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Increased bilateral occipitoparietal activity during retention of binary versus unary indexed lists in pair recognition

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Abstract

Cognitive complexity has been characterized by relations processed, rather than items stored. Separating these factors is difficult, because processing more complex relations often involves holding more items in memory. Previous research (Phillips and Niki, 2002, NeuroImage, 17, 1031–1055) identified parietal lobes with more item relationships, but not more items by varying index length—fewest number of positions having a unique combination of items. For example, AB CD EF is a unary (length one) indexed list of three pairs, because all items are unique at the first (or second) position; AB AD CB is a binary indexed list, because only pairs of items are unique. But, these lists also differ in number of associates. In this experiment, index length was varied independently of the numbers of items and associates. Subjects were asked to make a recognition judgment for each three-pair list: Was the test pair in the previous list? Random effects analysis contrasting two binary indexed lists (AB AC CB and AB AD CB) minus two unary indexed lists (AB BC CA and AB BC CD) revealed increased occipital and parietal activity (bilaterally) during the retention period for both binary indexed list types. This result is explained by index length, but not by item load or item fan, because the numbers of items and item associates were the same for the corresponding unary and binary list types. For peak voxels in left and right precuneus, activity during retention for both binary list types was also greater than for a third unary indexed list (AB CD EF). Because binary indexes require more positions (roles) to individuate pairs, we suggest that the increased activity in precuneus relates to spatial rehearsal in that more attention is directed to both positions to maintain the integrity of the memory trace.

Keywords: Pair recognition; Index length; Occipital; Parietal; Precuneus; Relational complexity; Association; Attention; Kanji

Introduction

Several theorists have converged on the idea that the complexity of cognitive tasks is characterized by the number of interacting task dimensions of variation (Halford and Wilson, 1980; Halford, 1993; Sweller, 1994; Robin and Holyoak, 1995; Halford et al., 1998). For example, in the balance scale task, subjects determine whether the scale will tip to the left or right given two weights at two distances either side of a fulcrum. If the distances are the same and fixed for all task instances, then the task reduces to determining the binary relationship between the two weights (i.e., the two dimensions of task variation). Hence, the relational complexity of computing the solution is said to be binary. However, the task becomes more difficult when both weights and distances vary independently across task instances. If the solution is to compute the four-way interaction of these variables, then complexity is quaternary (Halford et al., 1998).

From a review of the literature, Robin and Holyoak (1995) suggested that the prefrontal region, in particular, is responsible for processing high complexity relations. This view fits with relational complexity analysis (Halford et al., 1998) in that the ability to compute more complex relations increases with age and that the frontal lobes undergo protracted development (Thatcher, 1991). More direct support

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Table 1
Ternary relations with (a) unary, (b) binary, and (c) ternary indexes, and binary relations with (d) unary and (e) binary indexes

(a) Unary			(b) Binary			(c) Ternary			(d) Unary		(e) Binary	
A	B	C	**A**	**B**	C	**A**	**B**	**C**	$\mathbf{P_1}$	P_2	$\mathbf{P_1}$	$\mathbf{P_2}$
a_1	b_1	c_1	a_1	b_1	c_2	a_1	b_1	c_1	a	b	a	b
a_2	b_2	c_2	a_1	b_2	c_1	a_1	b_1	c_2	b	c	a	c
a_3	b_3	c_3	a_2	b_1	c_2	a_2	b_1	c_2	c	a	c	b
a_4	b_4	c_4	a_2	b_2	c_1	a_2	b_2	c_2				

Note. Positions constituting a unique index are indicated in bold. A relation may have more than one unique index.

comes from neuroimaging studies specifically designed to parametrically vary the number of task dimensions. In Raven's Progressive Matrices task, for example, the missing (choice) stimulus is the one that when placed in the vacant location of a 3×3 grid preserves the changes in stimulus features specified by the other eight sample stimuli. In the one-dimensional case, the eight samples differ in, say, size only, and the correct choice is the stimulus that preserves the change in size. In the two-dimension case, the choice stimulus must conform to changes specified along two dimensions, say, size and orientation. Greater activity was observed in anterior regions of the frontal lobes and well as regions in the parietal lobes when the stimulus choice was based on integrating more dimensions of variation (Prabhakaran et al., 1997; Christoff et al., 2001; Kroger et al., 2002).

Importantly, the process of integrating relationships may not be unitary and may involve components that are not specifically relational. Hence, care is needed when interpreting the link between relational complexity and the role of specific brain regions. For example, logically, transitive inference requires combining two binary relationships, such as Taller (John, Mary) and Taller (Mary, Sue), to infer a third, Taller (John, Sue)—in general, if R(a, b) and R(b,c), then R(a, c). But, complexity depends on whether the three dimensions (a, b, c) are integrated in one parallel step (ternary), or two serial steps of two dimensions each (binary) (Halford et al., 1998). Older children (>5 years) reliably make transitive inferences in both cases, whereas younger children make inferences only under conditions that permit serial integration (Andrews and Halford, 1998). Cowan (2001) has interpreted such differences as limits on memory capacity, rather than the capacity to integrate relations—ternary relationships are more difficult because they require keeping more items in a focus of attention to compute the relationship. By this view, the generate/self-evaluate model of intermediate relational processing attributed to prefrontal regions (Christoff and Gabrieli, 2000) could be interpreted more basically as an issue of intermediate memory load, particularly given that increased memory load also activates anterior regions of the frontal lobes (Rypma et al., 1999). For these reasons, it is also important to look at the details of relational processing to isolate relational components from components that are not specifically relational, such as memory load.

Relational components can be isolated from number of items by varying the index length (Phillips and Niki, 2002). Formally, a relation is a set of tuple instances, where each element of the tuple plays some role in the relation. So, for example, John likes Mary, and Sue likes Tom are instances of the binary relation Likes, with John and Sue in the Agent role, and Mary and Tom in the Patient role. Relations are often represented as tables, where each row corresponds to an instance and each column to a role of the relation. Where a task involves multiple instances, each role (column) can be considered a dimension of variation within the task. Index length is the number of roles at which there is a unique combination of elements. The relation Likes has a length one (unary) index, because all elements in the Agent (or Patient) role are unique. If the relation also contained the instance Sue likes Mary, then index length would be two (binary), because only the combinations of elements from both roles are unique. Relations with the same number of roles (i.e., arity) may have different length indexes. Table 1 shows three ternary relations with unary, binary, and ternary indexes, and two binary relations with unary and binary indexes. A longer index means that more position-specific cues are needed to individuate relational instances.

Index length is important for two reasons. First, it provides a theoretical basis (Halpin, 1995) for analyzing the complexity of relations in cognitive tasks (Phillips, 1997; Halford et al., 1998; Phillips et al., 1998). For example, the statements John owns a house, a cat, and a car and Mary owns a farm, a dog, and a bike could be interpreted as a quaternary relation (i.e., four dimensions of variation: Owner, Object1, Object2, Object3). However, since John and Mary are unique to each statement, the same relational information is captured by the binary relation Owns having just two dimensions: Owner, Object (i.e., Johns owns a house, John owns a cat, Mary owns a dog). (See, eg., Halpin, 1995; Phillips, 1997; Halford et al., 1998, for the technical reasons.) Second, by changing index length, the amount of relational information can be increased without increasing or changing the number of related items. For example, the three-pair list AB AD CB has a longer (binary) index than AB CD EF (unary) but fewer unique items (four versus six).

Using this type of manipulation, Phillips and Niki (2002) reported increased parietal and frontal lobe activity during encoding and retention of binary versus unary indexed pair

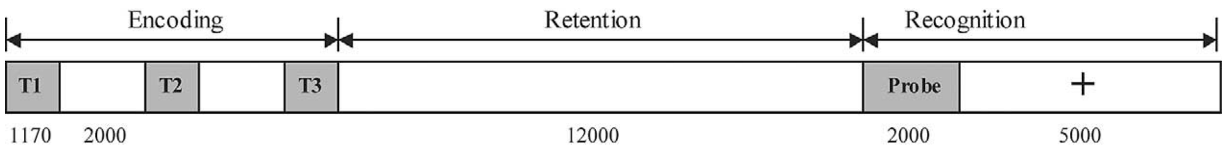

Fig. 1. Each trial was a sequence of three target pair events (1170 ms), separated by blank screens (2000 ms), and followed by the retention only delay period (12000 ms), a test probe pair (2000 ms), and an intertrial "+" event (5000 ms).

lists. Increased parietal activity was observed in visual, linguistic, and numeric domains for pair recognition, where subjects were given pair lists and asked to make a recognition judgment on a test pair following a delay (i.e., Was the test pair in the previous list?). One interpretation offered for the consistent increased activity was greater demand on spatial attention. A critical difference between relations and pure associations is role information (Phillips et al., 1995). In these experiments, role information was encoded by screen position (left, right). A longer index means that more role (position)-specific cues are needed to uniquely identify an instance of the relation. Awh and Jonides (2001) have argued that attention serves to maintain a better memory trace. A unary index means that only one position-specific cue is needed to uniquely access every instance; hence there is less demand on spatial attention. These results provided evidence that the effects of increasing relational information are not simply reducible to the number of items stored.

However, these results could also be interpreted in terms of number of associations independent of positional information (i.e., item fan)—the number of items associated to a given item (Anderson, 1974; Anderson and Reder, 1999b). Each item in the AB CD EF list has only one associate, but A and B in the AB AD CB list have two associates, B and D, and A and C, respectively. During retention, rehearsal of, say, the AD pair could reinstate B, a previously studied/rehearsed associate of A from the AB pair. Hence, the increased activity could be due to reactivation of other items, or inhibition of previous associates, a role that has been attributed to the frontal lobe (Shimamura et al., 1995). The purpose of the current work is to isolate relational from associative effects by contrasting lists with different index lengths but the same number of items and item associates. Table 1 (c and d) provides an example of two relations with different length indexes and the same number of items and item associates.

Materials and methods

Subjects were required to perform a pair recognition task, similar to Phillips and Niki (2002) Experiment 5; that is, subjects were given a sequence of kanji pairs and a test pair for which they were required to make a recognition judgment: Was the test pair in the previous list? Kanji are generally word units, often with multiple semantic and phonetic components.

Twelve Japanese university students (22 ± 2 years old; right-handed; two female) participated in the experiment, after providing informed consent, in accordance with AIST safety and ethics guidelines. Each subject session consisted of 50 trials. Each trial consisted of an encode phase when a list of three pairs was presented one pair at a time, followed by a retention phase when there was no stimulus presentation; followed by a recognition phase when a test pair (either a target or a distractor) was presented. During the recognition phase, the subject indicated whether the test pair was in the study list. The precise sequence of events is shown in Fig. 1. For example, the first target pair was presented for 1170 ms, followed by a blank screen (2000 ms), followed by the second target pair for 1170 ms. A cross indicated the end of the current trial. Subjects were permitted to respond to the test pair during this event. Pairs were presented horizontally, in black on a white background, and centered. Pairs were constructed from a list of low to medium frequency kanji and screened by a native Japanese speaker to minimize within-pair semantic and phonetic associations, and approximately balance stroke count. No pair formed a word, or was pronounceable as one by combining alternative pronunciations of individual kanji. Prior to entering the scanner, subjects were given written instructions regarding the experimental procedure and a brief practice session to ensure that they understood the task.

There were five list types that varied in index length (unary, binary) and number of unique items (3, 4, 6). They are labeled u3, u4, u6, b3, and b4. b6 is not possible with three-pair lists. The list types are shown in Table 2, and an example kanji pair (b4) list is given in Fig. 2. Each list type was tested with targets

Table 2
List conditions

Unique items	Index			
	Unary		Binary	
3	A	B	A	B
	B	C	A	C
	C	A	C	B
4	A	B	A	B
	B	C	A	D
	C	D	C	B
6	A	B		
	C	D		
	E	F		

Note. A binary indexed three-pair list of six unique items (b6) is not possible.

著 奈
著 為
角 為

Fig. 2. An example (b4) list of kanji pairs.

and distractors. Thus, we used a (2 [Index] × 2 [Item] + 1[u6]) × 2 [Probe] × 5 [Trial] design. Three of the five target probes matched the middle pair to minimize potential primacy and recency effects. Distractors for the u3 and b3 lists were reversed pairs. (With only three unique items, it is not possible to construct distractors with items in the same position as they appeared in the list.) The distractors for the u4 and b4 lists were AD and CD, respectively. Distractors for the u6 list were constructed with items in the same position as they appeared in the list (e.g., AD, CB). No kanji appeared in more than one trial, including practice trials. Conditions and pairs were randomly ordered, and balanced with the exception that there were two u3 distractor trials and eight u3 target trials, because three test pairs were accidently reversed in the software presentation program.

fMRI data acquisition/analysis

Scanning was performed on a 3.0-T MRI scanner (GE 3T Signa) with EPI capability. Eighteen axial slices (5.3 mm thick, interleaved) were set to cover the entire brain. A T2* weighted gradient echo EPI was employed. The imaging parameters were TR = 2 s, TE = 30 ms, FA = 70°, FOV = 20 × 20 (64 × 64 mesh). The image data were preprocessed (time slice adjusted, realigned, normalized, and smoothed), modeled, and analyzed using SPM99 (SPM, 1999). The preprocessed data were fitted by a general linear model where regressors were defined for each subject session event type. There were five list encoding events (i.e., one for each list type) modeled as the canonical hemodynamic response function convolved with a step function with the rising edge coinciding with the onset of the first target pair and the falling edge coinciding with the offset of the last target pair; five list retention events modeled as a step function coinciding with the duration of the retention-only period; and 5 [list] × 2 [Probe] + 1 [Error] recognition events modeled as the canonical hemodynamic response function with the onset coinciding with the onset of the test pair. Events are shown in Fig. 1. A high-pass filter with a cutoff of 120 s was used to remove low frequency noise. Model parameters were computed to minimize the squared error. Mixed between-subjects random effects within-subjects fixed effects analyses were performed to make population-level inferences about the contrasts of interest. The voxel threshold was set at $P < 0.001$, uncorrected. The locations reported by SPM99 were converted into Talairach coordinates (Talairach and Tournoux, 1988) by the transform specified in the mni2tal.m program (Brett, 1999). These coordinates were used to determine brain regions using Talairach Daemon program Version 1.1 (Lancaster et al., 2000).

Behavioral data acquisition/analysis

Response errors and reaction times were recorded using a three-button optical keypad attached to the subject's right leg. Subjects responded by pressing the left button with their index finger (right hand) to indicate a target, and by pressing either the middle or the right button with either their second or their third finger to indicate a distractor. The same finger–button combination was used throughout the scan, decided upon by the subject on the basis of what was most comfortable. Data were analyzed by Statistica (Statistica, 2000). Mean-value substitution was applied to missing response time data resulting from keypad failure. The mean was calculated from the remaining trials in the same List–Probe condition for that subject. Failure to response was regarded as a response error. Keypad failure was rare, with only one failure in 600 trials.

Acquisition of behavioral data was done to ensure that subjects were memorizing lists. Analysis of probe recognition is complicated by different types of distractors. For example, the only possible distractors without extra-list items (items not in the presented list) for u3 and b3 lists were reversals of list pairs, whereas distractors for the other lists were not reversals. Because the focus of this study is on index length, which is a property of lists not probes, distractor types were not balanced across lists as this would have unduly complicated the experimental design. Therefore, the analysis of response time data was limited to acceptance of target probes.

Results

For the fMRI data, three primary contrasts were conducted to measure the effects of the main factors (index length and number of unique items) and their interaction during the retention period. For conciseness, unary refers to the u3 and u4 conditions, which constitute the balanced part of the design. The conditions u3, u4, and u6 are explicitly referenced where unary refers to all three conditions. The primary contrasts were (a) binary minus unary (b − u) retention; (b) four minus three (4 − 3) retention; and (c) index length by item number (L×N) retention. Two follow-up contrasts were also performed to measure the influence on the encoding phase of the effects observed in the retention phase. The follow-up contrasts were (d) b-u encoding and (e) u-b encoding. All contrasts were thresholded at $P < 0.001$, uncorrected. A summary of the significant voxels for the respective contrasts is given in Table 3, which shows the number of voxels in each cluster, the cluster's significance level (corrected and uncorrected), the signifi-

Table 3
Significant voxels of activity for contrasts (a) b − u retention, (b) 4 − 3 retention, (c) Index × Item retention, (d) b − u encoding, and (e) u − b encoding

Cluster-level			Voxel-level			Location (mm)			Region	BA	Range
$P_{correct}$	Voxels	P_{uncorr}	$P_{correct}$	T	P_{uncorr}						
(a)											
0.000	484	0.000	0.203	8	0.000	−22	−70	37	Precuneus	7	3
			0.823	5.74	0.000	−20	−84	30	Cuneus	19	3
			0.999	4.33	0.001	−16	−85	15	Middle occipital gyrus		1
0.000	1149	0.000	0.245	7.74	0.000	24	−82	24	Cuneus	18	5
			0.27	7.61	0.000	22	−78	41	Precuneus	19	3
			0.723	6.05	0.000	34	−75	15	Middle occipital gyrus	19	7
0.845	28	0.192	0.966	5.06	0.000	32	−54	−1	Parahippocampal gyrus	19	7
0.611	47	0.097	0.97	5.03	0.000	0	−83	12	Cuneus	17	5
0.224	92	0.026	0.989	4.79	0.000	−36	−67	11	Middle occipital gyrus	19	9
			0.991	4.74	0.000	−30	−77	13	Middle occipital gyrus	19	11
0.985	10	0.436	0.997	4.51	0.000	30	−1	48	Middle frontal gyrus	6	3
0.985	10	0.436	0.998	4.48	0.000	−16	13	21	Caudate		9
0.991	8	0.489	0.998	4.47	0.000	−40	−76	−8	Middle occipital gyrus	18	3
(b)											
0.355	72	0.045	0.78	5.88	0.000	57	−41	0	Middle temporal gyrus		3
0.834	29	0.184	0.828	5.73	0.000	26	18	−23	Inferior frontal gyrus	47	3
0.949	17	0.306	0.994	4.64	0.000	−6	−55	18	Posterior gingulate	23	3
(c)											
0.737	38	0.158	0.892	5.34	0.000	16	−84	26	Cuneus	18	3
(d)											
0.332	78	0.045	0.293	7.4	0.000	55	−23	49	Postcentral gyrus	2	3
0.897	23	0.253	0.623	6.26	0.000	44	−24	33	Postcentral gyrus	2	5
0.661	44	0.12	0.986	4.77	0.000	38	−2	2	Claustrum		5
			0.995	4.56	0.000	38	−11	4	Claustrum		3
0.989	8	0.507	0.996	4.52	0.000	−34	−6	0	Claustrum		3
(e)											
0.42	67	0.061	0.484	6.68	0.000	18	−77	50	Precuneus	7	7
			0.825	5.66	0.000	20	−81	41	Precuneus	19	1
0.923	20	0.286	0.713	6	0.000	46	2	50	Middle frontal gyrus	6	3
0.989	8	0.507	0.973	4.92	0.000	6	−52	41	Precuneus	7	3

Note. The corrected and uncorrected cluster-level P values (i.e., chance probability of obtaining a cluster of that size), the number of supra-threshold voxels in the cluster, corrected and uncorrected voxel-level P values (i.e., chance probability of obtaining activation), T score, location of the most significant voxel in a cluster or subcluster (rows with empty Voxels column), region and corresponding Brodmann area of the nearest gray matter, and its Range from the cluster are shown. Range is the length of the smallest cube that contains gray matter, where the cube is centered on the most significant voxel in the cluster. For example, a range of 5 mm indicates gray matter two voxels from the most significant voxel.

cance level (corrected and uncorrected), and T value of the (sub)cluster's peak voxel and its location (Talairach coordinates), brain region, Brodmann area, and distance from the nearest gray matter. Only the most significant clusters are reported in the main text.

The contrast of b-u retention revealed two major clusters (484 and 1149 voxels) of activity extending from the precuneus to middle occipital gyrus bilaterally. The cluster sizes were significant to $P < 0.0001$ (corrected), and the peak voxels in left and right precuneus were significant to $P < 0.00001$ (uncorrected). For the 4-3 retention contrast, there was a cluster of 72 voxels at right middle temporal gyrus. The interaction of index length and item number revealed a cluster of 38 voxels at right cuneus.

For the follow-up contrasts, b-u encoding revealed a cluster of activity at right postcentral gyrus. No clusters were found in the occipital or parietal lobes of either hemisphere. However, a cluster of 67 voxels was observed at right precuneus for the u-b encoding contrast. The size of this cluster was marginally significant at the level of $P < 0.061$ (uncorrected), but not at the corrected level, $P < 0.42$.

Transverse sections of the T maps from each of the contrasts are shown in Fig. 3. The sections are centered on and 2 mm ventral and dorsal to the peak voxel in each contrast. The cross-hair indicates the *x, y* coordinate of the peak voxel. The cross-sections show a clear bilateral activation of precuneus with binary indexed lists, but activation of right middle temporal gyrus with increased number of unique items. The interaction observed in right cuneus was due to the greater activation of b4 lists than b3 lists. Right precuneus activity is also shown for the u-b encoding contrast. But, this activity is more dorsal than the b-u activity observed during retention.

Peristimulus time histories for the peak voxels in left and

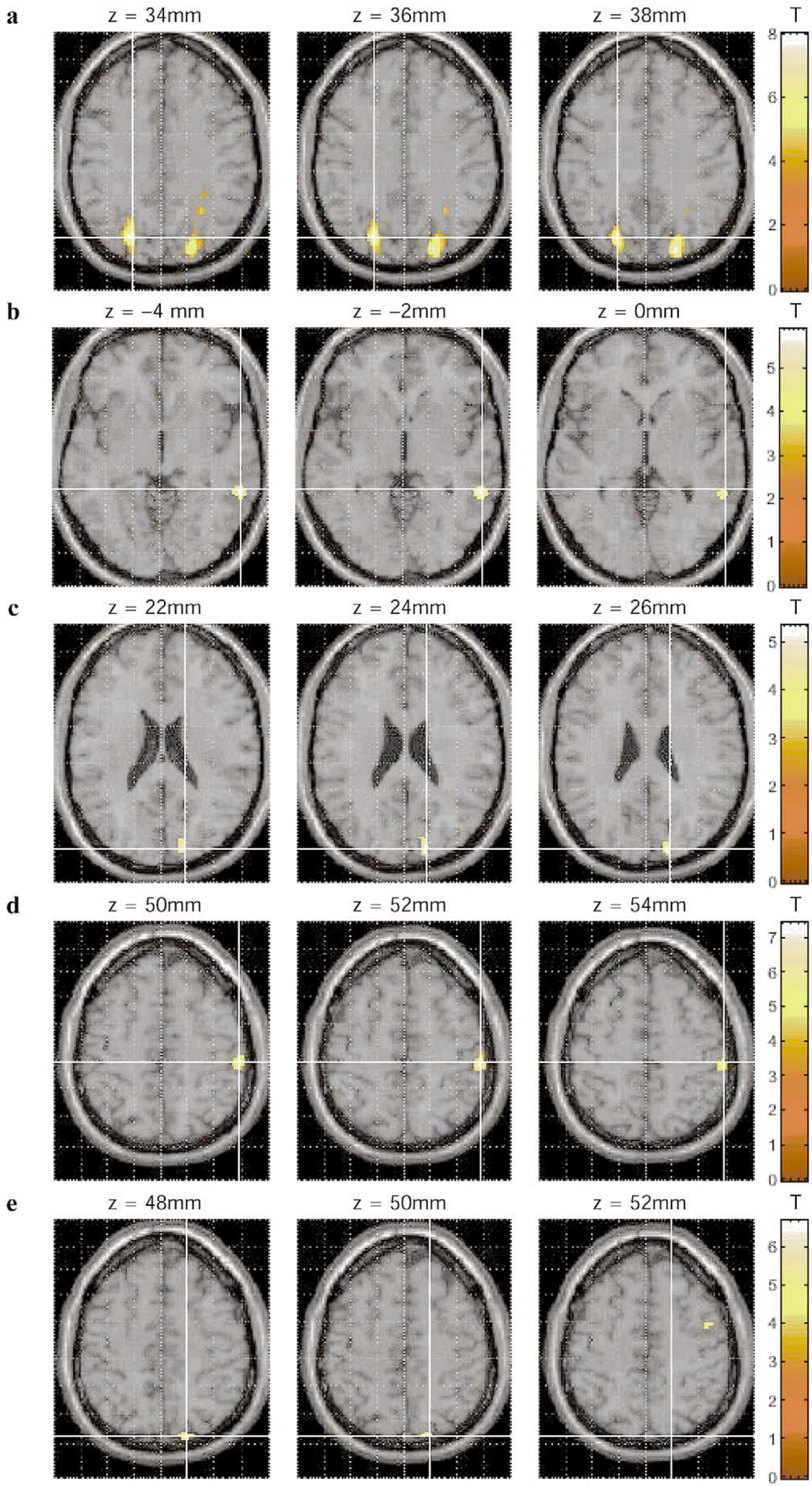

Fig. 3. Transverse sections at (middle), and 2 mm ventral (left) and dorsal (right) of peak voxels for contrasts (a) binary minus unary retention; (b) 4 minus 3 retention; (c) interaction of binary minus unary by 4 minus 3; (d) binary minus unary encoding; and (e) unary minus binary encoding.

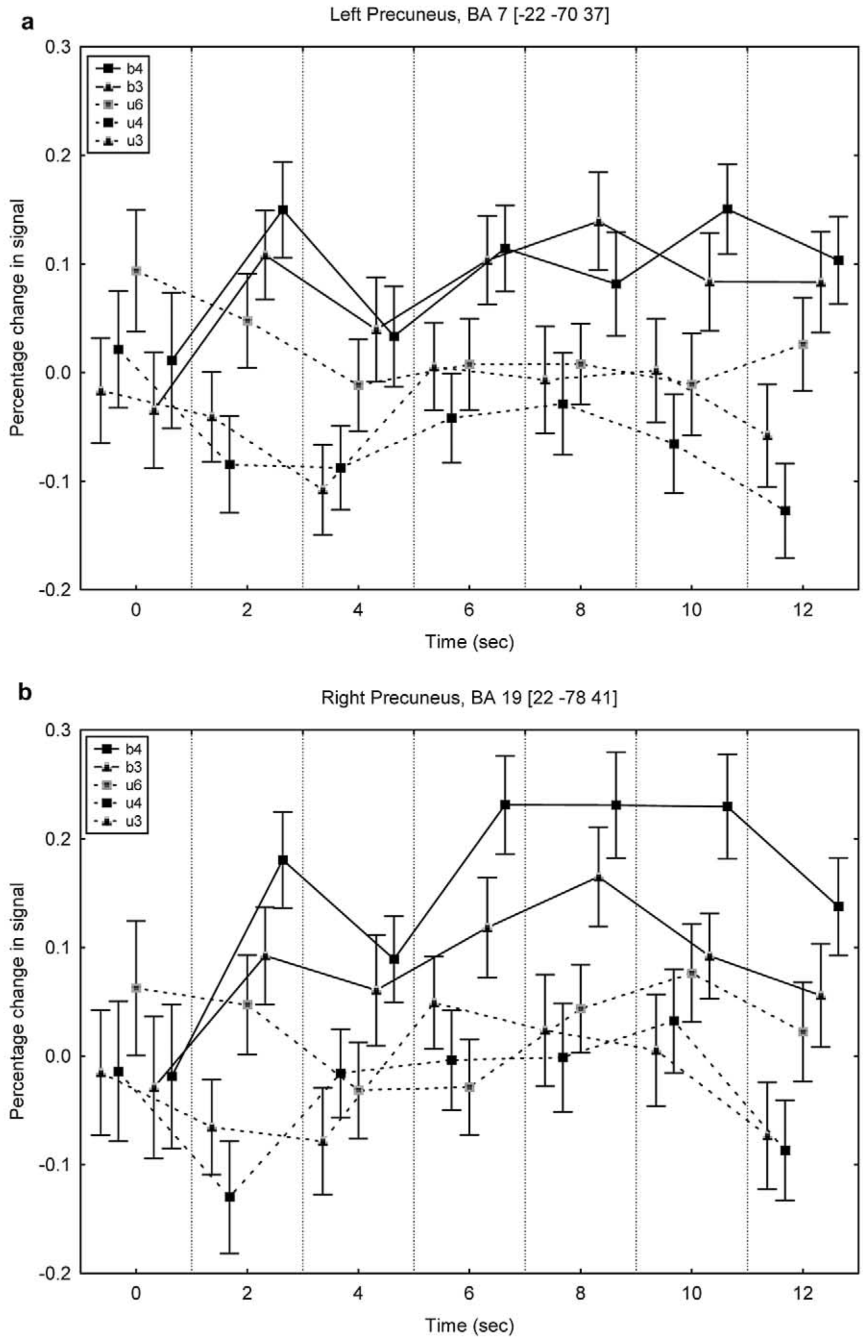

Fig. 4. Mean peristimulus time histories of peak voxels identified by the binary minus unary contrasts during the retention period. Unary lists (u3, u4, and u6) are indicated by dashed lines and binary lists (b3 and b4) by solid lines. Error bars indicate one standard error.

right precuneus observed in the b-u retention contrast were plotted for all five list types over the retention period (Fig. 4). Although the u6 retention event was not part of the b-u retention contrast, it is included to show the generality of the index length effect. During most of the retention period (from less than 2 s after onset to the end of the period) mean activity for b3 and b4 lists was greater than that for u3, u4, and u6 lists.

With regard to the behavioral data, a 5 (List) $\times$ 2 (Probe) repeated-measures ANOVA revealed no main effects for errors, $F(4, 44) = 0.42$, $P < 0.8$ (List); and $F(1, 11) = 2.51$, $P < 0.15$ (Probe). For reasons already mentioned, analysis of response time data was confined to the time to accept a target. A one-way ANOVA revealed a marginal effect on List, $F(4, 279) = 2.72$, $P < 0.03$. Post hoc analysis (Scheffe test, $\alpha = 0.05$) indicated that only the difference between b3 and u6 targets was significant, $P < 0.04$. Mean response errors for targets and mean response times to accept targets are shown in Table 4.

Table 4
Mean target error rates and response times (ms) to accept targets

List	u3	u4	u6	b3	b4
Error	0.19 (0.04)	0.17 (0.05)	0.08 (0.05)	0.18 (0.05)	0.13 (0.05)
Time	1409 (58)	1368 (72)	1223 (69)	1546 (73)	1357 (70)

Note. Parentheses indicate one standard error.

Discussion

Retention

The contrast results revealed an effect of index length, not attributable to item number or item fan. The contrast of binary (b3, b4) minus unary (u3, u4) indexed lists revealed bilateral activity in precuneus, as well as cuneus. For the peak voxels in left and right precuneus, greater activity was observed during retention of both b3 and b4 lists than for either u3 or u4 lists. This effect generalized to retention of u6 lists for which activity was also less than either binary list. It is unlikely that these results were due to processes related to item presentation, since the contrast of b-u encoding did not reveal parietal activity. However, a contrast of u-b encoding events did reveal activity in right precuneus that was close, but more dorsal, to the right precuneus activity observed for b-u retention. Inspection of peak voxel activity for the encoding phase revealed the difference was due to decreased activation of binary lists. These results provide further support for increased engagement of regions in the parietal lobes, specifically precuneus, during retention of binary indexed lists. They also show that the effect was not due to item fan, because the number of associates for u3 and b3, and u4 and b4 lists were the same.

The observed increased activity in precuneus during retention is interpreted in terms of spatial rehearsal. Although the occipital and parietal regions are generally associated with perceptual processes, the parietal regions in particular are also implicated in attention (Culham et al., 1998; Losier and Klein, 2001; Nagahama et al., 2001; Hopf et al., 2002) and memory (LaBar et al., 1999; Honey et al., 2000). More specifically, spatial attention mechanisms are supposed to be recruited to serve a rehearsal-like function that maintains information active in working memory (Awh and Jonides, 2001). The unary and binary indexed lists are very similar in structure: reversal of the BC pair in a u4 list results in a b4 list; reversal of any one pair in the u3 list results in a b3 list. The distributions of items to lists are identical. The lists differ in the number of positions that afford unique identification of each pair, and therefore in the way spatial cues can affect rehearsal of a memory trace. For AB AD CB (b4) lists, attending to the left position will yield an A item two-thirds of the time. Since A was paired with both B and D, both items would be reinstantiated. Attention to the second position maintains the information that B, not D, was paired with A in the first pair. (A similar situation occurs for attention first directed to the right position, and for b3 lists.) But for u3, u4, and u6 lists, cuing with an item in (say) the first position yields only one associate from the second position. In terms of rehearsal, then, this difference means that additional attention is directed to the other position as more items are reactivated during retention.

Several points favor the view that the observed activity in precuneus reflects a shift of attention role. If the difference only reflected reactivation, then activity should also be revealed in a contrast of number of associates, or number of items with index length constant. However, neither a u3-u6 (two associates per item versus one), nor a u6-u3 (six items versus three) contrast ($P < 0.001$, uncorrected) revealed activity in the same region (i.e., within a 10-voxel radius) of the peak voxels in precuneus. The only activity that appeared within precuneus was a small cluster of 5 voxels in BA 31. But, its location was more ventral ($xyz = -22, -70, 24$), registering close to the occipital lobe. Although Rugg et al. (1998) have suggested that precuneus was involved in retrieval success based on a contrast of many versus no associates in a cued recall task, their subsequent work (Allan et al., 2000) failed to replicate this observation, leading the authors to speculate that the activity was instead related to a task switching component that was only a part of their earlier experimental design.

Previous studies (e.g., Christoff and Gabrieli, 2000; Kroger et al., 2002) reported activity in and anterior to the dorsolateral prefrontal cortex (BA 9/46 and BA 10) with increasing relational complexity, yet little or no such activity was observed in the contrasts reported above. There are differences, however, between the current experiment and earlier studies. In those studies, relational complexity was measured as the number of dimensions of variation. In the current task, the number of dimensions of variation is the same across all conditions (i.e., two). What differs is index length, which is a measure of the interaction between those dimensions. Furthermore, in the Kroger et al. (2002) study, the number of dimensions was contrasted at five levels from zero to four. Here, only two levels were contrasted. Therefore, effects are likely to be smaller. Random effects analysis for retention of binary minus unary lists at a less stringent threshold ($P < 0.05$, uncorrected) revealed three clusters (>20 voxels) of frontal activity in the left superior frontal gyrus, BA 9 ($xyz = -20, 56, 29$; 55 voxels); right medial frontal gyrus, BA 10 ($xyz = 22, 45, 11$; 152 voxels); and right middle frontal gyrus, BA 46 ($xyz = 46, 42, 26$; 24 voxels). Thus, increased index length also activated prefrontal regions, but the significance was lower.

Recognition

The only significant difference in response times was between b3 and u6 lists, where the acceptance was longer for targets from b3 lists. While this observation suggests an effect of index length on recognition, it is also consistent with an item fan effect, since every target in a b3 list had a 2-2 fan (i.e., both left and right probe items were associated to two items in the study list), whereas every target probe in a u6 list had a 1-1 fan. Moreover, an index length effect during retention may be compatible with item fan effect during recognition, because fan effects—increased response time with increased item fan—are supposed to reflect only retrieval processes (Anderson and Reder, 1999a).

Summary and further work

In this article we reported greater bilateral parietal and occipital activity for retention of binary in contrast to unary indexed lists. These results provide further evidence for an index length effect that is not due to the number of items or item associates in the list. Because binary indexed lists require more cues in more positions to uniquely identify pairs, the increased activity observed in precuneus may reflect spatial rehearsal processes. Binary indexes require additional attention to both positional cues, whereas unary indexes only require attention to one positional cue. This hypothesis can be tested in future studies by a dual-task paradigm, where subjects are given a spatial attention task during the retention period. A secondary task that requires shifts in spatial attention would modulate retrieval performance on the primary memory task for binary, more than unary, indexed lists.

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