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Sensitivity to effective relational complexity in the occipitoparietal lobe

Steven Phillips* and Kazuhisa Niki

Cognitive and Behavioral Sciences Group, Neuroscience Research Institute, National Institute of Advanced Industrial Science and Technology (AIST), Tsukuba Central 2, 1-1-1 Umezono, Tsukuba, Ibaraki 305-8568, Japan

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Previous work identified bilateral regions in the occipitoparietal lobe sensitive to the complexity of relational information [Phillips, S., Niki, K., (2003). Increased bilateral occipitoparietal activity for retention of binary versus unary indexed lists in pair recognition. NeuroImage 20 (2), 1226–1235]. Here, we investigate the effect of learning on sensitivity to relational complexity. Eight subjects were scanned on a pair recognition task before, during and after a 2-week training period when subjects learned to recognize a set of shape pairs. For each trial of the pair recognition task, subjects determined whether a probe pair appeared in a list of learned or novel pairs. In the low/high relational complexity condition, every pair in list AB CD EF/AB AD CB was uniquely identifiable by an item in either/both the first or/and second position. Whole-brain and region of interest contrasts revealed a significant interaction between complexity and learning in the occipitoparietal lobe. The increase in activity for the retention of high versus low complexity lists was greater for learned than novel pair lists. Subjects were more likely to respond to low complexity lists as though they were high complexity prior to training. The results suggest that this region provides a window into effective relational complexity, that is, complexity of relational information as processed by the subject, not as presumed by task design.

Keywords: Relational complexity; Parietal lobe; Occipital lobe; Learning; Relation; Pair recognition

The ability to utilize relationships between tasks items is central to theories of higher cognitive functions, including analogy (Gentner, 1983; Hummel and Holyoak, 1997), inference (Goodwin and Johnson-Laird, 2005) and learning transfer (Hummel and Holyoak, 2003). And the capacity to process relational information is central to a theory explaining performance differences between and within age groups (Andrews and Halford, 2002; Halford et al., 2005) on the basis of the complexity of relations processed (Halford et al., 1998). Formally, a relation is a set of tuples, and the position of each item in a tuple identifies its role in the relation. According to relational complexity theory (Halford et al., 1998), the roles or positions within relations may constitute dimensions of variation across task instances, and that tasks involving more dimensions are more difficult. For example, the balance-scale task (i.e., judging whether two weights either side of a fulcrum will balance) is more difficult when both weights and distances from the fulcrum are varied over successive task instances than when weights (or distances) only are varied. In terms of the theory (Halford et al., 1998), the first case involves a more complex quaternary relationship between the two weights and two distances, whereas the second case only requires computing a less complex binary relationship between two weights (or distances) (Halford et al., 2002).

A number of researchers have manipulated dimensions of variation in different ways to identify brain regions responsive to relational complexity (Christoff et al., 2001; Kroger et al., 2002; Phillips and Niki, 2002, 2003; Prabhakaran et al., 1997; Waltz et al., 2001). In tasks adapted from Raven's Progressive Matrices tests, for example, the objective was to fill the empty square of a 3 × 3 grid containing eight display items with a choice item that preserves the relationships between the display items. In the 0-relation condition, the display and correct choice items were the same. Thus, there were no dimensions of variation. In the 1-relation condition, display items within but not between rows were the same. In this case, there was just one dimension of variation along columns. (Alternatively, items within columns were the same, and the dimension of variation was along the rows.) In the 2-relation case, items differed systematically within and between rows so that the dimensions of variation were two, and so on. Increased prefrontal and parietal activity was observed with increased dimensions (Christoff et al., 2001; Kroger et al., 2002; Prabhakaran et al., 1997). Inferring the missing item in a Raven's Matrices task consists of several component steps, including search for the dimension(s) of variation; selection of the target feature(s);

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* Corresponding author. Fax: +81 298 61 5857.
E-mail address: steve@ni.aist.go.jp (S. Phillips).
URL: http://www.staff.aist.go.jp/steven.phillips (S. Phillips).

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and match to the correct choice item. One step that appears to be a critical function of the frontal lobe is the integration of multiple relations to make an inference. Subjects with prefrontal but not temporal lobe damaged failed to make inferences that required integrating two or more relations (Waltz et al., 2001).

To identify relational complexity effects with other components of relational processing, an alternative method was developed contrasting short-term storage of relations with different indexes (or keys), meaning the number of roles or positions that afford unique reference to every relational instance (Phillips and Niki, 2002, 2003). For example, the relation (pair list) AB CD EF has a unary index because every pair is identifiable by a single cue at one position, whereas relation AB AD CB has a binary index because cues at both positions are necessary, in general. (For example, with AB CD EF in memory, cuing with A at the first position retrieves pair AB. With AB AD CB in memory, cuing with A at the first position retrieves both AB and AD. Cuing with A at the first position and B at the second position retrieves pair AB.) Thus, a list with a binary index requires more positional information to maintain the relationship between items. The roles spanned by the index are the dimensions of variation. A contrast of activity during retention of two binary index lists (AB AC CB and AB AD CD) versus two unary index lists (AB BC CA and AB BC CD) revealed greater activity in the occipitoparietal lobe (Phillips and Niki, 2003). Activity for both binary lists was greater than both unary lists for most of the retention period and also greater than a third unary index list (AB CD EF) for a bilateral region in the superior parietal lobule. This result suggests that the occipitoparietal lobe is sensitive to the complexity of relational information as manipulated by relational index.

A major difficulty with establishing complexity metrics (relational or otherwise) for cognitive science is distinguishing between complexity as apparent in task design and complexity as processed by the subject. Task strategy, background knowledge or familiarity with task materials can influence how relationships between task items are processed. To illustrate, the list black ball, black mail, foot ball has a binary index when interpreted as a lists of word pairs, but a unary index when interpreted as the word list blackball, blackmail, football. In the latter case, effective complexity (unary) is less than apparent complexity (binary). Effective complexity may also exceed apparent complexity when, for example, individual items are difficult to distinguish, causing say the unary index list ⩽⇂, ⩽↿, ⩾↾ to be recognized as the binary index list <↓, <↑, <↑ of more familiar items. Learning is one factor that can influence effective relational complexity. Here, we extend our earlier work by investigating the effect of learning on the maintenance of relational information by measuring activity for retention of binary versus unary index lists of learned versus novel pairs of items.

Materials and methods

Eight Japanese subjects (20–30 years old; right handed; two females) were recruited for the experiment after providing informed consent in accordance with AIST safety and ethics guidelines. Over a period of 4 months, subject performance was recorded in two types of sessions: (1) in learning sessions, subjects were trained to recognize specific pairs of shapes. (2) In scanning sessions, subjects performed pair recognition from lists of pairs from the learning session and lists of novel pairs. Both learning and scanning sessions used a pair recognition format where each trial consisted of a pair list followed by one or more probes, and subjects indicated whether the probe(s) appeared in the previous list. The timing for scanning trials is shown in Fig. 1, along with example shapes that were generated from Fourier descriptors (Zahn and Roskies, 1972).

Paired recognition task (learning sessions)

Each learning session consisted of eight blocks: two test blocks (first and last); and six study blocks. Each study block consisted of eight unique shape pairs. Within each study block, there were five study–test cycles. Each cycle commenced with the word “Study” (4000 ms) to indicate the start of the study phase. During this phase, the eight pairs were presented one at a time for 2170 ms followed by a 2000-ms interval when nothing was presented on the screen. After the eighth interval, the word “Test” appears (4000 ms) indicating the start of the test phase of the study block. The 16 shapes were paired so that four were studied and four were not. These test pairs were presented with the same timing as for the study phase. During test presentation, subjects were required to respond with the left arrow key if the test probe was a study pair (target) or the right arrow key if it was not (distractor). The order of study pairs and the choice of targets and distractors were randomized across cycles. At the end of each block, subjects were given a short 2- to 3-min rest before studying a new block of eight unique shape pairs. No shape appeared in more than one block. Therefore, subjects studied 48 unique shape pairs in one session. The six study blocks were preceded and followed by test blocks. There was a 30-min rest between the test and study blocks. All 96 study shapes were included in the test blocks and arranged into 24 pairs that appeared in study blocks as studied

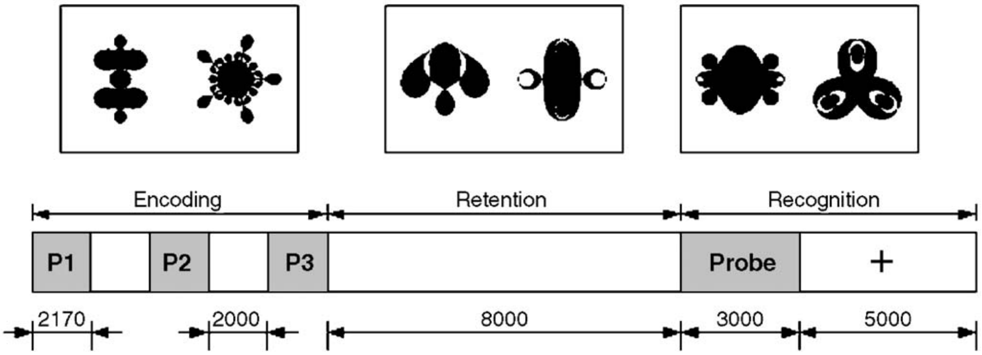

Fig. 1. Sample shape pairs and trial timing (scanning session).

pairs and 24 pairs that were not studied as pairs. Presentation was the same as for the study blocks. In total, one learning session lasted about 1 h. Subjects studied the same set of 48 study pairs in every learning session. But the selection of targets and distractors was randomized across and within sessions. The order of study blocks was also randomized.

Paired recognition task (scanning sessions)

The general format of a paired recognition task consists of presenting subjects with a list of pairs followed, after some delay, by a probe to which they respond depending on whether the probe was in the presented list. Here, lists consisted only of shapes from the learning session. In the learned condition, all three list pairs were studied in the learning session. In the novel condition, all pairs were not study pairs. As in previous studies (Phillips and Niki, 2002, 2003), lists were also arranged into unary and binary index conditions. A unary list consisted of six unique items in the form AB CD EF. A binary list consisted of four unique items in the form AB AD CB. Binary lists were randomly ordered so that the first and second pair always shared an item (i.e., all orders except AD CB AB and CB AD AB). The probe pair either appeared in the list (target) or did not (distractor) Thus, we used a 2 (learn, novel) × 2 (unary, binary) × 2 (target, distractor) design. A total of 32 trials (four per condition), randomly ordered, were administered for each scanning session. The 16 learned pair list trials were generated by randomly selecting 48 study pairs (=16 × 3 [pairs]) from the learning session. The 16 novel pair list trials were generated by random recombination of remaining shapes from the learning session to make up 48 novel pairs. The proportion of first, second and third position targets was 0.25, 0.5 and 0.25, respectively. Distractors were generated by repairing shapes from the presented list.

During each trial, subjects were given a list of three pairs of shapes. Each list pair was presented one at a time for a period of 2170 ms, separated by a 2000-ms interval where nothing appeared on the screen (encoding phase). Following the last pair, there was an 8000-ms delay period, where nothing was presented to the subject (retention phase). After the retention period, a probe pair was presented for 3000 ms, followed by a "+" symbol (5000 ms) to indicate the end of the trial (probe phase). The timing for each trial is shown in Fig. 1. During the probe phase, subjects were required to determine whether the probe paired appeared in the list. All materials were presented centrally, in black on a white background. All probe items, whether in target or distractor pairs, appeared in the same screen position (either left of right of center) as studied. The construction of lists was the same for all subjects within sessions but randomized across sessions.

Session schedule

Learning sessions preceded or followed scanning sessions by 1 or 2 days. There were four scanning sessions. The first three were 1 week apart, and the final scan was 3–4 months after the third scan. The schedule for scanning and learning sessions was S_1, L_1, L_2, S_2, L_3, L_4, S_3, S_4, where S_i and L_j are the scanning and learning sessions, respectively. The first learning session (L_1) did not start with a test block, since subjects had no prior pair learning on which to test. In total, then, we employed a 4 (session) × 2 (learned) × 2 (index) × 2 (probe) design for the scanning task and a 3 (session) × 2 (delay) × 2 (probe) design for the balanced part of the test blocks in the learning sessions. The two levels for the delay factor are the test blocks administered 30 min and 3 days after the study blocks. That is, the last (test) blocks in learning sessions L_1, L_2 and L_3 belong to level 1 (30-min delay between study and test) and the first (test) blocks of learning sessions L_2, L_3 and L_4 belong to level 2 (3-day delay between study and test).

Behavioral data acquisition/analysis (scanning sessions)

Subject responses and times were recorded with a three-button optical keypad attached to the subject's right leg. Subjects pressed the left button with their index finger (right hand) to indicate a target and either the middle or right button with their second or third finger to indicate a distractor. The finger–button combination used throughout the scan was decided upon by the subject based on what was most comfortable. Data were analyzed by Statistica (2000). Failure to respond within the allotted time was regarded as an error. When no response was recorded, response time was calculated as the mean of the times for the remaining trials in the same condition for that subject.

fMRI data acquisition/analysis

Scanning was performed on a 3.0-T MRI Scanner (GE 3 T Signa) with EPI capability. 18 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). SPM99 (Friston et al., 1995) was used to analyze the image data. Data were preprocessed (timeslice adjusted, realigned, normalized and smoothed) and fitted by a general linear model where regressors were defined for each subject session event type. There were 11 events types, including four (List × Learn) encoding events; four (List × Learn) retention events; and three (target, distractor, error) probe events. Encoding events were modeled by a step function convolved with a canonical hemodynamic response function, where onset and offset of the step function coincided with the presentation onset of the first pair and offset of the last pair. Retention events were modeled by a step function lasting for the interval between the offset of the last list pair and onset of the probe pair. Probe events were model by the canonical hemodynamic response function. 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. Whole-brain contrasts were conducted for each individual, and contrast values were entered into second-level t tests to obtain random effects analyses. The threshold was set at $P < 0.01$, uncorrected. Region of interest (ROI) analysis was conducted using MarsBar, version 0.23 (Brett et al., 2002) on a region identified as sensitive to index length from a previous study that used the same pair recognition procedure (Phillips and Niki, 2003). Regions are reported in Talairach coordinates (Talairach and Tournoux, 1988) after conversion from MNI coordinates using the algorithm specified in Brett (1999).

Results

Behavioral data

Learning sessions

A within-subjects repeated measures ANOVA for the test blocks in the learning sessions revealed a significant effect on errors for

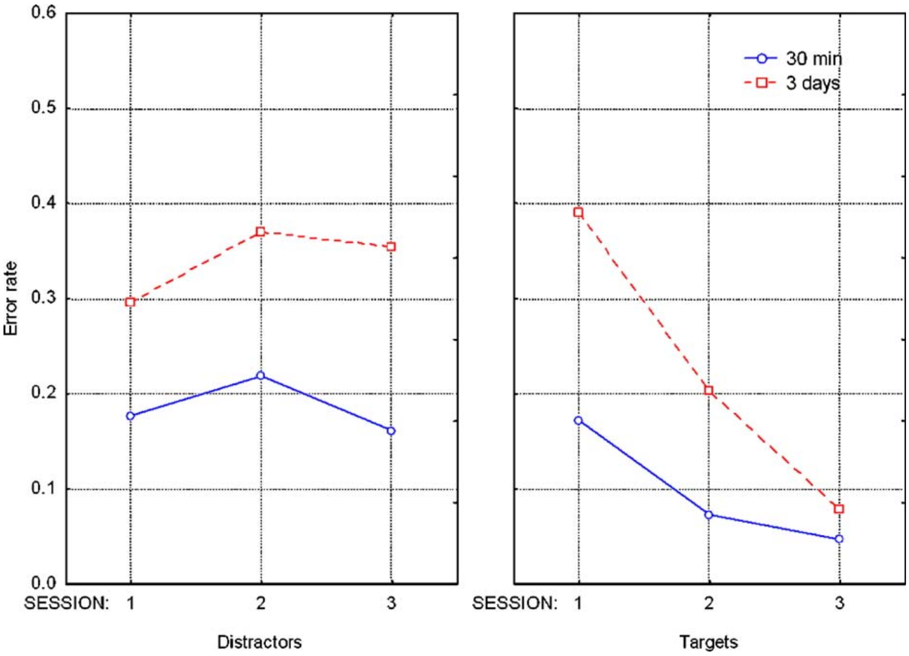

Fig. 2. Probe errors for learning session test blocks.

session, $F(2,14) = 7.27$, $P < 0.01$; delay, $F(1,7) = 115.11$, $P < 0.00001$; and probe, $F(1,7) = 18.36$, $P < 0.005$. There was also a session by probe interaction, $F(2,14) = 24.85$, $P < 0.00005$. Post hoc comparisons (Scheffe test, $\alpha < 0.05$) revealed within-session performance on targets was better than distractors for sessions 2 and 3 ($P < 0.05$). There was also a session by delay by probe interaction, $F(2,14) = 7.47$, $P < 0.01$ (Fig. 2). An ANOVA also revealed significant effects on response times for session, $F(2,14) = 9.70$, $P < 0.05$; delay, $F(1,7) = 9.80$, $P < 0.05$; and probe, $F(1,7) = 70.55$, $P < 0.00001$. There was also significant delay by probe, $F(1,7) = 9.27$, $P < 0.05$ and session by probe, $F(2,14) = 11.97$, $P < 0.001$ interactions. Post hoc comparisons (Scheffe test, $\alpha < 0.05$) revealed performance on targets was better than distractors for sessions 2 and 3 ($P < 0.05$) (Fig. 3).

Scanning sessions

Data for the first three sessions were analyzed separately because there was no training between the 3rd and 4th sessions. A within-subjects repeated measures ANOVA revealed a significant effect on errors for session, $F(2,14) = 8.14$, $P < 0.005$ and learned

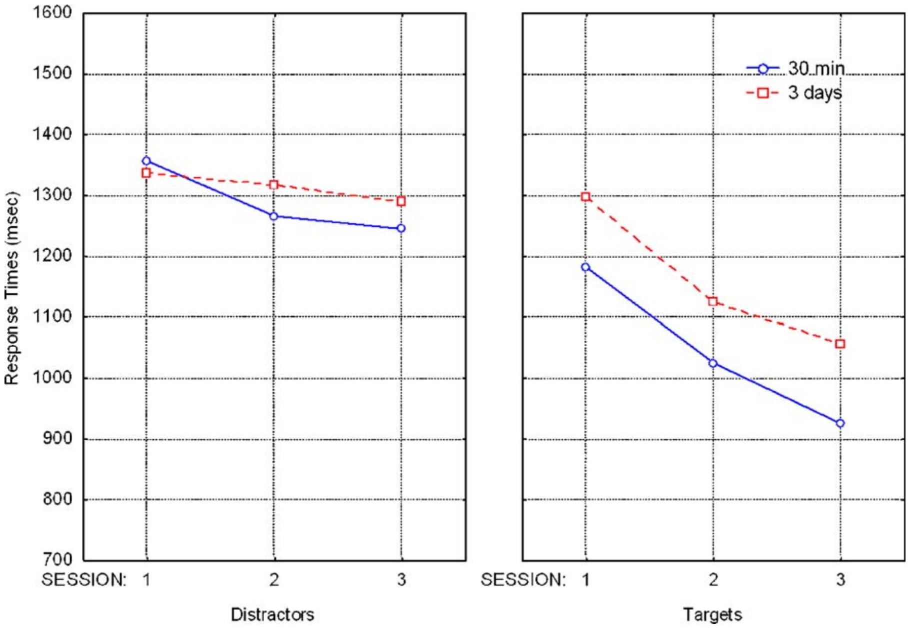

Fig. 3. Probe times for learning session test blocks.

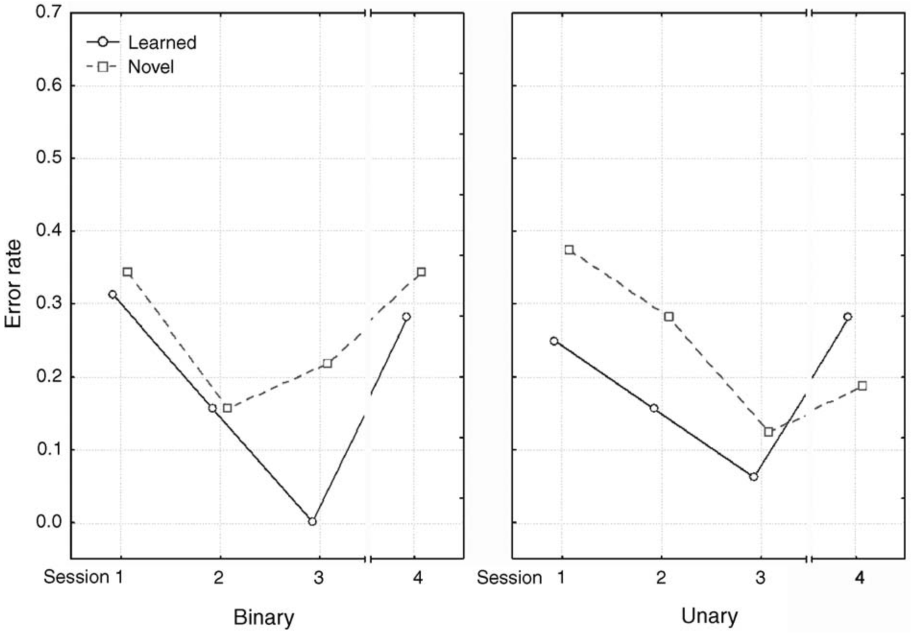

Fig. 4. Probe errors for scanning sessions.

factors, $F(1,7) = 16.53$, $P < 0.005$, but no effect for index, $F(1,7) = 1.64$, $P = 0.25$. (In one condition, all subjects responded without error. So, to perform a repeated measures ANOVA, performance for one subject was perturbed slightly by setting the mean to 0.01.) Mean error rates are shown in Fig. 4. Mean errors for the 4th session were not lower than for the 1st session. That is, 3–4 months after training ceased, performance returned to pretraining levels. An ANOVA revealed a significant effect on response times for session, $F(2,14) = 6.27$, $P < 0.02$ and learned factors, $F(1,7) = 18.44$, $P < 0.005$, but no effect of index, $F(1,7) = 0.26$, $P = 0.63$. Mean response times are shown in Fig. 5. Response times on the 4th session were not significantly faster than the 1st session.

Because all shapes were novel to the subjects at the start of training, between-session improvements in performance may result from either shape or shape pair learning. However, an interaction between session and learned factors implies additional improvement afforded by pair learning. For errors, there was no interaction ($P = 0.99$), but for response times, a two-way ANOVA contrasting 1st versus 3rd sessions revealed a marginally significant session by learned interaction, $F(1,7) = 5.34$, $P = 0.055$. Post hoc

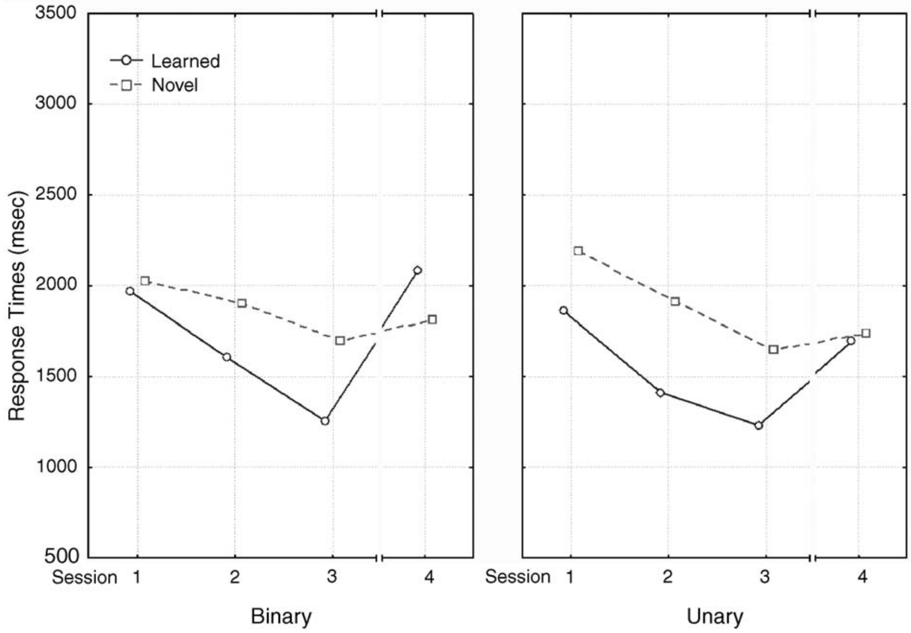

Fig. 5. Probe times for scanning sessions.

comparisons (Scheffe test, $\alpha < 0.05$) indicated that response times for lists of learned pairs in session 3 were significantly faster than the lists of learned (actually novel) pairs ($P < 0.05$) or novel pairs ($P < 0.05$) in session 1. Response times for learned pairs lists were faster than novel pair lists in session 3, but the difference was not significant ($P = 0.4$).

Discussion

The significant effect of session on errors and response times for the test blocks of the learning sessions indicates that training was effective. Furthermore, the convergence of response errors for test blocks administered 30 min and 3 days after study blocks indicates transfer into longer term memory. Increase in response time for distractors over targets is typical of search tasks, where search can be terminated immediately upon locating the target, but must continue against all list elements to correctly reject a distractor.

The significant effect of session and learned factors on errors and response times for the scanning sessions indicates that training also transferred to the scanning sessions. Improvements in performance across sessions reflect both shape and pair learning. The interaction between session and learned factors reflects pair learning only because shapes in learned and novels sets were given equal exposure during study and test blocks in the learning sessions. However, any behavioral gains acquired through training were lost by the 4th session, indicating that the effects were not permanent.

The lack of an index effect at the behavioral level for the scanning sessions is probably because both levels are well within relational processing capacity limits, given empirical data for a capacity of up to quaternary relations (i.e., four dimensions of variation) (Halford et al., 2005). In addition, there was only one possible distractor in the binary conditions compared to six possible distractors in the unary conditions. This difference may make it easier to reject distractors for binary than unary index lists. An ANOVA revealed a marginally significant index by probe interaction on response time ($P < 0.06$), where the response time on targets was slower for binary (1793 ms) than unary lists (1710 ms), but faster for binary (1794 ms) than unary lists (1862 ms) on distractors.

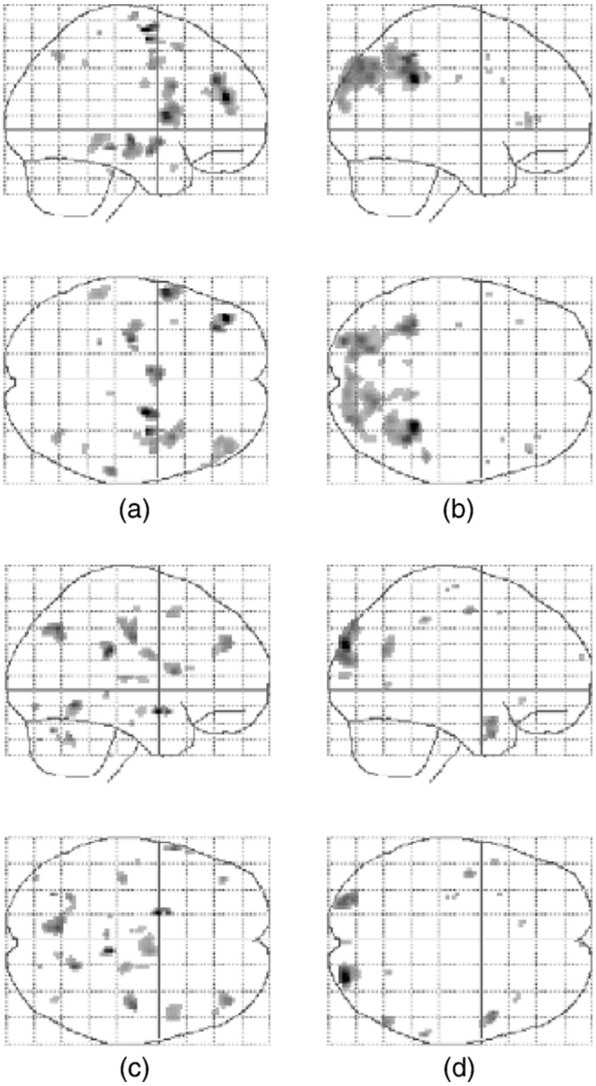

Fig. 6. Contrasts for (a) binary minus unary lists in session 1, (b) binary minus unary lists of learned pairs in sessions 2 and 3, (c) binary minus unary lists of novel pairs in sessions 2 and 3, and (d) (binary minus unary) by (learned minus novel) lists in sessions 2 and 3.

fMRI data

Both whole-brain and region-of-interest contrasts were conducted to assess the effects of learning on brain regions sensitive to changes in index.

Whole-brain contrasts

A contrast of binary minus unary indexed lists for the first session (i.e., before any training) is shown in Fig. 6(a). Locations and significance levels of the peak voxel from clusters containing more than 10 contiguous voxels exceeding the significance threshold of $P < 0.01$, uncorrected, are shown in Table 1(a). Clusters of increased activity for binary in contrast to unary index lists were observed in bilateral middle frontal gyrus (BA 6/9/10), bilateral superior frontal gyrus (BA 6/8/9), bilateral precentral gyrus (BA 6/44), bilateral middle temporal gyrus (BA 21), right superior temporal gyrus (BA 22), left anterior cingulate (BA 25) and right inferior parietal lobule (BA 7).

A contrast for retention of binary minus unary indexed lists for lists of learned pairs in sessions two and three (i.e., sessions following 1 or 2 weeks of pair training) is shown in Fig. 6(b), and voxel locations and significance levels are shown in Table 1(b). Increased binary list activity was observed in bilateral inferior parietal lobule (BA 40), right superior parietal lobule (BA 7), bilateral cuneus (BA 19) and right precuneus (BA 7/19).

A contrast of retention activity for binary versus unary lists of novel pairs for sessions two and three is shown in Fig. 6(c). Voxel locations and significance levels are shown in Table 1(c). Clusters of significant activity were found in bilateral parahippocampal gyrus (BA19/34), right posterior cingulate (BA 23), left precuneus (BA 7), bilateral precentral gyrus (BA 4/6/44) and right middle frontal gyrus (BA 8/10).

A contrast yielding the interaction between index and learning is shown in Fig. 6(d), and voxel locations and significance levels are shown in Table 1(d). Significant clusters were observed at bilateral cuneus (BA 19), bilateral precuneus (BA 7/19), right middle temporal gyrus (BA 21/38), right superior temporal gyrus (BA 39) and left precentral gyrus (BA 6).

Table 1
Significant voxels (a) session 1 binary minus unary lists, (b) sessions 2 and 3 binary minus unary lists of learned pairs and (c) novel pairs and (d) (binary minus unary) by (learned minus novel) lists in sessions 2 and 3

	Voxels	T	P_{uncorr}	Location (mm)			Region	BA
(a)	30	8.23	0.000	22	−5	61	Middle frontal gyrus	6
		5.89	0.000	24	3	62	Superior frontal gyrus	6
	120	8.14	0.000	−40	44	16	Middle frontal gyrus	10
		6.43	0.000	−34	38	28	Superior frontal gyrus	9
	125	6.98	0.000	−55	6	7	Precentral Gyrus	44
	29	6.72	0.000	34	−3	55	Middle Frontal Gyrus	6
	90	6.07	0.000	−26	−18	−4	Lentiform Nucleus	
		4.30	0.002	−36	−14	−11	Caudate	
	91	5.68	0.000	−6	−4	−12		
		5.44	0.000	−4	2	−7	Anterior cingulate	25
	53	5.27	0.001	38	11	25	Middle frontal gyrus	9
	14	5.11	0.001	59	−30	−9	Middle temporal gyrus	21
	45	4.20	0.002	42	−2	39	Precentral gyrus	6
		3.55	0.005	34	−2	46	Middle frontal gyrus	6
	133	4.17	0.002	44	46	18	Middle frontal gyrus	10
		3.99	0.003	48	47	9	Middle frontal gyrus	10
		3.91	0.003	40	42	29	Superior frontal gyrus	9
	30	4.02	0.003	32	16	49	Superior frontal gyrus	8
	17	4.00	0.003	46	−2	−8	Superior temporal gyrus	22
	27	3.90	0.003	38	−62	47	Inferior parietal lobule	7
	46	3.88	0.003	−55	−37	−3	Middle temporal gyrus	21
	13	3.33	0.006	42	−6	28	Precentral gyrus	6
(b)	556	9.06	0.000	32	−41	33	Inferior parietal lobule	40
		6.82	0.000	40	−44	43	Inferior parietal lobule	40
		4.63	0.001	28	−56	45	Superior parietal lobule	7
	762	6.38	0.000	−26	−86	34	Cuneus	19
		6.36	0.000	−36	−40	46	Inferior parietal lobule	40
		6.27	0.000	−34	−45	39	Inferior parietal lobule	40
	642	5.56	0.000	16	−66	42	Precuneus	7
		5.47	0.000	26	−82	34	Cuneus	19
		5.23	0.001	28	−78	41	Precuneus	19
	23	4.60	0.001	51	−33	33	Inferior parietal lobule	40
	12	4.13	0.002	48	31	4	Inferior frontal gyrus	
(c)	17	7.45	0.000	−18	−1	−10	Parahippocampal gyrus	34
	33	6.12	0.000	8	−28	24	Posterior cingulate	23
	99	5.60	0.000	−8	−58	40	Precuneus	7
	39	5.52	0.000	18	−54	−2	Parahippocampal gyrus	19
	73	5.08	0.001	42	−14	30	Precentral gyrus	6
	17	4.93	0.001	−58	10	10	Precentral gyrus	44
	56	4.51	0.001	40	44	21	Middle frontal gyrus	10
	25	4.33	0.002	−28	−56	−16		
	59	4.19	0.002	8	−4	20	Caudate	
	21	3.95	0.003	−40	−18	40	Precentral gyrus	4
	15	3.81	0.003	18	−20	8	Thalamus	
	40	3.64	0.004	46	12	42	Middle frontal gyrus	8
(d)	177	6.63	0.000	26	−86	30	Cuneus	19
		3.88	0.003	22	−79	45	Precuneus	7
	174	4.83	0.001	−26	−86	25	Cuneus	19
		4.59	0.001	−26	−79	43	Precuneus	19
	50	4.42	0.002	51	7	−24	Middle temporal gyrus	21
		4.38	0.002	48	7	−17	Middle temporal gyrus	38
	48	4.09	0.002	53	−59	27	Superior temporal gyrus	39
	13	4.05	0.002	−44	−5	48	Precentral gyrus	6

Note. The table shows the cluster size, peak voxel T score, P value (uncorrected), location, region and corresponding Brodmann area of the nearest gray matter.

Region-of-interest (ROI) contrasts

ROI analysis was based on a bilateral region centered in the superior parietal lobe at or near the precuneus identified as sensitive to list index from our previous study, which used the same recognition procedure (Phillips and Niki, 2003). In that study, the activities for retention of two types of binary index lists (AB AC CB and AB AD CB) were greater than for three types of unary index lists (AB BC CA, AB BC CD and AB CD EF). For this study, each ROI was defined as the intersection of the region from the previous study and a 5-mm sphere centered on the peak voxels, located at [−22 −70 37] and [22 −78 41], which border on the occipitoparietal sulcus. ROI activity was defined as the mean activity over all voxels within a region. Contrast values for each subject specific contrast were entered into second-level t tests to obtain random effects analyses. The significance of binary minus unary lists for learned and novel pair list conditions in each session and region is given in Table 2. For the left hemisphere, there was a significant index effect for session 2 lists of learned ($P < 0.003$) and novel pairs ($P < 0.05$) but not for the other sessions. The index by learned interaction for session 2 was not significant ($P = 0.21$). There was also a significant three-way index by learned by session (1 and 3) interaction ($P < 0.03$). For the right hemisphere, the effect of index on regional activity was marginally significant in session 2 ($P < 0.06$) and significant in session 3 ($P < 0.007$), but not significant in other sessions, or for novel pair lists. There was a significant index by learned interaction for session 2 ($P < 0.05$) and session 3 ($P < 0.05$) but not for session 1 ($P = 0.94$) or 4 ($P = 0.47$). There was also a marginally significant three-way index by learned by session (1 and 3) interaction ($P < 0.15$). Pooling contrast values for left and right hemisphere regions yielded a significant three-way index by learned by session (1 and 3) interaction ($P < 0.009$).

Discussion

Whole-brain contrasts revealed an interaction between index and learning. There was greater activity for retention of binary than unary index lists, and this difference was greater for lists of learned than novel pairs. Although the significance threshold was set at a relatively less conservative level, confirmation of the effect was obtained by ROI analysis. Because we used novel shapes, training involved both shape and pair learning. However, the within-session index by learned interaction in the 2nd and 3rd sessions suggests that this difference was due to pair learning, not just increasing familiarity with individual shapes, since the shapes in learned and novel pair list conditions had the same amount of exposure over the training sessions. Moreover, the three-way interaction indicated that the within-session interaction was not an artifact of a particular set of shapes because the same sets of learned and novel shapes were used in all sessions. If the effect was just a consequence of a particularly difficult to recognize set of shapes, then we would expect the same within-session interaction in session 1 and therefore no between-session three-way interaction. The difference between binary and unary indexed lists was no longer significant in session 4, 3 to 4

Table 2
ROI (superior parietal lobule) contrasts of binary minus unary indexed lists (P values)

Session	Left			Right		
	Learn	Novel	All	Learn	Novel	All
1	0.48	0.19	0.36	0.36	0.32	0.16
2	0.70	0.76		0.06	0.37	
3	0.003	0.05		0.007	0.47	
4	0.75	0.67		0.94	0.44	

months after training. The behavioral data indicated that the learning of shape pairs was forgotten, which adds further supports the link between learning and index.

We expected to observe parietal activity for the whole-brain contrast of binary versus unary lists for the first session (i.e., prior to learning), since this contrast is equivalent to that used in our previous study, even though we used different materials. However, for the first scanning session, pairs from both learned and novels sets were actually novel, since scanning took place prior to any training. ROI analysis indicated that the effect of index approached significance when contrast values for left and right regions for learned and novel lists on the first session were pooled ($P < 0.09$).

Some further support for effective relational complexity in the occipitoparietal region was found in an analysis of individual differences by correlating the directions of the learning by index interactions between each individual's behavior and contrast data. Linear regressions of target probe response time on amount of training (i.e., the first three sessions) of learned pair lists revealed greater slopes for binary than unary conditions for six of the eight subjects. For these six subjects, there was greater improvement in response to targets from unary than binary lists with training, which is consistent with a change in effective relational complexity with learning. For the right ROI in the occipitoparietal lobe, there was a greater contrast value for binary minus unary lists of learned pairs in the third session compared to the first session in five subjects. That is, the difference between binary and unary activation after training was greater than before. The directions of the interactions for response time and contrast data were the same in seven of the eight subjects ($P = 0.035$, where P is the chance probability that two random two-state variables coincide at least seven out of eight times). For the left ROI, seven subjects showed greater binary minus unary activity after training than before. But the interaction was in the same direction as the behavioral data in only five subjects ($P = 0.36$).

General discussion

The influence of learning on the difference between binary and unary index lists suggests that subjects were responding to effective relational complexity rather than complexity as specified by task design. Task design can place bounds on relational complexity, but within those bounds, there is still scope for variation in the way relations are processed. For example, suppose the task was to determine the serial position of each pair from the binary index list AB AD CB CD. A single (unary relational) cue-retrieval process implies chance-level performance at 50%. Therefore, in the case that subject performance is above this chance-level baseline and in the absence of task-specific strategies to reduce complexity, task design ensures that the effective complexity is at least binary. Conversely, though, there is no logical requirement to use a single cue-retrieval process to determine pair positions in the unary index list AB BC CD DA when a double (binary relational) cue-retrieval process will also work. The additional (apparently redundant cue) may compensate for the difficulty in distinguishing unfamiliar items. In this case, the effective complexity of an apparently unary relational condition would be binary.

Although the pair recognition task in this study only required maintaining item–item links independent of position information because probe items always appeared in the same position as studied, attention to positional information can still be employed to enhance list memory. The parietal lobes are often associated with visual/spatial attention (Corbetta et al., 1995; Losier and Klein, 2001; Nagahama et al., 1999). Awh and Jonides (2001) have argued that attention serves to maintain a better memory trace, for example, when spatial attention is directed toward the location where an item was presented. Given the lack of familiarity with the materials before training, it is reasonable to suppose that subjects enhance their memory for lists by increased attention to positional information for both unary and binary index lists. After training, when stronger item–item links have been established, less attention to positional information is needed in the unary case because each item is paired with only one other item. In the binary case, additional attention to positional information can prevent mixing traces for the two items paired with a single item. (To prevent, say, retaining a trace AE for pairs AB and AD, where E is some mixture of B and D.) In our previous study, we used Japanese kanji characters which were, naturally, easier for Japanese subjects to recognize and retain than the shapes used here. Importantly, though, the relative lack of an index effect in the first session was not because subjects could not do the task, implying that activity simply converged on a chance-level baseline. The mean error rate of 0.28 was significantly below the 0.5 chance response rate, $t = 4.58$, $P < 0.003$.

One consequence of this explanation is that if familiarity influences effective relational complexity, then we should see greater occipitoparietal activity for lists of novel than learned pairs even though list index is kept at the constant unary baseline. Indeed, a contrast of unary lists of novel minus learned pairs for session two ($P < 0.01$, uncorrected) revealed a 41 voxel cluster of activity with the peak voxel in the left cuneus (BA 19, [−28 −82 34]), and a 52 voxel cluster of activity with the peak voxel in the right cuneus (BA 19, [−20 −84 37]) that extended into the precuneus.

Several studies have interpreted changes in cortical activity with relational complexity in terms of the number of relational instances that must be integrated to make an inference (Christoff et al., 2001; Kroger et al., 2002; Prabhakaran et al., 1997; Waltz et al., 2001). Although relational integration is an important determinant of relational complexity (Halford et al., 1998), it is unlikely to be the aspect of relational complexity that caused the differences observed here. The pair recognition task employed here does not require integrating relations. In relational calculus terms (Codd, 1990), pair recognition involves select/project operations, whereas relational integration as in combining aRb and bRc to make the transitive inference aRc involves a join operation on common items (Halford et al., 1998; Phillips et al., 1995). Even if subjects integrate relations along shared items during retention, this factor was controlled for in our previous study (Phillips and Niki, 2003) from which the ROIs for the current study were defined. That is, the number of shared items in binary and unary lists was the same. Hence, we have interpreted the changes observed here in terms of differences in relational indexes.

Other regions

We have focused primarily on a region in the occipitoparietal lobe because we had strong evidence from our previous study that this region was sensitive to differences in relational index. However, other regions are also likely to be involved. As mentioned earlier, others have observed increased prefrontal activity in conditions of greater relational complexity, and the prefrontal cortex has also been implicated in the maintenance of spatial short-term memory (Smith and Jonides, 1998; Koch et al., 2005). The binary minus unary by learned minus novel contrast did not reveal significant clusters of activity in the prefrontal cortex (Table 1(d)). However, prefrontal activity was observed for binary minus unary lists in session 1 (Table 1(a)), and binary minus unary lists of novel pairs in sessions 2 and 3 (Table 1(c)). These contrasts suggest increased prefrontal activity with index before pair learning, rather than after learning. Consistent with this suggestion, a contrast of binary minus unary lists of novel minus learned pairs in sessions 2 and 3 ($P < 0.01$, uncorrected) revealed bilateral middle frontal gyral activity (74 voxels, BA 10 [−42 44 22]; 71 voxels, BA 10, [40 44 25]).

A possible role of the prefrontal cortex in this context is the inhibition of competing memory associates. Frontal and parietal lobes often co-activate under demanding conditions, yet a number of specific functional differences are evident. Koch et al. (2005) reported differential interference effects using repetitive transcranial magnetic stimulation during a memory task–memory performance was affected by stimulation of both regions during the delay period, but only by stimulation of the prefrontal cortex during the retrieval period. Prabhakaran et al. (2000) observed increased prefrontal activity for maintenance of integrated versus unintegrated item(letter)–position information but increased parietal and temporal activity for the reverse contrast. And Shimamura et al. (1995) found that subjects with frontal lobe lesions are more susceptible to intrusions from competing associations compared to normals. Both unary and binary list conditions require the integration of item–item information, but only the binary list condition contains items with multiple associates. Prior to training, the maintenance of binary index lists is more likely to incur the activation of competing associates, hence, the greater activity in prefrontal cortex. With training, the difference between binary and unary list activation of prefrontal cortex would be reduced if subjects learned to re-represent item pairs as unique single item chunks.

Consistent with the role of inhibiting competing associates for the prefrontal region is our observation of activity at the anterior end of ventrolateral temporal lobe with learning. In a pair associates task using the same type of shapes, Sakai and Miyashita (1991) found neurons in monkey anterior temporal cortex that responded only in the presence of trained pairs but not when the shapes that made up those pairs were presented individually. These neurons can be interpreted as re-representing item pairs as unique single items. A contrast of learned minus novel pair lists for session three ($P < 0.01$, uncorrected) revealed a 27 voxel cluster of activity with a peak voxel in the right inferior temporal gyrus (BA 20, [48 −3 −22]) and a subcluster with a peak voxel in the right middle temporal gyrus (BA 21, [50 6 −28]). It is possible that this region of right inferior/middle temporal gyrus is the human analogue of visual chunk learning observed in monkeys, which is consistent with the reduced need to inhibit competing associates for binary versus unary index lists in the prefrontal lobe.

This role for the prefrontal lobe, however, appears to be at odds with our interpretation of the effects in the occipitoparietal lobe—if the differential need to inhibit competing associations between binary and unary lists is reduced with learning, then it raises the question of why there is also an increased differential need to maintain positional information. The use of unusual shapes meant that subjects were likely exposed to two levels of learning – learning to recognize novel items and learning to recognize novel item pairs – during the 2-week training course. A composite bottom-up hierarchy/top-down reverse hierarchy model of visual perception and learning (Ahissar and Hochstein, 2004; Hochstein and Ahissar, 2002) admits multiple concurrent representations, and the transition from representing relations as item pairs to item pair chunks is unlikely to be an all-or-nothing process. In this regard, the progressive familiarity with individual items that drives the increased differential attention to positional information for item pair representations of binary/unary lists may be reconciled with the progressive availability of chunk representations of item pairs that drives the decreased differential need for top-down inhibition of competing associates.

Further work is needed to establish exactly what role the occipitoparietal region plays in the maintenance of relational memory and how that role interacts with those of the prefrontal and temporal lobes. Capacity for visual short-term memory appears to be localized to the occipitoparietal region (Marois and Ivanoff, 2005). However, it is not likely to just reflect a store for items because the unary list had more unique shapes. Nor is it likely to be just reactivation of associates during rehearsal because the number of associates was matched in contrasts of two binary versus two unary index lists in our previous studies. Instead, the increase in activity for binary index lists may reflect (attention to) additional positional cues to retain the correct pairing of items. Whatever the precise role of this region, though, its sensitivity to learning and index provides a window into the effective complexity of relational information.

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