups, while the rightmost column shows results for high and low K_{WR} groups.

Figure 3: ROIs shown to be commonly activated by short-term memory tasks in previous studies. All ROIs were defined as 10mm spheres around peak activation reported in the following studies: MD regions (IFS = inferior frontal sulcus; IPS = intraparietal sulcus) are drawn from Duncan and Owen (2000). inf. IPS (inferior intraparietal sulcus), sup. IPS (superior intraparietal sulcus) and LOC (lateral occipital cortex) are drawn from Xu and Chun (2006). Silver-IPS (intraparietal sulcus) is drawn from Silver, Ress and Heeger (2005) and the MFG region is drawn from McNab and Klingberg (2008). Activity from these ROIs was extracted and correlated with estimates of short-term memory capacity.

Figure 4: Regions activated by the five neuroimaging studies included in the meta-analysis during encoding and maintenance. Red indicates that activity in the respective voxels was found in all five studies while blue indicates that only one study showed activity in that region. The figure was created by adding the binary t-maps (FDR corrected, $p < 0.05$) for the five different studies.

Figure 5: Correlation plots for all ROIs (standardized values depicted) during encoding (first row) and maintenance (second row). Significant correlations between mean BOLD activity (y-axis) and estimates of short-term memory capacity (x-axis) are marked by an asterisk (* $p < 0.05$, ** $p < 0.005$, *** $p < 0.001$). Correlations were not significant for any of the ROIs during the maintenance phase of the tasks but are shown here for comparison.

Table 1: Overview of all experiments included in this paper. CD = Change Detection; WR = Whole Report; PR = Partial Report

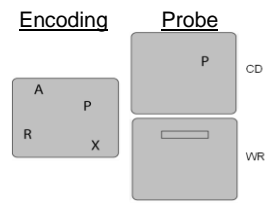
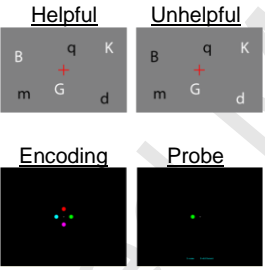
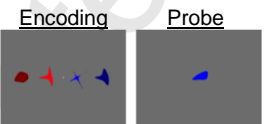
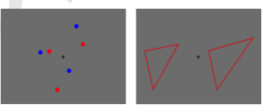

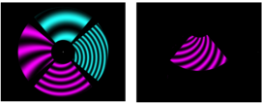
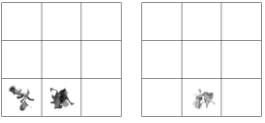
Experiment	fMRI?	N	Stimuli	Set-sizes	Task	Probe (if CD)	Encoding Duration	Maintenance Duration	
1. Blocked vs. Intermixed Probes	No	16	Letters		2,3,4,6,8	WR+CD	Single letter	183ms	1200ms
2. Perceptual Grouping	No	16	Letters (WR) Colours (CD)		3,6 (WR & PR) 1,2,3,4,6,8 (CD)	WR, PR,CD	Single colour	183ms (WR/PR) 150ms (CD)	0ms (WR/PR) 1200ms (CD)
3. Lateralised Retrocuing	Yes	15	Red or blue shapes		2, 4	CD	Single shape	750ms	1.5 – 17.4s (randomly selected without replacement from set of intervals of exponentially increasing duration)
4. Parts & Wholes	Yes	17	3 or 6 points		1, 2 triangles	CD/2AFC	Triangle	1, 6 or 11s	1, 6 or 11s
5. Retinotopy 1	Yes	31	Four gratings		2	CD	Two gratings	300ms	1, 6 or 11s
6. Retinotopy 2	Yes	26	Four gratings		2	CD	Single grating	300ms	1, 6 or 11s
7. Item Familiarity	Yes	23	Abstract shapes		1, 2	CD	Single shape	1000ms	1, 6, or 11s

Table 2: ROIs included in the meta-analysis.

Coordinates are given in MNI152 space, converted from Talairach space where necessary using tal2mni (<http://imaging.mrc-cbu.cam.ac.uk/downloads/MNI2tal/tal2mni.m>).

ROI	Full Description	Peak Coordinates (MNI)	Source
superior IPS	superior intraparietal sulcus	-21, -70, 42 23, -56, 46	Xu, & Chun (2006)
inferior IPS	inferior intraparietal sulcus	-21, -89, 24 26, -84, 28	Xu, & Chun (2006)
“Silver” IPS	intraparietal sulcus (Silver)	-23, -80, 38 23, -80, 38	Silver, Ress, & Heeger (2005)
MD-IPS	intraparietal sulcus (Multi Demands network)	-37, -56, 41 37, -56, 41	Duncan, & Owen (2000)
MD-IFS	inferior frontal sulcus (Multi Demands network)	-42, 23, 28 42, 23, 28	Duncan, & Owen (2000)
LOC	lateral occipital cortex	-44, -71, 5 42, -69, 0	Xu, & Chun (2006)
MFG	middle frontal gyrus	-42, -10, 52 48, -8, 42	McNab, & Klingberg (2008)

Figure1

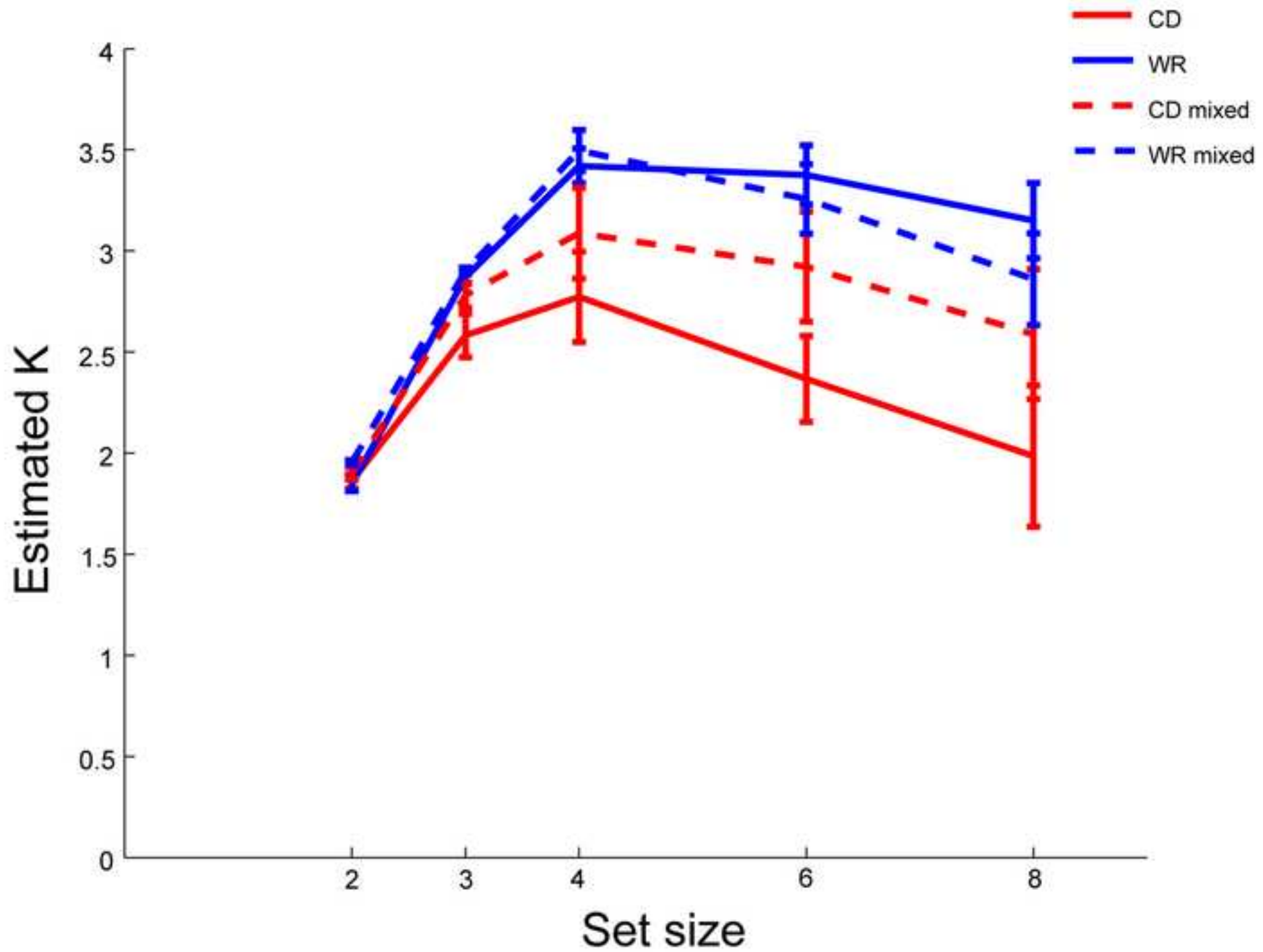
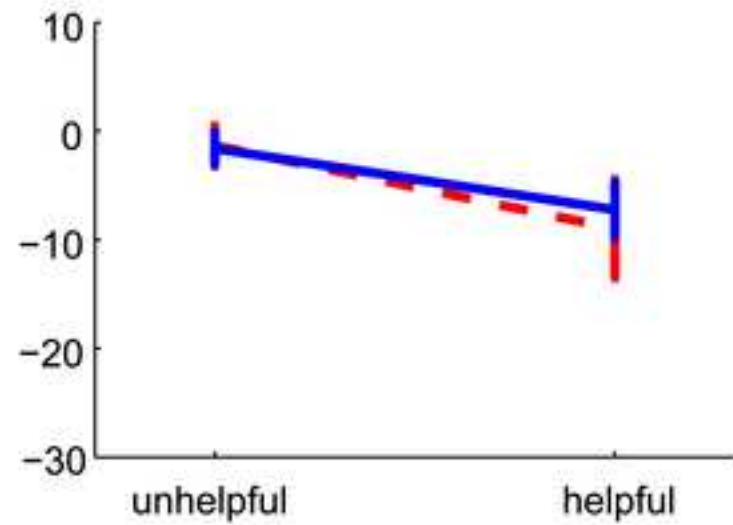
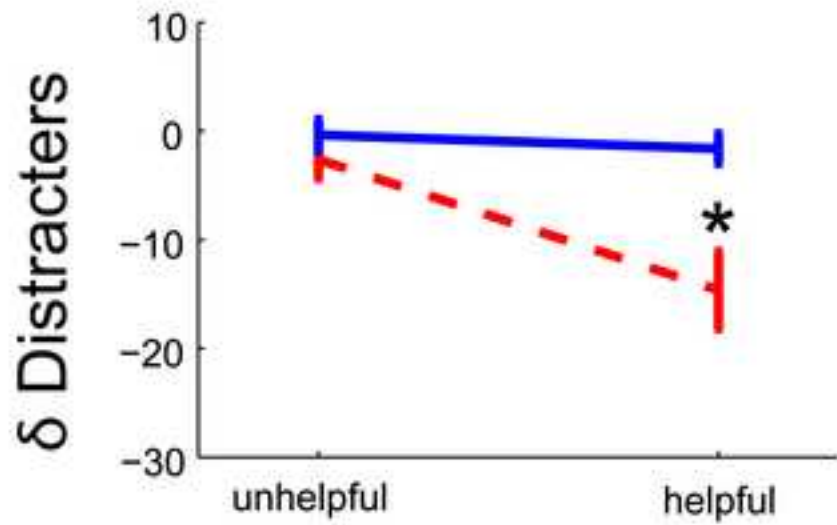
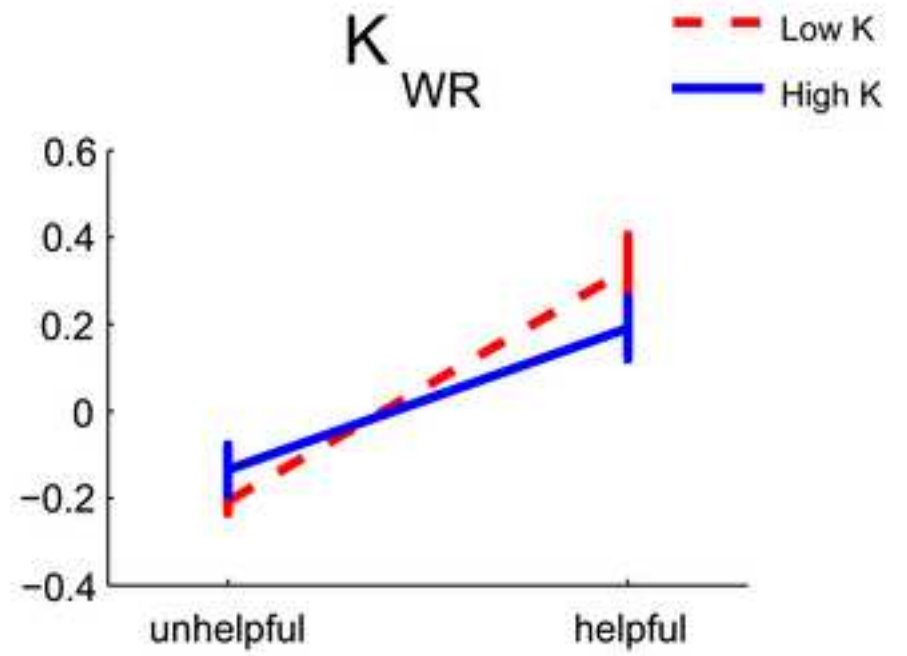
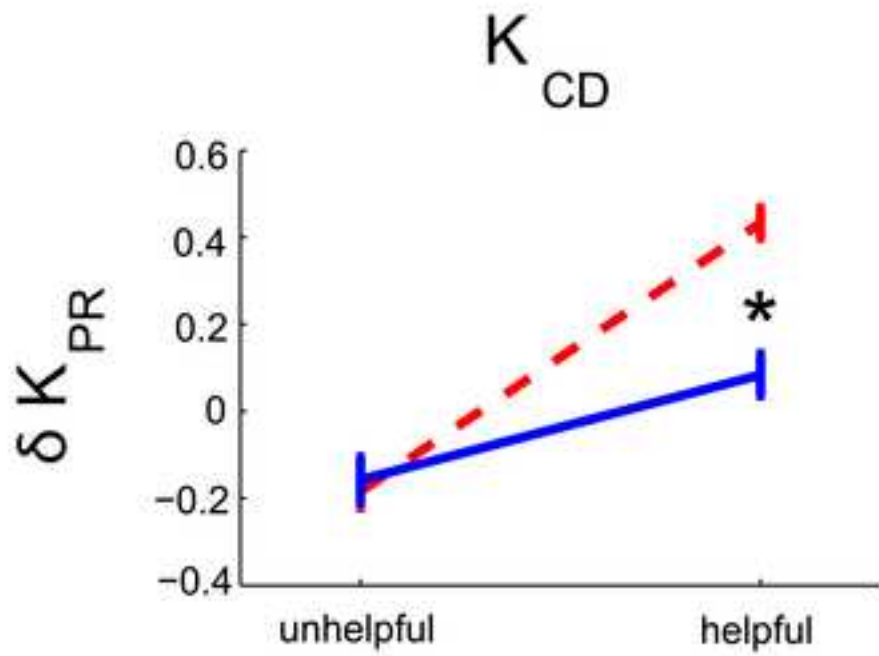
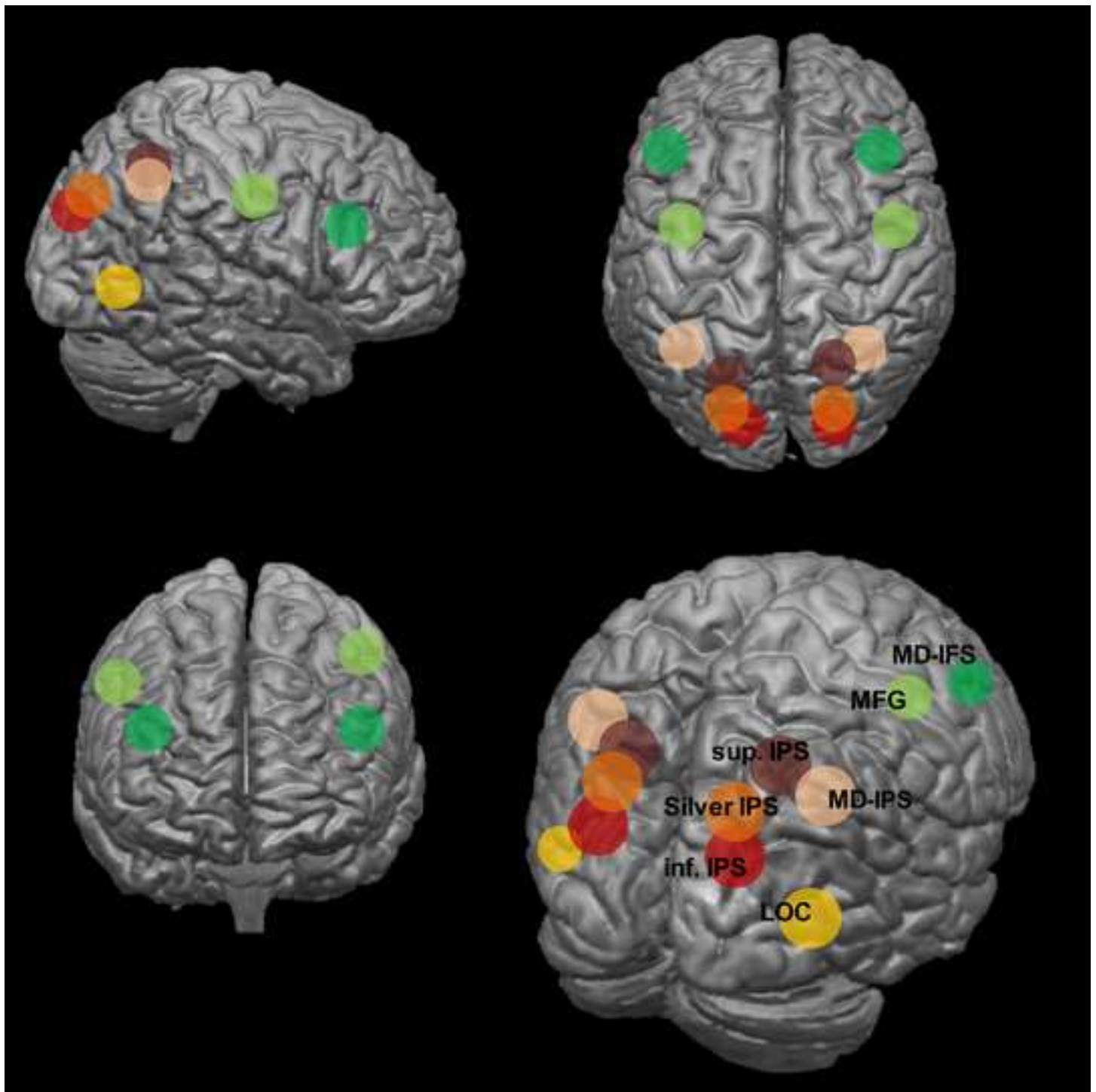
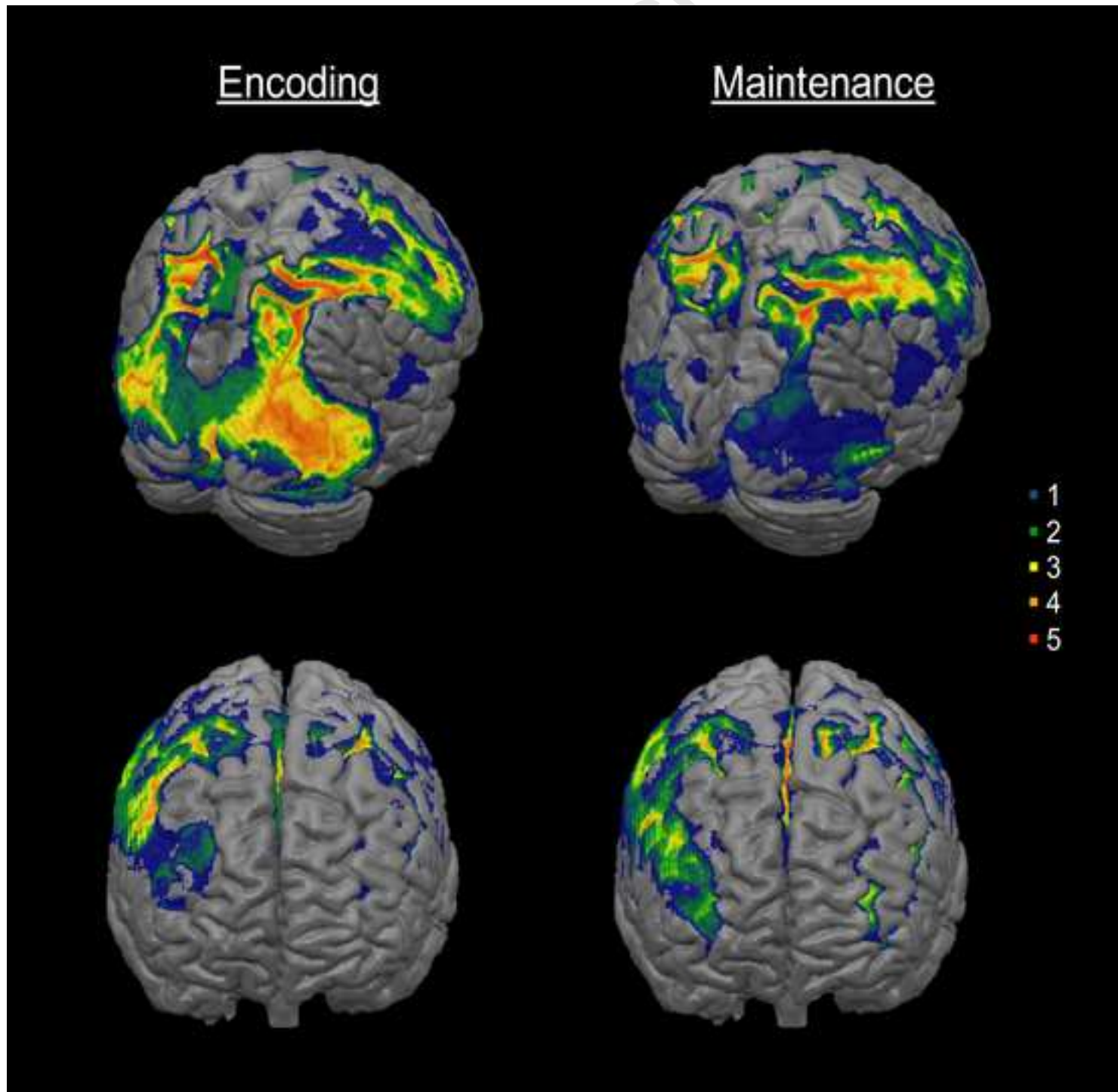


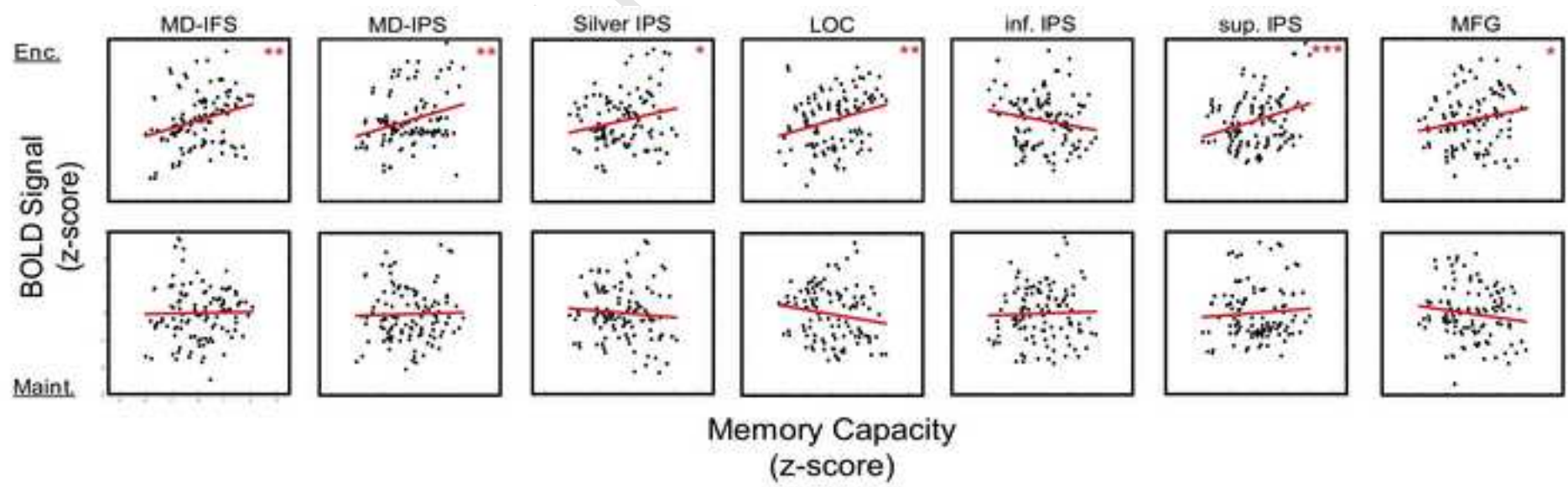
Figure2







Manuscript



Research Highlights

- Change detection (CD) measures of VSTM are strongly influenced by encoding strategy
- Whole report VSTM measures are unaffected by differences in attentional selection
- Aiding selection improves performance of people with low CD estimates of capacity
- Brain activity during encoding, not maintenance, best predicts CD performance

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