

Separating Relational from Item Load Effects in Paired Recognition: Temporoparietal and Middle Frontal Gyral Activity with Increased Associates, but Not Items during Encoding and Retention

Steven Phillips and Kazuhisa Niki

Neuroscience Research Institute, AIST, Tsukuba Central 2, Tsukuba, Ibaraki 305-8568, Japan
E-mail: steve@ni.aist.go.jp

Received November 2, 2001

Working memory is affected by items stored and the relations between them. However, separating these factors has been difficult, because increased items usually accompany increased associations/relations. Hence, some have argued, relational effects are reducible to item effects. We overcome this problem by manipulating index length: the fewest number of item positions at which there is a unique item, or tuple of items (if length >1), for every instance in the relational (memory) set. Longer indexes imply greater similarity (number of shared items) between instances and higher load on encoding processes. Subjects were given lists of study pairs and asked to make a recognition judgement. The number of unique items and index length in the three list conditions were: (1) AB, CD: four/one; (2) AB, CD, EF: six/one; and (3) AB, AD, CB: four/two, respectively. Japanese letters were used in Experiments 1 (kanji—ideograms) and 2 (hiragana—phonograms); numbers in Experiment 3; and shapes generated from Fourier descriptors in Experiment 4. Across all materials, right dominant temporoparietal and middle frontal gyral activity was found with increased index length, but not items during study. In Experiment 5, a longer delay was used to isolate retention effects in the absence of visual stimuli. Increased left hemispheric activity was observed in the precuneus, middle frontal gyrus, and superior temporal gyrus with increased index length for the delay period. These results show that relational load is not reducible to item load. © 2002 Elsevier Science (USA)

Key Words: paired recognition; inferior parietal lobe; middle frontal gyrus; association; relation; complexity; chunking; Fourier descriptor; kanji.

INTRODUCTION

Since Miller's classic paper (Miller, 1956), many researchers have tried to characterize working memory through load effects, such as changes in error rates and reaction times as a function of number of study items.

Two such characterizations are distinguishable by their focus on relational versus item information. The relational processing view characterizes working memory load in terms of the arity of the relations computed between items (Halford *et al.*, 1998b). So, for example, tasks that require computing ternary relations (e.g., Gives[John, Mary, book]) induce higher error rates and longer reaction times than tasks requiring at most binary relations (e.g., Loves[John, Mary]). Alternatively, the item storage view characterizes load in terms of the number of items concurrently held in working memory (Cowan, 2001). This capacity limit is attributed to the maximum number of items that can be maintained within a focus of attention—the locus of accessibility by putative executive-control processes of working memory.

Cowan has noted that both theories place the limit of working memory capacity at approximately the same quantity, four. He argued that relational complexity effects are reducible to storage effects, because determining an *n*-ary relation between items requires keeping all *n* items within the focus of attention. However, relational complexity involves more than storage of items. It also involves processes for computing those relations (Halford *et al.*, 2001).

Brain imaging offers a potentially more sensitive technique than behavioral methods, because neurological regions may be distinguishable even when error rates and reaction times are not. However, there are some problems with attempting to separate potential item and relational effects. First, for a single relational instance, the arity of the relation is the number of items related. Second, experimental procedures used in behavioral studies to isolate relational complexity effects (see Halford, 1993) do not easily fit within the constraints of brain imaging. Third, tasks involving high arity relations are considerably more difficult in terms of error rates and reaction times. Thus, relational complexity effects may be confounded by neurological effects related to difficulty, such as arousal or

stress (Christoff, personal communication). In this paper, we overcome these problems with a concept taken from relational database theory called index length (see Halpin, 1995). The concept of index length and its link to relational complexity are detailed next to provide the conceptual background for the rest of the paper.

Relational Complexity and Index Length

A critical feature of relational complexity theory (Halford *et al.*, 1998b) is that it applies to the cognitive processes engaged in a task, rather than the relations that may be employed to specify the task. Consequently, two apparently similar tasks can involve processing relations of different arity (e.g., binary versus ternary), and two apparently dissimilar tasks may engage relations of the same arity (Halford *et al.*, 1998a). So, for example, the statement, "John owns a house and a car and a cat" does not imply that subjects must process the quaternary relation $\text{Owns}(\text{Owner}, \text{Object1}, \text{Object2}, \text{Object3}) = \{(\text{John}, \text{house}, \text{car}, \text{cat})\}$, because the same relational information is also captured by the binary relation $\text{Owns}(\text{Owner}, \text{Object}) = \{(\text{John}, \text{house}), (\text{John}, \text{car}), (\text{John}, \text{cat})\}$. This distinction captures the intuition that simply stringing together lists of items does not necessarily increase memory load. The reducibility of relational arity is determined by the length of the unique index on the relation (see Halpin, 1995). If a relation can be split and then rejoined so as to retain the original set of relational instances, then the relation is reducible. This procedure has been used to evaluate relational information in psychological tasks (see Phillips, 1997; Phillips *et al.*, 1998; Halford *et al.*, 1998b, for examples).

Unique index length (hereafter simply referred to as index length) is the fewest number of item positions at which there is a unique item, or item tuple (if length is greater than one), for every instance in the relational (memory) set. For example, the ternary relation $\text{Gives1}(\text{Agent}, \text{Patient}, \text{Object}) = \{(\text{John}, \text{Mary}, \text{book}), (\text{Sue}, \text{Tom}, \text{pen}), (\text{Paul}, \text{Ann}, \text{hat})\}$ permits a length one (unary) index at the Agent position, because no items in that position are repeated. The same applies to the other positions. However, the ternary relation $\text{Gives2}(\text{Agent}, \text{Patient}, \text{Object}) = \{(\text{John}, \text{Mary}, \text{book}), (\text{John}, \text{Mary}, \text{pen}), (\text{Sue}, \text{Tom}, \text{pen})\}$ does not, because each position has a repeated item. Instead, there is a unique length two (binary) index spanning Agent and Patient, because no pair of items at these positions is repeated. Whereas Gives1 is reducible, Gives2 is not.

The concept of index length is important for two reasons: (1) Index length explains why apparently high arity tasks do not necessarily impose high memory load with loss of performance—because they are reducible to lower arity relations (Halford *et al.*, 1998b). (2) The length of the index is not necessarily the arity of the

relation and therefore not necessarily the number of items bound within a single relational instance. Hence, relational complexity, as it is expressed in terms of index length, can be decorrelated from item number.

The second point is illustrated by the following example. The binary relation $R_1(P_1, P_2) = \{(A,B), (C,D), (E,F)\}$ has a unary index, because every pair has a unique item in the first (second) position. Logically, access to any pair requires at most one cue, either from the first or from the second position. The first pair, for instance, is retrievable by providing cue A (B) in the first (second) position. By contrast, the binary relation $R_2(P_1, P_2) = \{(A,B), (A,D), (C,B)\}$ has a binary index, because items are not unique across pairs in either position. Therefore, retrieval of only the first pair requires both cue A and cue B in the first and second positions, respectively. Separately, cue A (B) identifies both first and second (first and third) pairs. In going from the first to the second relation, the number of items per relational instance (two), the number of relational instances (three), and the total number of items (six) remain the same; and the number of unique items decreases (from six to four); but the index length increases (from one and two).

These differences have implications for both memory encoding and retrieval. For encoding, the number of item positions with common items (overlap) is at most the index length minus one. No pairs overlap in the unary indexed list, but one item is common to first and second and first and third pairs in the binary list. Increased index length implies increased similarity (in terms of shared items) between relational instances. Therefore, a longer index increases the likelihood of incorrect formation and hence retrieval of relational information. Or conversely, it increases the resources needed to maintain the same level of encoding fidelity. For retrieval, index length is the number of cues necessary to uniquely target a relational instance. How index length affects retrieval depends on whether the cues are applied to the memory set in parallel or in series. In the parallel case, a longer index increases the number of cues that must be simultaneously applied to obtain at most a single match. In the serial case, a longer index increases the number of intermediate retrievals that must be matched against the other cues.

For the purpose of direct comparison to Cowan's theory, one can think of the presented cues and retrieved items as symbols occupying a limited number of attentional slots (for a neural network level model of relational processes, see Halford *et al.*, 1998b). However, this interpretation does not mean that relational complexity is reducible to item complexity (i.e., number of items), because the two theories have different implications. Cowan argued that the effects of relational complexity can be accounted for in terms of the number of related items that must be kept in a focus of attention: processing a ternary relational instance imposes

greater load than a binary relational instance because it consists of more items. Depending on the interpretation, this argument implies either no difference between processing R_1 and R_2 relations, if the focus of attention is delimited to single relational instances, or greater load for the R_1 relation, if the focus of attention is expanded to include the entire relation. By contrast, index length implies greater load for the R_2 relation.

Introducing index length as an experimental variable addresses the methodological problems cited previously in that index length is not correlated with number of items; it can be manipulated within a simple Sternberg list recognition paradigm (Sternberg, 1966); and, as we shall see, manipulation of index length did not greatly impact upon error rates and reaction times. The next question is whether subjects are in fact sensitive to increases in index length. But, first, we review neurological studies related to this question before presenting our experiments.

Related Neurological Studies

A review of the neurophysiology literature for animals and humans suggested prefrontal cortex (PFC) as the site implicated in relational processes (Robin and Holyoak, 1995), which includes the integration of multiple relations (Waltz *et al.*, 2001). Relational complexity correlates with age and fluid intelligence (Andrews, 1997; Andrews and Halford, in press), and imaging studies have found increased frontal activity on fluid intelligence tests (Prabhakaran *et al.*, 1997; Duncan *et al.*, 2000). More specifically, contrasts of tasks requiring subjects to identify 0, 1, and 2 arithmetic operations needed to solve mathematics problems revealed more frontal activity in the 2-operation case (Prabhakaran *et al.*, 2001). Contrasts of 0, 1, and 2 binary relations in a Raven's matrices task revealed greater activity in the anterior regions of PFC for the 2-relation condition (Christoff *et al.*, 2001). A similar study using behavioral measures showed higher errors and longer times with more relations (Waltz *et al.*, 2000). These results are consistent with the relational theory (see Halford, 1993; Halford *et al.*, 1998b, for details) that was developed out of numerous experiments on adults, like transitive inference (Maybery *et al.*, 1986), requiring integration of (binary) relations (e.g., $>(x,y)$ and $>(y,z)$ implies $>(x,z)$); and children (Halford and Wilson, 1980; Halford, 1984; Andrews and Halford, 1998), where the frontal lobes undergo a protracted development throughout the first decade of life (Thatcher, 1991). Neural responses on an apparently dissimilar task such as n -back, where dorsolateral prefrontal cortex was activated for $n \geq 2$ (Cohen *et al.*, 1997; Smith *et al.*, 1998), can also be interpreted as the integration of multiple (successor) relations analogous to transitive inference (e.g., 2-back(x_t, x_{t-2}) \leftrightarrow Succ(x_t, x_{t-1}) and Succ(x_{t-1}, x_{t-2}) and Same(x_t, x_{t-2})).

Yet, the PFC is generally regarded as functionally heterogeneous. Many complex reasoning tasks as well as less complex short-term memory tasks invoke activity (see, for example, Cabeza and Nyberg, 2000; Christoff and Gabrieli, 2000; Nyberg *et al.*, 1996; Rugg and Wilding, 2000, for recent reviews). Raven's matrices tasks may modulate processes not specific to relational complexity. Instead, tasks involving multiple relations may invoke self-evaluating processes that operate on the products of other processes (Christoff *et al.*, 2001), where the dorsal/rostral region of PFC may be involved when information is internally generated (Fletcher *et al.*, 1998; Christoff and Gabrieli, 2000). However, if these intermediate relations are interpreted as items kept in a temporary store, then the effects can also be attributed to number of items stored.

Memory experiments have also been directly or indirectly concerned with possible item number and relational effects. For example, age-related dysfunction has been related to binding of feature information (Mitchell *et al.*, 2000a,b). Although memory experiments are typically concerned with associative processes where, in contrast to relational processes, positional information is generally irrelevant, they nonetheless share an important component, i.e., the binding of multiple items. (For formal definitions of associative and relational processes and their differences, see Phillips *et al.*, 1995.) Memory tasks consistently implicate prefrontal and parietal regions, although many factors influence the degree and location of activity. Rypma *et al.* (1999) contrasted one-, three-, and six-letter item loads in a recognition task and found more anterior prefrontal activity with higher load. This study varied the number of items, but not the relationships to other items. Hunkin *et al.* (2000) contrasted the number of associates in a recall task and found greater right inferior frontal activity in the two versus one associated targets condition, but greater left inferior frontal activity in the four versus one target condition. This study suggests greater frontal activity with number of associates, but the number of targets to be retrieved also increased. Furthermore, subjects were given repeated training on the cue-target pairs before testing. Training also affects prefrontal activity (Klingberg and Roland, 1998) and differs from relational tests where items are presented only once. Along similar lines, Rugg *et al.* (1998) and Allan *et al.* (2000) found greater right anterior PFC activity in a word-stem (many associates) versus word-fragment (few associates) completion task in the zero-target condition (none of the associates was a target, i.e., appeared in the study list), suggesting a monitoring role for this region, since more associates must be checked to see whether they appeared in the study list. This study can also be interpreted as varying number of items. In a recognition test, Rugg *et al.* (1999) also found greater right anterior PFC activity in the high-

density (80% of test words in study list) versus low-density (20% of test words in study list) recognition condition, but not in the source condition, where subjects must determine on which side of the display the test word appeared in the study list. Instead, left inferior frontal gyrus was more active in the source relative to the high-density recognition condition. The source versus recognition contrast appears to manipulate relational complexity, since it can be interpreted as a binary relation between item and position information in the source condition ($R_{WP}(\text{Word}, \text{Position})$), and a unary relation in the recognition condition ($R_W(\text{Word})$). But, the number of items in the relation also varies, with two items for each instance in the source (location) condition and only one item in the other condition. In both conditions, Word provides a unique index into the memory set, so index length is unchanged. Pair-associate learning has also been investigated with brain damaged patients using the AB-AC and AB-ABr paradigms. Subjects learn two lists of associates, where cues A from the first list AB are paired with new associates C in the second list (AB-AC) or repaired with another associate from the first list (AB-ABr). (In both paradigms index length is two, since list [i.e., first, or second] and cues A uniquely identify all associates.) Subjects with frontal lobe damage perform poorly on the second list, with many errors arising from intrusions of first-list associates. These results suggest that the frontal lobes may also play a role in inhibiting irrelevant associations (Shimamura *et al.*, 1995). Finally, Prabhakaran *et al.* (2000) found greater activity in the right middle and superior frontal gyri for the maintenance of integrated versus unintegrated letter and position information, but bilateral parietal and temporal activity for the reverse contrast. In the integrated conditions, letters were presented at the locations to be memorized. In relational terms, this corresponds to a binary relation $R_{LP}(\text{Letter}, \text{Position})$. In the unintegrated conditions, letters were presented separately from the locations to be memorized. This arrangement can be interpreted as two unary relations $R_L(\text{Letter})$ and $R_P(\text{Position})$, since neither is a cue for the other.

Outline of the Paper

We conducted five experiments designed to isolate relational effects, in terms of index length, from item effects. All experiments have the same general structure and follow the Sternberg list recognition paradigm. That is, subjects were given a study list of two or three pairs of items from which they made a recognition judgement on a test pair. There were three types of study lists: u4 = AB, CD—four unique items, unary index; u6 = AB, CD, EF—six unique items, unary index; and b4 = AB, AD, CB—four unique items, binary index. A test pair (probe) was either a target—

items appeared together in the study list—or a distractor—items did not appear together in the study list (e.g., in the u4 condition, AB is a target and AD is a distractor). All test items appeared in the same position as presented in the study list (i.e., there were no reversals). Japanese letters were used in Experiments 1 (kanji—ideograms) and 2 (hiragana—phonograms), digits in Experiment 3, and shapes generated from Fourier descriptors (Zahn and Roskies, 1972) in Experiment 4. Between experiment analysis is provided on these four experiments, followed by conjunction analysis to establish population-level inferences. The cause of the index length effect is discussed, and a further experiment is reported. Kanji were used in Experiment 5 with a longer delay to isolate the effect of index length of retention in the absence of visual stimuli.

EXPERIMENT 1: KANJI PAIRED RECOGNITION

Japanese kanji characters were used as items in this paired recognition experiment. Kanji are roughly word units. A character may constitute a word individually or when combined with another character; and each kanji may have one or more pronunciations.¹ One advantage of using kanji is that there are many of them. With approximately 2000 for standard usage, many trials can be generated without repetition, minimizing possible priming, or learning, effects across trials.

Method

Eight Japanese university students (seven male, one female; right-handed) undertook the experiment, after providing informed consent, in accordance with AIST safety and ethics guidelines. Timing data for two subjects were unusable due to an equipment problem. Response error analysis was performed on all eight subjects, but response time and fMRI analysis was performed on the remaining six male subjects. Each subject undertook one session of 60 trials, consisting of an encode/study phase when a study list of two or three pairs of items (kanji) was presented one pair at a time, followed by a probe phase when a test pair (either a target or a distractor) was presented, followed by a response phase when the subject indicated whether the test pair was in the study list. The precise sequence of events is shown in Fig. 1, including additional events for punctuation. For example, the first target pair is presented for 1170 ms, followed by a blank screen (1000 ms), followed by the second target pair for 1170 ms, and so on. A question mark indicates that the next pair is a probe, and a cross indicates the end of the current trial. Pairs were presented horizontally, in black on a white background, and centered. Pairs were

¹ Historically, kanji derived their shape from the objects they denote. But, this link is all but lost in modern script.

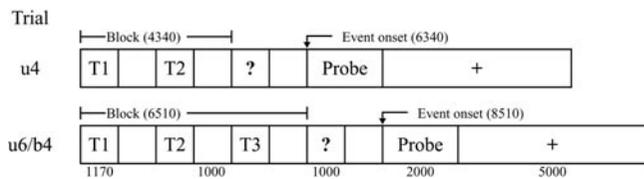


FIG. 1. Block and event timings (ms) for each trial. Arrows indicate event onset times relative to the start of the trial. All other numbers indicate block or event durations. For example, on u4 trials, a subject was shown study/target pair (T1), followed by a blank screen, followed by study pair (T2), and so on. The “?” screen indicates that the next pair is a probe, requiring a recognition response. The “+” screen indicates the end of the trial.

constructed from a list of low- to medium-frequency kanji and screened by a native Japanese speaker, so as to be meaningless, minimizing semantic and phonetic associations, and roughly balanced by stroke count. No pair formed a word or was pronounceable as one. 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. We used a 3 (Complexity) \times 2 (Probe) \times 10 (Trial) design. In the three-pair conditions (u6 and b4), 8 of 10 target probes matched the middle pair, to avoid potential primacy and recency effects. In the two-pair condition (u4), target probes were evenly selected from first and second pairs. In condition b4, 8 of 10 targets where the (A,B) pair, where both items appeared in more than one pair in the study list. No kanji appeared in more than one trial, including practice trials. Conditions and pairs were randomly ordered. See Fig. 2a for a sample trial.

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 fingers (right hand) to indicate a target and by pressing either the middle or right button with either their second or third fingers 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 complexity-probe condition for that subject. Keypad failures were rare, with only one in each of the first three experiments and two in the last experiment from a total of 1500 trials.

fMRI data acquisition/analysis. Scanning was performed on a 3.0-T MRI scanner (GE 3T Signa) with EPI capability. Eighteen axial slices (5.5 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 = 32 ms, FA = 70°, FOV = 20 \times 20 (64 \times 64 mesh). Images were preprocessed (timeslice adjusted, realigned, normalized, and smoothed) by SPM99 (SPM, 1999). Data were estimated to establish a fixed model in which there were three block types corresponding to the list type (u4, u6, b4) defined for the encode phase, and 3 (u4, u6, b4) \times 2 (target, distractor) + 1 (error) event types were defined for the probe phase. Block types were modeled using a boxcar function convolved with the canonical hemodynamic response function. Event types were modeled with the canonical hemodynamic response function. For the purposes of this study, detailed contrast analyses were reported for the encoding phase only (but, see also General Discussion for the probe phase). Block

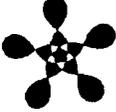
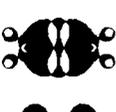
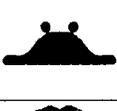
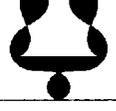
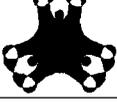
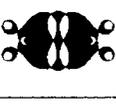
T1	著 奈	け ら	8 7		
T2	著 為	つ ひ	3 4		
T3	角 為	れ な	3 7		
Probe	著 為	つ な	8 4		
	a	b	c	d	

FIG. 2. Sample trials for (a) kanji, (b) hiragana, (c) number, and (d) shape paired recognition experiments. The top three rows show study pairs presented during the study phase. The bottom row shows test probes, where (a) and (d) are targets (appeared in the study list), and (b) and (c) are distractors (did not appear in the study list).

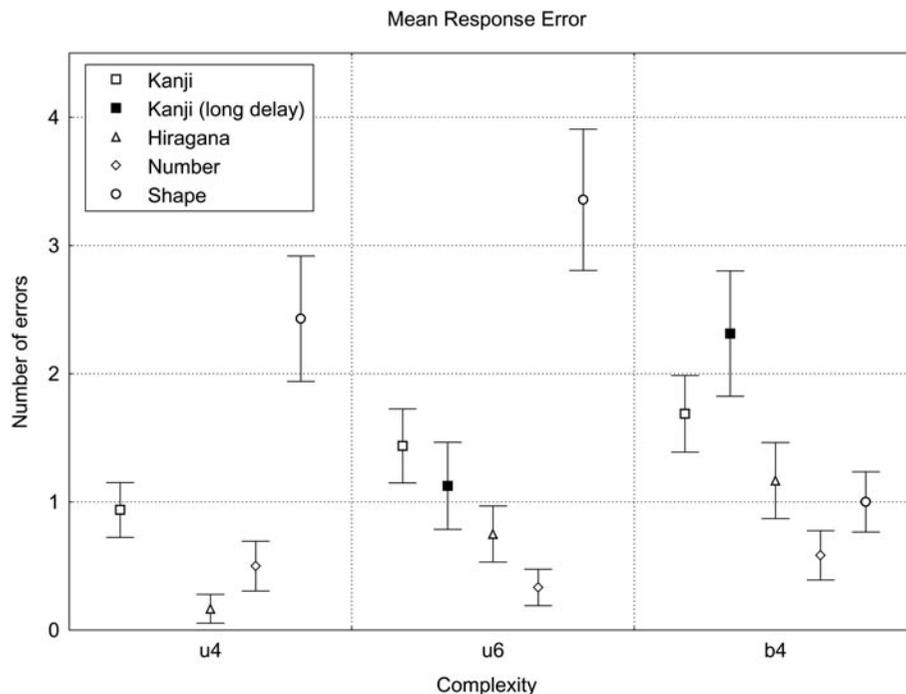


FIG. 3. Mean response errors by Complexity, collapsed over targets and distractors. Error bars indicate one standard error.

durations and event onsets are shown in Fig. 1. Event intervals were slightly longer than multiples of the scan rate to maximize the sampling rate. Conditions and pairs were randomly ordered and counter balanced (i.e., 10 trials of each of the six condition–probe combinations). For contrast analysis, locations reported by SPM99 were converted into Talairach coordinates (Talairach and Tournoux, 1988) by the transform specified in the *mnit2tal.m* program (Brett, 1999). These coordinates were used to determine brain regions using the Talairach Daemon program version 1.1 (Lancaster *et al.*, 2000).

Our initial method of analysis for this and the other experiments was by summary contrasts to identify differences in activation averaged over all subjects. Summary contrasts provide a first pass through the data. Because activity may arise from just one subject with a highly significant difference, or several subjects with more moderately significant differences, it can be regarded as a disjunctive contrast. That is, it addresses the question of whether any subject exhibits significant activity for the contrast investigated. In a later section, we followed up with conjunction contrasts to address the more specific issues of whether any of these differences were common across all subjects and in what proportion of the population we can expect them to occur. Since to our knowledge this study is the first attempt to directly distinguish relational from item load effects in the brain, and we had few expectations regarding the regions of difference, we adopted a standard cutoff threshold of $P < 0.05$, corrected for multiple

comparisons, when reporting statistical parameter maps throughout this paper. Because analysis was performed over the entire brain, this threshold was stricter than the alternative standard of $P < 0.001$, uncorrected.

Results

Behavior. A 3 (Complexity) \times 2 (Probe) repeated-measures ANOVA revealed no main effects and no interactions for errors, $F(2,14) = 2.58$; $P > 0.1$ (Complexity); $F(1,7) = 0.20$; $P > 0.6$ (Probe). Because there was no effect for Probe on errors for this and the other experiments, mean errors are reported collapsed over targets and distractors (Fig. 3). A 3 (Complexity) \times 2 (Probe) \times 10 (Trial) repeated-measures ANOVA revealed a main effect of Probe on reaction time, $F(1,5) = 8.08$; $P < 0.05$, with mean response times of 1070 ms (targets) and 1140 ms (distractors). There was no effect for Complexity $F(2,10) = 1.89$; $P > 0.2$. There was also a two-way interaction between Probe and Trial, $F(9,45) = 4.2$; $P < 0.001$. Post-hoc analysis (Scheffe test, $\alpha = 0.05$) revealed no significant differences between Probe by Trial means. Mean response times for Probe by Complexity collapsed over Trial are shown in Fig. 4a.

fMRI. The following four summary contrasts were performed on the fMRI data: (1) u6 versus u4; (2) u6 versus b4; (3) b4 versus u4; and (4) b4 versus u6. The common difference between the first and second contrasts is the number of unique items (six versus four);

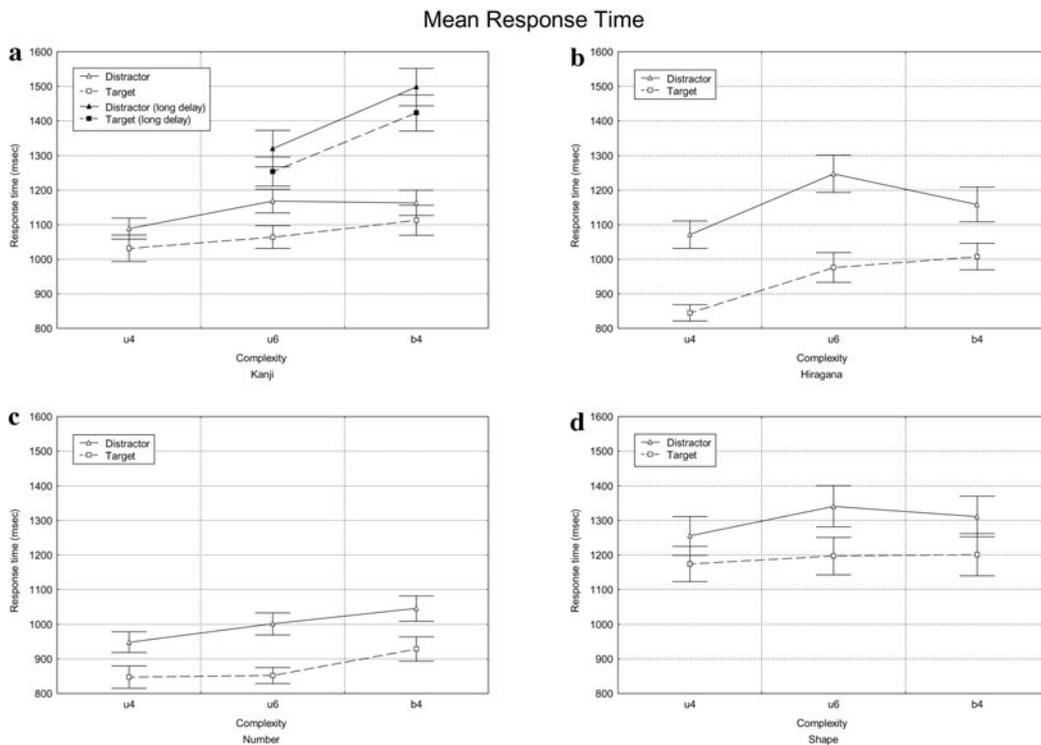


FIG. 4. Mean response times (ms) by Experiment and Complexity for target and distractor trials. Error bars indicate one standard error.

and the common difference between the third and fourth contrasts is index length (two versus one). Therefore, voxels common to both first and second (third and fourth) contrasts indicate sensitivity to item number (index length), independent of index length (item number). These contrasts were relabeled six versus four item number and binary versus unary index length, respectively. Figure 5a (top two rows) shows the statistical parameter map for the six versus four contrast, that is, the u6 versus u4 contrast ($P < 0.05$, corrected) masked by inclusion of only those voxels that also satisfied the u6 versus b4 contrast ($P < 0.05$, uncorrected). Figure 5a (bottom two rows) shows the statistical parameter map for the binary versus unary contrast, that is, the b4 versus u6 contrast ($P < 0.05$, corrected) masked by inclusion of only those voxels that also satisfied the b4 versus u4 contrast ($P < 0.05$, uncorrected). Locations are given in Table 1. The significance level of the primary contrast (e.g., b4 versus u6) is not affected by the secondary mask contrast (i.e., b4 versus u4), because the search and therefore the correction is only done by the primary contrast, which specifies the voxels to be checked by the mask. Since no search is involved for the secondary contrast its threshold is uncorrected. (The main text only refers to the more significant clusters of activity.)

For the six versus four contrast, the most significant increases ($P < 0.001$, corrected) in activity occurred

medially at or near the superior frontal gyrus (BA 6/8) and left middle frontal gyrus (BA 8). For the binary versus unary contrast, the most significant increases ($P < 0.001$, corrected) occurred at or near the right middle and superior frontal gyri (BA 6), right angular gyrus (BA 39), right inferior parietal lobule (BA 39/40), left precuneus (BA 7), and left superior parietal lobule (BA 7).

Discussion

The binary versus unary contrast showed the largest cluster of voxels of increased activity in the right inferior parietal lobule, including the angular gyrus. These results are consistent with an earlier study² using the same two experimental conditions, but a different baseline, where study lists had the form AA, BB, CC (Phillips *et al.*, 2001). The location (36 -74 31), size (1336 voxels), and significance ($Z = 7.54$) of this cluster are similar to that of the earlier study (37 -66 36; 1305 voxels; $Z = 7.07$). Two other clusters of increased activity were also comparable to the earlier study: left superior parietal lobule (30 -68 48; 210 voxels; $Z = 5.59$) compared with left inferior parietal lobule (37 -66 36; 245 voxels; $Z = 5.65$); and right middle frontal

² None of the six subjects in the earlier study took part in this experiment.

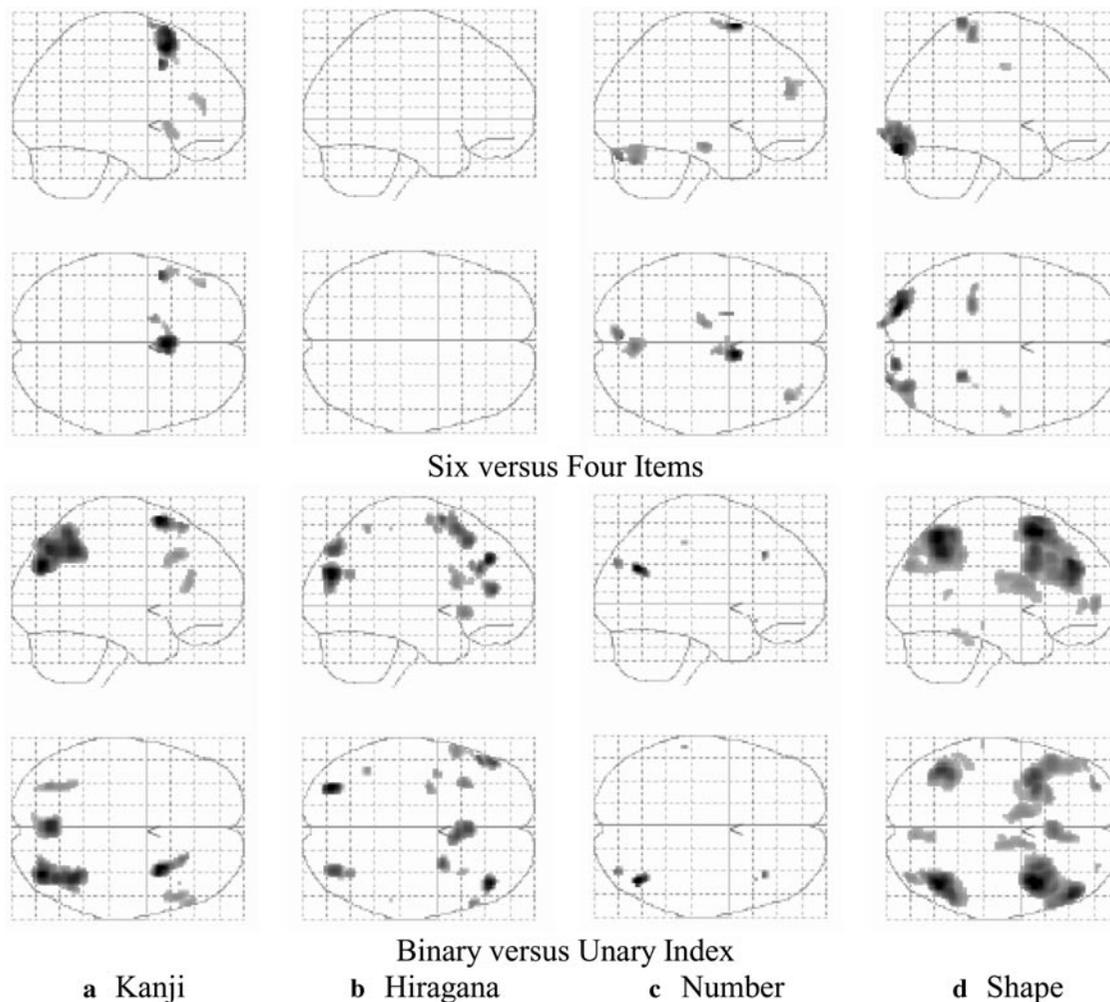


FIG. 5. Sagittal (top) and transverse (bottom) views of six versus four items and binary versus unary index for (a) kanji, (b) hiragana, (c) number, and (d) shape paired recognition.

gyrus (32 13 58; 175 voxels; $Z = 7.72$) compared with the same gyrus (42 3 55; 277 voxels; $Z = 5.69$). These comparisons indicate that the increased activity observed for the binary condition (particularly in the right inferior parietal lobule) is robust. Increased activity in the right middle frontal gyrus and right inferior parietal lobule was also reported by Klingberg and Roland (1998) for encoding versus recognition of pair associates of shapes generated from Fourier descriptors. Although their study did not manipulate index length, it suggests that the effect is not specific to kanji.

One possible role of the right parietal lobule in this task is to invoke increased shifts of spatial attention brought about by the overlap of study pairs in the binary, but not unary conditions. A number of studies have implicated the parietal lobes in shifts of spatial attention, for example, in visual search (Corbetta *et al.*, 1995; Ashbridge *et al.*, 1999) and memorization of locations (Kessels *et al.*, 2000). A review of the literature

suggested that the left parietal lobe is home to one module of visual attention to objects in the right hemifield, whereas the right parietal lobe houses two modules, one for each hemifield (Losier and Klein, 2001). Increased left parietal activity was also observed, but to a lesser extent than right parietal activity. This is consistent with the report that while left parietal activity has also been implicated in shifts of spatial attention, disruption of this area has less impact on reaction times for visual search than disruption of the right parietal lobule (Walsh *et al.*, 1999). Awe and Jonides (2001) have suggested that attention operates in the service of maintaining a better memory trace. It is reasonable to suppose that subjects repeatedly attend to left and right items in order to enhance their memory trace of a pair that overlaps with previously studied pairs.

The additional frontal activity observed in the binary condition, in particular BA 9/46 (dorsolateral PFC), may serve to monitor retrieval of incidental associates

TABLE 1

Significant Voxels of Activity for Kanji Contrasts (a) Six versus Four and (b) Binary versus Unary

P_{corr}	Z	Voxels	Location (mm)			Region	BA	Range
(a)								
0.000	7.15	401	2	16	51	Superior frontal gyrus	8	3
0.000	6.72		0	18	58	Superior frontal gyrus	6	5
0.011	4.89		-12	17	64	Superior frontal gyrus	6	5
0.000	6.29	24	-49	12	40	Middle frontal gyrus	8	1
0.001	5.36	12	-18	7	66	Superior frontal gyrus	6	3
0.007	5.00	61	-49	13	-2	Superior temporal gyrus	22	3
0.010	4.91		-53	19	-9	Inferior frontal gyrus	47	3
0.009	4.93	36	-44	41	9	Inferior frontal gyrus	46	3
(b)								
0.000	7.72	175	32	13	58	Middle frontal gyrus	6	3
0.000	5.86		24	28	54	Superior frontal gyrus	6	3
0.000	7.54	1336	36	-74	31	Angular gyrus	39	3
0.000	7.16		38	-50	41	Inferior parietal lobule	40	3
0.000	6.79		38	-62	40	Inferior parietal lobule	39	3
0.000	7.12	393	-2	-66	42	Precuneus	7	1
0.000	5.59	210	-30	-68	48	Superior parietal lobule	7	3
0.001	5.32		-30	-57	56	Superior parietal lobule	7	5
0.003	5.15		-30	-68	29	Precuneus	19	11
0.001	5.37	87	51	25	34	Middle frontal gyrus	9	3
0.005	5.05		51	17	30	Middle frontal gyrus	9	3
0.003	5.16	55	55	32	15	Middle frontal gyrus	46	1
0.006	5.03		53	34	22	Middle frontal gyrus	46	3
0.043	4.57	1	42	26	47	Middle frontal gyrus	8	1

Note. Each table of locations shows the corrected P value, Z score, number of voxels, and location of the most significant (generally central) voxel for each supercluster (i.e., unconnected cluster), its connected subclusters (rows with empty Voxel column), region and corresponding Brodmann area of the nearest gray matter, and its range from the cluster. Range is defined as the length of the smallest cube, centered on the most significant voxel, containing gray matter. Thus, a (maximum) range of 11 mm indicates gray matter at a distance of 5 mm along one or more axes. Empty columns indicate no gray matter within the maximum range along any axis.

during encoding (i.e., retrieval of previously studied associates to either of the currently presented items). Other studies have implicated dorsolateral PFC in the monitoring of externally (Christoff and Gabrieli, 2000) or internally (Fletcher *et al.*, 1998) generated information, or the inhibition of irrelevant associates (Shimamura *et al.*, 1995). Although these studies were concerned with cued recall of paired associates, some retrieval of associate information must also occur during encoding of overlapping pairs; otherwise subjects could not be sensitive to differences between unary and binary conditions. Furthermore, there is evidence that paired recognition and cued recall are based on common processes (Nobel and Shiffrin, 2001). In the binary condition, the AB pair (typically, the second pair) has one item common to the other two pairs (AD, CB). This permits either A or B to act as an implicit one for incidental retrieval of a first pair associate (i.e., D or C, depending on whether AD or CB was the previous pair). In this case, frontal regions could act to either inhibit the incidentally retrieved associate or enhance the trace of the current pair by repeated attention via excitatory connections back to the parietal lobes.

The increase in item load, six versus four unique kanji, activated the medial superior, middle, and left

inferior frontal gyri. Increased activity at these gyri was also reported on a letter memory load task (Rypma *et al.*, 1999). However, activity was more lateralized and right hemisphere dominant in their six versus one letter contrast, but not in their three versus one contrast. Following their explanation, this difference may be because the three versus one contrast does not transcend the putative four-item capacity limit. These regions become activated only when the limit is exceeded. The same situation applies to the six versus four unique kanji contrast, since all conditions are at or above this limit. Therefore, this contrast will be less sensitive to changes in item load. A cluster of activity (40 40 20; BA 10) was revealed, although, for the u6 versus u4 contrast, at a lower level of significance ($P < 0.001$, uncorrected).

At least in the domain of Japanese kanji, relational effects in the form of the number of items to which an item is related (associated) are not reducible to item effects, contrary to Cowan's (2001) claim. It cannot be explained by item (storage) load, because in the b4 (binary) condition the number of unique (or presented) items was less than (or equal to) the number of items in the u6 and u4 (unary) conditions. The next three experiments examined the generality of these results.

TABLE 2

Significant Voxels of Activity for Hiragana Contrasts (a) Six versus Four and (b) Binary versus Unary

P_{corr}	Z	Voxels	Location (mm)			Region	BA	Range
No suprathreshold voxels								
(a)								
(b)								
0.000	6.32	194	-30	-74	26	Superior occipital gyrus	19	9
0.000	6.15	93	42	40	31	Superior frontal gyrus	9	1
0.000	5.66	135	32	-72	42	Precuneus	19	3
0.000	5.60	321	2	24	43	Medial frontal gyrus	8	3
0.000	5.52		6	18	53	Superior frontal gyrus	8	3
0.000	5.59	70	-48	41	9	Inferior frontal gyrus	46	1
0.000	5.54	32	-49	32	26	Middle frontal gyrus	46	5
0.001	5.48	59	26	7	59	Superior frontal gyrus	6	5
0.003	5.14	59	-32	19	-4	Inferior frontal gyrus	47	1
0.004	5.08	34	34	-61	25	Middle temporal gyrus	39	3
0.004	5.08	20	55	29	26	Middle frontal gyrus	46	1
0.005	5.02	86	-57	14	16	Inferior frontal gyrus	44	3
0.032	4.59		-55	24	15	Inferior frontal gyrus	45	3
0.007	4.93	14	-40	3	55	Middle frontal gyrus	6	3
0.008	4.92	29	-28	-1	59	Middle frontal gyrus	6	3
0.011	4.84	18	-42	-48	56	Inferior parietal lobule	40	1
0.020	4.70	15	34	17	-4	Inferior frontal gyrus	47	1
0.032	4.59	5	-26	-74	42	Precuneus	19	3
0.041	4.53	1	53	-30	55	Postcentral gyrus	2	3

Note. For definition of entries see Table 1.

EXPERIMENT 2: HIRAGANA PAIRED RECOGNITION

Japanese kanji characters may have multiple meanings and pronunciations. Hiragana, by contrast, are a set of 51 characters representing only Japanese phonemes (see Fig. 2b for examples). Each character has only one reading and no semantic content, although they may be combined to form words, like letters of the alphabet. In this and following experiments, we tested the generality of the effects observed in Experiment 1 with materials that have reduced semantic and phonetic information.

Method

Six Japanese university students (three male, three female; right-handed) undertook the experiment after providing informed consent. None of the six subjects undertook the first experiment. With the exception of the materials used, the method of data acquisition and analysis was identical to Experiment 1, so the details are not repeated here.

As with kanji, hiragana pairs were screened by a native Japanese speaker so that no pair pronounced a word. However, because the set of eligible pairs was small, pairs appeared in more than one trial, although each list of pairs was unique. A sample list is shown in Fig. 2b.

Results

Behavior. There was a main effect of Complexity on errors $F(2,10) = 5.09$; $P < 0.05$, but not for Probe $F(1,5) = 2.87$; $P > 0.1$. There were main effects of Complexity on response time $F(2,10) = 10.07$; $P < 0.005$, and Probe on response time $F(1,5) = 11.23$; $P < 0.05$. There was also a three-way interaction among Complexity, Probe, and Trial on response time $F(18,90) = 1.76$; $P < 0.05$. Post hoc analysis (Scheffe test, $\alpha = 0.05$) revealed no significant differences between Complexity by Probe by Trial means. Subject errors are shown in Fig. 3 and response times in Fig. 4b.

fMRI. The same contrasts performed in the previous experiment were also conducted here. In the six versus four contrast, there were no differences significant to $P < 0.05$, corrected. Figure 5b (top two rows) and corresponding Table 2a show increased activity at the less conservative threshold of $P < 0.001$, uncorrected. At this level, increased activity was observed at or near the lingual gyrus, bilaterally (BA 17/18), left superior frontal gyrus (BA 6/8), left superior temporal gyrus (BA 22), and left precentral gyrus (BA 4). Figure 5b (bottom two rows) and Table 2b show the binary versus unary contrast, significant to $P < 0.05$, corrected. Of these differences, the most significant increases ($P < 0.001$, corrected) occurred at or near the left superior occipital gyrus (BA 19), right superior frontal gyrus (BA 8/9), right precuneus (BA 19), right

medial frontal gyrus (BA 8), and left inferior and middle frontal gyri (BA 46).

Discussion

In the binary versus unary contrast, three regions of increased activity stand out as being in the same vicinity as those found in the kanji experiment: bilateral activation of the posterior lobes and the right frontal lobe. The cluster located in the right precuneus (32 -72 42; 135 voxels; $Z = 5.66$) is close to, but more dorsal to the cluster at the angular gyrus in the kanji experiment (36 -74 31; 1336 voxels; $Z = 7.54$). The cluster at the left superior occipital lobe (-30 -74 26; 194 voxels; $Z = 6.32$) is close to the precuneus subcluster for kanji (-30 -68 29), but more ventral to the parent supercluster at the superior parietal lobule (-30 -68 48; 210 voxels; $Z = 5.59$). In the right frontal lobe, the cluster at (26 7 59; 59 voxels; $Z = 5.48$) is in the same superior frontal gyrus, but more anterior for the kanji cluster (24 28 54) and its parent supercluster (32 13 58; 61 voxels; $Z = 7.72$) in the middle frontal gyrus. These similarities suggest common processes. However, the effect was generally stronger for kanji than hiragana, as seen by the cluster sizes and Z scores, particularly in the right parietal lobule, which was linked to the processing of visual information. Kanji convey more visual information than hiragana, in terms of both the number of strokes and their components. For example, the kanji characters for the words hold, hit, throw, and catch all contain the common component representing hand. There is no such structural organization for hiragana.³ Hence, visual information is likely to play a more prominent role in discriminating kanji than hiragana. By contrast, increased activity was found in the left inferior frontal gyrus (BA 44/45) for hiragana, but not kanji. This region is known for its role in phonological processes and rehearsal (phonological loop, Baddeley, 2000) and the maintenance of verbal in contrast to spatial information (see Prabhakaran *et al.*, 2000, and the cited references therein). The natural interpretation that follows is that discrimination of hiragana relies more on phonological processes, hence the increased significant difference in this area. This point is reinforced by the fact that kanji typically have multiple readings making phonetic information a weaker source for differentiation; and a planned comparison showing the difference in response times between u4 and u6 conditions was significant for hiragana $F(1,5) = 8.44$; $P < 0.05$, but not for kanji $F(1,5) = 0.04$; $P > 0.8$.

There were no suprathreshold voxels for the six versus four contrast. At a lower level of significance ($P <$

0.001, uncorrected), activity was observed in superior frontal gyrus (-6 3 68) close to clusters observed for kanji (-12 17 64 and -18 7 66), suggesting common storage-related processes when the putative capacity limit of four items is exceeded. For kanji, but not hiragana, a subcluster (-53 19 -9) was also observed in the left inferior frontal gyrus (BA 47), a region also linked to phonological processes. This difference may be due to the fact that a single reading of a single kanji character may consist of more than one phoneme (e.g., mountain = yama = ya + ma). Therefore, on average, the phonological difference between six and four items will be two in the case of hiragana, but more than two for kanji.

EXPERIMENT 3: NUMBER PAIRED RECOGNITION

Method

Six Japanese university students (four male, two female; right-handed) were recruited for the experiment after providing informed consent. Five subjects also undertook Experiment 2. The sixth subject did Experiment 1 only. The method was identical to Experiments 1 and 2. Single digit numbers in the range 3 to 9 (inclusive) were used as items for this experiment (see Fig. 2c). Pairs of numbers appeared in more than one trial, but each pair list was unique.

Results

Behavior. There were no main effects for errors, $F(2,10) = 1.00$; $P > 0.4$ (Complexity); $F(1,5) = 1.92$; $P > 0.2$ (Probe). Errors are shown in Fig. 3. There was a main effect of Probe on response time $F(1,5) = 36.10$; $P < 0.005$. There were no other effects. Response times are shown in Fig. 4c.

fMRI. The results of contrast analysis are shown in Fig. 5c and Table 3. For the six versus four contrast, the most significant increases in activity ($P < 0.001$, corrected) were observed at or near the left and right superior frontal gyri (BA 6) and middle frontal gyrus (BA 10). For the binary versus unary contrast, the most significant increase occurred near the right middle temporal gyrus (BA 39).

Discussion

The binary versus unary contrast revealed a cluster of activity similar in location to clusters observed in both kanji and hiragana experiments for the same contrast. The cluster was observed at the right superior occipital gyrus (34 -78 32; 20 voxels; $Z = 4.91$), which is close to the cluster (32 -72 42; 135 voxels; $Z = 5.66$), located in the precuneus (hiragana), and the cluster (36 -74 31; 1336 voxels; $Z = 7.54$), located in the angular gyrus (kanji). The right middle frontal gyrus was also a common gyrus of activity for this

³ Phonetically similar characters (e.g., ka and ga) differ only by marking the top right corner of the character. Only unmarked characters were used.

TABLE 3

Significant Voxels of Activity for Number Contrasts (a) Six versus Four and (b) Binary versus Unary

P_{corr}	Z	Voxels	Location (mm)			Region	BA	Range
(a)								
0.000	7.58	89	8	7	66	Superior frontal gyrus	6	3
0.002	5.27		6	-2	68	Superior frontal gyrus	6	3
0.024	4.72		-2	3	68	Superior frontal gyrus	6	5
0.000	5.89	34	-4	-79	-20			
0.000	5.87	173	4	-69	-22			
0.001	5.41		2	-67	-15			
0.000	5.55	7	-22	3	64	Superior frontal gyrus	6	1
0.001	5.45	40	-14	-18	-14			
0.001	5.33	93	42	46	18	Middle frontal gyrus	10	5
0.032	4.65		34	52	23	Superior frontal gyrus	10	3
(b)								
0.001	5.45	53	42	-65	27	Middle temporal gyrus	39	7
0.008	4.97	8	38	27	34	Middle frontal gyrus	9	1
0.011	4.91	20	34	-78	32	Superior occipital gyrus	19	3
0.023	4.74	2	-57	-29	44	Inferior parietal lobule	40	3
0.035	4.63	1	40	19	-11	Inferior frontal gyrus	47	1

Note. For definition of entries see Table 1.

contrast in all three experiments, although activity was more anterior and ventral for number pairs (38 27 34; 8 voxels; $Z = 4.97$), than for hiragana (26 7 59; 59 voxels; $Z = 5.48$) and kanji (32 13 58; 175 voxels; $Z = 7.72$).

In the six versus four contrast, the superior frontal gyrus was active. This region also exhibited clusters or subclusters in close proximity for the same contrast in both kanji and hiragana experiments, including locations (-2 3 68), (-6 3 68), and (-12 17 64) for number, hiragana, and kanji experiments, respectively.

Although this experiment also showed similar regions of activity, the strength of the difference was generally weaker for numbers compared to kanji and hiragana. One difference is that there were fewer numbers from which to generate trials for number pairs (7) than hiragana (40) and kanji (320). Yet, smaller sets are more likely to cause interference between trials resulting in poorer performance, as Mewhort and Johns (2000) suggested to explain differences between materials in their item recognition experiments. Since performance on numbers was better than hiragana or kanji, the difference is more likely to be with the processing of numbers than set sizes. Related to this possibility is that pairs of digits have a natural interpretation as single double-digit numbers, which potentially reduces the perceived overlap between items during storage. We return to this point in more detail in the General Discussion, because the final experiment also bears upon these issues. Where novel or meaningless materials are used subjects are less likely to reinterpret pairs as single items, in which case the index length effect should be stronger.

EXPERIMENT 4: SHAPE PAIRED RECOGNITION

In the final experiment, we used shapes generated from Fourier descriptors (see Fig. 2d), using the algorithm by Zahn and Roskies (1972), which have been used to study neural regions involved in paired associate learning in monkeys (Sakai and Miyashita, 1991) and humans (Klingberg and Roland, 1998). Hiragana and single-digit numbers convey less semantic information than kanji, but there are fewer of them. With Fourier descriptors, an unlimited number of unique, but meaningless shapes can be generated.

Method

Seven Japanese university students (four male, three female; one left-handed⁴) performed the experiment after providing informed consent. One subject also undertook Experiment 2. No other subject did any of the other experiments. A trial experiment indicated that recognition of shape pairs was more difficult than for the other experiments. For this reason, subjects were given more time to encode and recognize pairs. Pairs and probes were presented for 2000 and 3000 ms, respectively. The period for the intertrial (“+”) event was 3170 ms. Two practice sessions (5 min each) were also administered to each subject prior to scanning for familiarization. None of the shapes in the practice trials was used during scanning. All other aspects of experiment, acquisition, and analysis were the same as for the other experiments.

⁴ She expressed no difficulty in responding with her right hand.

TABLE 4

Significant Voxels of Activity for Shape Contrasts (a) Six versus Four and (b) Binary versus Unary

P_{corr}	Z	Voxels	Location (mm)			Region	BA	Range
(a)								
0.000	6.65	390	-26	-88	-14	Inferior occipital gyrus	18	1
0.001	5.46		-14	-99	-3	Lingual gyrus	18	1
0.035	4.61		-28	-95	5	Middle occipital gyrus	18	1
0.000	6.01	61	16	-90	-6	Inferior occipital gyrus	17	3
0.000	5.66	53	24	-37	70	Postcentral gyrus	2	7
0.000	5.65	276	34	-82	-4	Inferior occipital gyrus	18	1
0.000	5.57		28	-95	0	Cuneus	18	1
0.007	4.98		44	-80	-8	Inferior occipital gyrus	18	1
0.001	5.40	105	-30	-32	61	Postcentral gyrus	3	1
0.009	4.92		-40	-30	59	Postcentral gyrus	3	3
0.023	4.71	13	50	-10	39	Precentral gyrus	4	5
0.044	4.55	2	32	-28	70	Postcentral gyrus	3	7
(b)								
0.000	(Inf)	2529	40	10	51	Middle frontal gyrus	6	3
0.000	(Inf)		50	38	28	Middle frontal gyrus	46	1
0.000	7.51		30	17	58	Middle frontal gyrus	6	3
0.000	(Inf)	1533	42	-58	51	Superior parietal lobule	7	1
0.000	(Inf)		40	-54	41	Inferior parietal lobule	40	1
0.000	6.01		51	-43	37	Inferior parietal lobule	40	5
0.000	(Inf)	735	-42	-54	47	Inferior parietal lobule	40	1
0.000	7.75	1899	-38	12	36	Precentral gyrus	9	3
0.000	7.53		-36	11	29	Middle frontal gyrus	9	9
0.000	7.41		-30	14	45	Middle frontal gyrus	6	1
0.000	6.78	350	2	25	43	Medial frontal gyrus	8	3
0.000	5.94		8	31	37	Medial frontal gyrus	8	3
0.000	6.13	72	-30	54	-1	Superior frontal gyrus	10	1
0.000	5.87	244	-12	3	15	Caudate		1
0.006	5.01		-14	12	7	Caudate		1
0.000	5.66	231	12	3	18	Caudate		3
0.001	5.49		12	-7	21	Caudate		3
0.002	5.26		14	6	11	Caudate		3
0.001	5.48	175	6	-74	42	Precuneus	7	3
0.001	5.32		8	-64	44	Precuneus	7	1
0.002	5.22		6	-62	51	Precuneus	7	3
0.001	5.33	30	-46	47	0	Inferior frontal gyrus	10	3
0.004	5.11	7	30	54	-3	Superior frontal gyrus	10	1
0.008	4.93	39	-46	-38	-20	Fusiform gyrus	36	1
0.010	4.90		-53	-45	-15	Inferior temporal gyrus	37	1
0.009	4.93	13	48	-52	12	Superior temporal gyrus	39	1
0.025	4.69	8	-63	-28	-10	Middle temporal gyrus	21	1

Note. For definition of entries see Table 1.

Results

Behavior. There was a main effect of Complexity on response errors (Fig. 3), $F(2,12) = 6.93$; $P < 0.01$. There was a main effect of Probe on response time (Fig. 4d), $F(1,6) = 10.48$; $P < 0.05$. There were no other effects.

fMRI. Contrast analysis results are shown in Fig. 5d and Table 4. The most significant increases ($P < 0.001$, corrected) in the six versus four contrast occurred at or near the left inferior occipital and lingual gyri (BA 18), right inferior occipital gyrus (BA 18), right cuneus (BA 18), and left postcentral gyrus (BA 3). Many of the regions reported in the binary versus unary contrast were also significant to a much stricter

criterion ($P < 0.0001$, corrected). These regions were at or near the right middle frontal gyrus (BA 6/8), right superior parietal lobule (BA 7), right inferior parietal lobule (BA 40), right middle frontal gyrus (BA 46), left inferior parietal lobule (BA 40), left middle frontal gyrus (BA 6/9), right medial frontal gyrus (BA 8), right inferior frontal gyrus (BA 9), left superior frontal gyrus (BA 10), right superior occipital gyrus (BA 19), and left caudate.

Discussion

The most obvious feature in these contrasts is the strength of the effect in the binary versus unary con-

ditions. Four regions of highly significant difference ($P < 0.0001$, corrected) were observed bilaterally in the parietal and frontal lobes. Regions at the right inferior parietal lobule were active in all four experiments: kanji (36 -74 31; 1336 voxels; $Z = 7.72$, including 38 -50 41), hiragana (32 -72 42; 135 voxels; $Z = 5.66$), number (34 -78 32; 20 voxels; $Z = 4.91$), and shape (42 -58 51; 1533 voxels; $Z \rightarrow \infty$, including 40 -54 41), although differences extended into regions more posterior for kanji and shape pairs than for hiragana or number pairs. The right middle frontal gyrus was also consistently activated in all four experiments: kanji (32 13 58; 175 voxels; $Z = 7.72$, including 24 28 54), hiragana (26 7 59; 59 voxels; $Z = 5.48$), number (38 27 34; 8 voxels; $Z = 4.97$), and shape (40 10 51; 2529 voxels; $Z \rightarrow \infty$, including 30 17 58). Regions at or near the left inferior parietal lobule were activated for kanji (-30 -68 48; 210 voxels; $Z = 5.59$, including -30 -68 29), hiragana (-30 -74 26; 194 voxels; $Z = 6.32$), and shape pairs (-42 -54 47; 735 voxels; $Z \rightarrow \infty$), but not for number pairs. Activation of the left middle frontal gyrus (-38 12 36; 1899 voxels; $Z \rightarrow \infty$, including -36 11 29) also occurred for hiragana pairs (-49 32 26; 32 voxels; $Z = 5.48$), but not for kanji and number pairs. Consistent differentiation at the right parietal and frontal areas provides strong support that index length effects are common across visually presented materials, a point we look at in more detail in the next section.

The most notable feature of the six versus four contrast was the extent of the difference observed in the inferior occipital gyrus (bilaterally) and left lingual and middle occipital gyri. The extent of this activity was unique to shape pairs and probably reflects a dependence on visual features for differentiation of shapes, since they were mostly devoid of semantic and phonetic information. Activation at or near these regions also occurred in the other three experiments, but to a weaker extent.

BETWEEN-EXPERIMENT COMPARISONS/CONTRASTS

Behavior

The relative strength of the effects was correlated with relative error rates and response times.⁵ In order of highest to lowest, mean number of errors and response times were 2.3, 1247 ms (shape); 1.4, 1105 ms (kanji); 0.7, 1051 ms (hiragana); 0.5, 937 ms (number). A mixed-effects 4 (Experiment) between-groups \times 3 (Complexity) \times 2 (Probe) repeated-measures ANOVA, treating Experiment as a random effect, revealed a significant effect of Experiment on error rate $F(3,23) =$

11.63; $P < 0.0001$. There were no other main effects on error rate. A mixed-effects 4 (Experiment) between-groups \times 3 (Complexity) \times 2 (Probe) \times 10 (Trial) repeated-measures ANOVA revealed no significant effect of Experiment on response time $F(3,21) = 1.98$; $P > 0.1$. But, there were main effects of Probe $F(1,3) = 18.56$; $P < 0.05$ and Complexity $F(2,6) = 8.66$; $P < 0.05$ on response time. This effect of Complexity was due to the low response times for the u4 condition. In a planned comparison, there was a significant difference for u4 versus u6 and b4 $F(1,21) = 12.56$; $P < 0.001$, but not for b4 versus u6 $F(1,21) = 0.43$; $P > 0.5$, with Experiment treated as a fixed effect. In terms of error rates and response times, subjects found u6 and b4 conditions equally difficult (but, see also General Discussion for further analysis). Therefore, it is unlikely that regional effects were due to stress or arousal arising from increased task difficulty.

fMRI

Since the same design was used for all materials, and contrast analysis revealed similar regions of activity, it is reasonable to perform contrast analysis on the data pooled from all four experiments. We performed fixed model estimation and analysis for all 25 subject sessions using the same parameters and block/event types that were used for the individual experiments. Regions that responded to increased index length across all materials were revealed by a binary versus unary contrast for kanji ($P < 0.05$, corrected) masked by the inclusion of only those voxels that satisfied the same contrast in the other three experiments ($P < 0.05$, uncorrected). In other words, the resulting voxels showed significant increased activity in the b4 versus u6 and b4 versus u4 contrasts for kanji, hiragana, number, and shapes. (Because this contrast actually consists of eight component contrasts, chance co-occurrence of significant activity for a single location was very low and less than $1/20^8 < 10^{-10}$.) Consistent with the individual experiment contrasts, clusters of increased activity containing more than one voxel were found at or near the right precuneus (34 -74 33; 142 voxels; $Z = 6.66$) with a subcluster at the right inferior parietal lobule (38 -64 38; $Z = 6.60$); right middle frontal gyrus, BA 6 (32 10 56; 20 voxels; $Z = 7.31$ and 28 18 56; 23 voxels; $Z = 6.38$) and BA 9 (51 25 34; 106 voxels; $Z = 5.71$); left inferior parietal lobule, BA 7 (-30 -66 46; 40 voxels; $Z = 5.25$); and left precuneus, BA 19 (-30 -68 29; 18 voxels; $Z = 5.09$). The binary versus unary contrast for the number experiment did not reveal left parietal activity at the $P < 0.05$ corrected level of significance, but it was observed at $P < 0.05$ uncorrected, hence its presence in the pooled contrast.

Domain-specific effects were also investigated for index length, focussed on the right temporoparietal re-

⁵ The strength of the effect for shape pairs was not due to the extra subject. It was also stronger than the other experiments for summary contrasts over the first four subjects.

gion, since it was the site that showed the strongest effects. The contrasts for individual experiments suggested that activity in this region was more dorsal for the kanji and shape pairs, but more ventral for hiragana and number pairs. Accordingly, we performed b4 versus u6 contrast for kanji pairs ($P < 0.05$, corrected) masked by exclusion of those voxels that satisfied the same contrast for hiragana and number experiments ($P < 0.05$, uncorrected). The same was also done for shape versus hiragana and number pairs. In other words, the two contrasts test for voxels specific to kanji, but not hiragana or number pairs and voxels specific to shape, but not hiragana or number pairs. For kanji, the contrast revealed a cluster at the inferior parietal lobule, BA 40 (38 –50 41; 441 voxels; $Z \rightarrow \infty$). For shapes, the contrast revealed activity at the superior parietal lobule, BA 7 (42 –56 54; 348 voxels; $Z = 7.65$), including a subcluster at the inferior parietal lobule, BA 40 (40 –50 39; $Z = 7.20$) in almost the same location as for kanji. In the same way, we also tested for voxels specific to hiragana (and number), but not kanji or shape. At the same level of significance, the two contrasts revealed activity at middle temporal gyrus, BA 39 for both hiragana (32 –61 23; 13 voxels; $Z = 5.29$); and number pairs (36 –59 21; 2 voxels; $Z = 4.60$). These two clusters overlap in that there were no voxels specific to one contrast, but not the other, at this level of significance.

Because these contrasts were constructed by masking the within-experiment summary contrasts, the appropriate interpretation of these results is with respect to *some* subjects. In the first case, where summary contrasts were masked by inclusion, the results are to be interpreted as identifying significant activity common to all subjects who showed significant activity in any of the four experiments. In other words, for example, there were at least four subjects (at least one from each experiment) who all showed significant right inferior parietal activity with increased index length. In the case of domain-specific effects, where summary contrasts were masked by exclusion, there were at least two subjects (at least one each for kanji and shape) who showed significant activity in the right parietal lobule that was not shown in any of the 12 subject sessions for hiragana and number. Likewise, there were at least two subjects (at least one each for hiragana and number) who showed significant activity in the middle temporal gyrus that was not revealed in any of the other 13 subject sessions for kanji and shape. In the next section, we investigate the more specific questions of whether this activity was also common to all subjects both within and between experiments, and if so, what proportion of the population can be expected to exhibit these effects.

CONJUNCTION CONTRASTS AND POPULATION-LEVEL INFERENCES

Conjunction contrasts can be used to identify regions of significant activity common to *all* subjects by specifying the contrast of interest for each subject and performing the conjunction of these contrasts (Friston *et al.*, 1999a,b). In the uncorrected case, the resulting parameter map threshold at p indicates that all subjects activated at the same locations thresholded at $p^{1/n}$, where n is the number of subjects. The resulting map in the corrected case further accounts for chance cooccurrence of activity throughout the volume of interest, which in our case is the entire brain.

Conjunction Contrasts

Our primary concern here was to determine whether the right parietal, temporal, and middle frontal gyral activity observed in the binary versus unary summary contrasts was evident in all subjects and experiments. For each material type, we performed b4 versus u6 conjunction contrasts, thresholded at $P < 0.05$ corrected. Figures 6a and 6b (bottom) show the resulting statistical parameter maps for kanji and shape, respectively. Locations for conjunction contrasts are given in Table 5. Major clusters (>10 voxels) were observed at the precuneus, BA 7 (–2 –66 40; 71 voxels; $Z = 6.93$), right angular gyrus, BA 39 (38 –74 30; 80 voxels; $Z = 6.80$), and right inferior parietal lobule, BA 40 (36 –47 41; 66 voxels; $Z = 5.71$) for kanji. For shape, major clusters were observed at the left precentral gyrus, BA 9 (–34 9 31; 108 voxels; $Z = 7.84$), right inferior parietal lobule, BA 40 (42 –47 41; 50 voxels; $Z = 6.43$), right middle frontal gyrus, BA 6/8 (32 20 47; 80 voxels; $Z = 6.11$), medial frontal gyrus, BA 8 (4 26 45; 30 voxels; $Z = 5.97$), and left middle frontal gyrus (–26 10 46; 12 voxels; $Z = 5.37$). There were no clusters in these areas for hiragana and number. A b4 versus u6 conjunction contrast of all subjects in both kanji and shape experiments revealed two major clusters of activity (Fig. 6c (bottom)), one in the right inferior parietal lobule, BA 40 (40 –47 41; 109 voxels; $Z \rightarrow \infty$) and the other in right middle frontal gyrus, BA 6 (32 11 55; 72 voxels; $Z = 6.82$). These two clusters were highly significant, peaking at $P < 9 \times 10^{-10}$ and $P < 3 \times 10^{-6}$, corrected, respectively. There was also a smaller cluster at the right middle temporal gyrus (40 –70 29; 9 voxels; $Z = 5.25$). The b4 versus u4 conjunction contrast also revealed similar regions of activity, although right parietal activity was more anterior for shape and so not revealed in the conjunction of kanji and shape (Fig. 6, top).

Population-Level Inferences

These results are used to infer the expected proportion of the population likely to exhibit these effects.

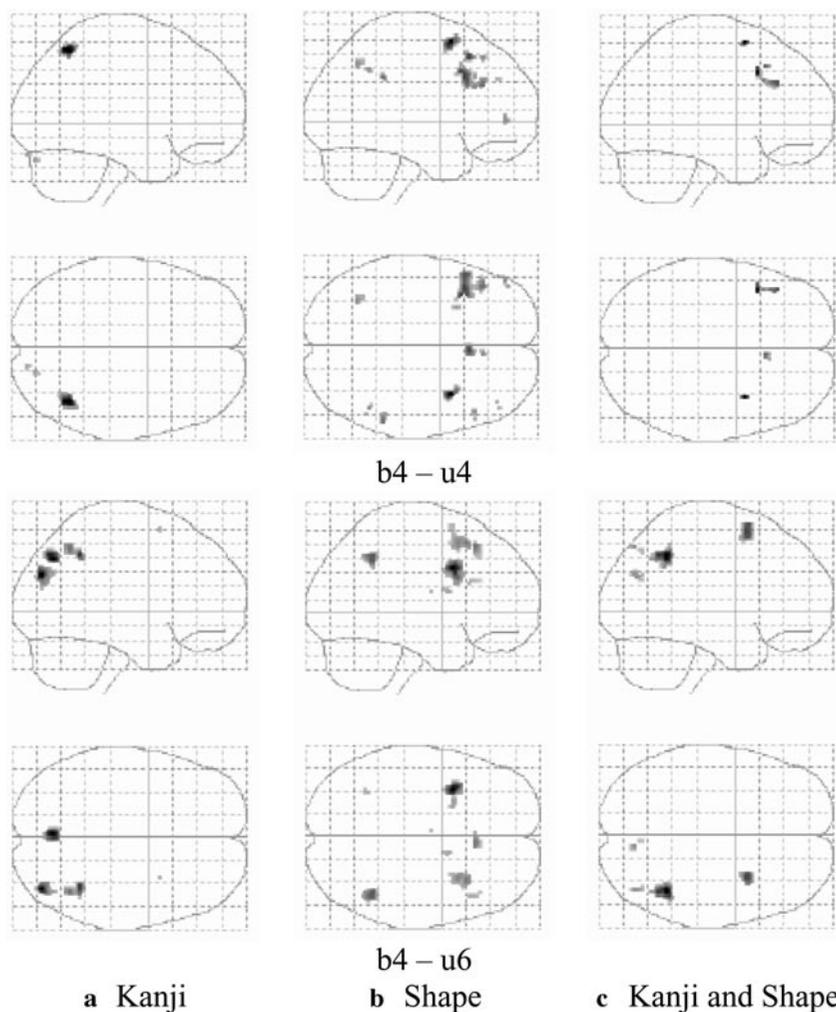


FIG. 6. Sagittal (top) and transverse (bottom) views of b4 – u4 items and b4 – u6 conjunction contrasts for (a) kanji, (b) shape, and (c) kanji and shape.

Population-level inference by random-effects analysis generally overestimates the between-subject variance and therefore requires more subjects to establish an effect and introduces the pragmatic problem of obtaining sufficient time in the scanner. Friston *et al.* (1999a) introduced a new method for obtaining population-level inferences using the sensitivity of fixed-effect models by taking the conjunction of subject-specific contrasts. So, for example, six subjects are sufficient to establish with probability $P < 0.05$ (specificity, population level) that roughly more than 60% (typicality) of the population will exhibit the effect with a test at $P < 0.05$ (specificity, subject-level) and sensitivity 100% (i.e., the test will always reveal the effect in those subjects who have it). For a less sensitive test (e.g., 80%), six subjects are sufficient to infer that more than 75% of the population exhibit the effect (Friston *et al.*, 1999b, Fig. 2). Friston *et al.* (1999a) extended this work to corrections for multiple comparisons. The proportion

γ_c of the population likely to exhibit an effect not explainable by the null hypothesis with probability $P > 1 - \alpha_c$, corrected, is given by the expression

$$\gamma_c \geq \frac{\left(\frac{\alpha_c - P_n}{1 - P_n}\right)^{1/n} - \alpha_m}{1 - \alpha_m},$$

where n is the number of subjects, α_m is minimum threshold specificity for each subject in the conjunction, and P_n is the corrected P value for the region of interest (Friston *et al.*, 1999a, Eq. [6]). Because the sensitivity of the test cannot be directly measured, this expression conservatively assumes a test sensitivity of one. Note that while the subject-specific thresholds may not be low, their conjunctions may be highly significant.

TABLE 5

Significant Voxels of Activity for Conjunction Contrast b4 versus u6 for (a) Kanji; (b) Shape; (c) Kanji and Shape; (d) Hiragana; and (e) Number

P_{corr}	Z	Voxels	Location (mm)			Region	BA	Range
(a)								
0.000	6.93	71	-2	-66	40	Precuneus	7	1
0.000	6.8	80	38	-74	30	Angular gyrus	39	1
0.000	6.22	66	36	-47	41	Inferior parietal lobule	40	1
0.001	5.71		40	-54	45	Inferior parietal lobule	40	1
0.030	5.03	2	30	11	57	Middle frontal gyrus	6	3
(b)								
0.000	7.84	108	-34	9	31	Precentral gyrus	9	7
0.000	6.43	55	42	-47	41	Inferior parietal lobule	40	1
0.000	6.11	80	32	20	47	Middle frontal gyrus	8	1
0.030	5.05		28	11	57	Middle frontal gyrus	6	1
0.000	5.97	30	4	26	45	Medial frontal gyrus	8	1
0.007	5.37	12	-26	10	46	Middle frontal gyrus	6	5
0.010	5.29	5	12	7	14	Caudate		1
0.011	5.27	7	36	17	25	Middle frontal gyrus	9	11
0.015	5.2	5	44	22	21	Middle frontal gyrus	46	7
0.032	5.04	4	-32	-51	38	Inferior parietal lobule	40	9
0.042	4.98	1	-4	-7	15	Thalamus		5
(c)								
0.000	Inf	109	40	-47	41	Inferior parietal lobule	40	1
0.000	6.82	72	32	11	55	Middle frontal gyrus	6	1
0.003	5.67	4	8	-69	48	Precuneus	7	3
0.003	5.66	9	40	-70	29	Middle temporal gyrus	39	5
0.021	5.25	3	4	-66	46	Precuneus	7	1
0.045	5.08	1	38	-65	29	Middle temporal gyrus	39	7
(d)								
0.010	5.23	9	-53	14	16	Inferior frontal gyrus	44	3
0.036	4.94	3	10	16	54	Superior frontal gyrus	6	7
(e)								
0.035	5.01	1	-34	22	12	Insula	13	1

Note. For definition of entries see Table 1.

From this expression we infer that for the peak voxels in the right inferior parietal lobule observed for kanji in the b4–u6 conjunction contrast, which activated with chance probability $P < P_n = 6 \times 10^{-5}$, corrected, with all six subject-specific parameter maps thresholded at $\alpha_m = 0.09$, uncorrected, more than 56% of the population are expected to exhibit this activity with probability $P > 0.95$, corrected. This is a very conservative estimate of the population, since it relies on perfect detection of the effect when it occurs. For the peak voxels observed in the right inferior parietal lobule and right middle frontal gyrus in the b4 versus u6 contrast for shape, more than 60% of the population are expected to exhibit this activity with probability $P > 0.95$, corrected ($n = 6$, $P_n = 1.2 \times 10^{-4}$, $\alpha_m = 0.12$).

The conjunction contrasts for kanji and shape revealed common regions of activity. A b4 versus u6 conjunction contrast including both kanji and shape contrasts confirmed that activity in the right inferior parietal lobule and right middle frontal gyrus was common to both experiments. For the peak voxels in these two clusters, at least 70% of population are expected to exhibit this activity with probability $P > 0.95$, cor-

rected ($n = 13$, $P_n = 3 \times 10^{-6}$, $\alpha_m = 0.3$). Hence, the index length effect is highly robust for kanji and shape. The peak voxel in the smaller cluster in the right middle temporal gyrus, although activated with a higher chance probability, also has a typicality of at least 70%.

GENERAL DISCUSSION

There are two patterns that emerge from this series of four experiments. The first is the consistent increase in activation of the right temporoparietal lobule and right middle frontal gyrus in the binary versus unary conditions across different stimuli. Together with the earlier study, we now have five experiments providing evidence for the same effect. The second is that the strength of this increase and its more precise location within the temporoparietal region varied depending on the stimuli and were correlated with task difficulty in terms of error rate and response time. These domain-general and domain-specific effects are further discussed in the context of possible retrieval and chunking processes, respectively.

Retrieval of Incidental Associates

As discussed in the kanji experiment, these common patterns suggest that the right inferior parietal lobule subserves repeated shifts of spatial attention to left and right elements so as to enhance the memory trace of overlapping pairs, induced by the binary index condition. Increased shifts of spatial attention invoked by parietal activity may in turn be driven by monitoring of incidental retrieval of associates in the right middle frontal gyrus. Although the primary focus of this paper was on an encoding phase, so as to identify relational effects not accountable by item storage effects, we can nevertheless explore the possibility that implicit retrieval of incidental associates was also a factor during explicit recognition by contrasting events during the probe phase.

Behavioral results showed that response times were consistently longer for distractors than targets across all materials and list types. An initial contrast of distractors versus targets for correct responses on all trials and materials ($P < 0.05$, corrected) revealed strong activity in the left inferior frontal gyrus (BA 45) and bilateral (predominantly left) parietal lobes (BA 40). However, this difference was evident in u4 and u6, but not b4 lists. Continuing the theme of incidental associate retrieval, a possible explanation for this difference lies with the studied associates of the individual probe items. In unary lists (u4 and u6), a distractor (e.g., AD) has two incidental associates (in this example, C and B) whereas a target (e.g., AB) has none. Hence, the frontal and parietal areas were activated in response to distractor probes, but not target probes. But, for binary list (b4), both the distractor (CD) and the targets (e.g., AB) have two incidental associates (A and B and C and D, respectively). Therefore, these regions will be active in both conditions and not revealed by their contrast. If this indifference is indeed the result of activity for both distractor and target probes, rather than the lack of activity, then this explanation has two further implications. First, b4 targets have two incidental associates, but u4 and u6 targets have none. Therefore, a contrast of b4 versus u4 and u6 targets should also reveal similar regions of activity. Consistent with this reasoning, a contrast of b4 versus u4 and u6 targets also revealed activity in the left inferior frontal gyrus and parietal lobes, bilaterally ($P < 0.05$, corrected). Second, since b4, u4, and u6 distractor probes all have two incidental associates, and the previous contrasts implied activity in the same regions in these cases, then a contrast of b4 versus u4 and u6 distractor should reveal no activity in these regions. Again, consistent with this reasoning, no activity was found in any of these regions for a b4 versus u4 and u6 distractor contrast ($P < 0.05$, corrected).

Note that these two implications were not logically necessary. Given distractor versus target activity for

unary (u4/u6[d] > u4/u6[t]), but not binary (b4[d] \approx b4[t]) lists, five logically possible relations exist between binary distractors/targets (b4[d/t]) and unary distractors (u4/u6[d]) and targets (u4/u6[t]). They are: (1) b4[d/t] > u4/u6[d] > u4/u6[t]; (2) b4[d/t] \approx u4/u6[d] > u4/u6[t]; (3) u4/u6[d] > b4[d/t] > u4/u6[t]; (4) u4/u6[d] > b4[d/t] \approx u4/u6[t]; and (5) u4/u6[d] > u4/u6[t] > b4[d/t]. Only the observed relation (2) is consistent with the incidental associates account. Also, implied by (2) is activity for binary distractors versus unary targets (b4[d] > u4/u6[t]), but not for binary targets versus unary distractors (b4[t] \approx u4/u6[d]). Corresponding contrasts ($P < 0.05$, corrected) revealed activity at the left inferior frontal gyrus (BA 45), left precuneus (BA 19), and right superior parietal lobule (BA 7), for the first, but not the second implied contrast, although there was a small cluster of activity in right precuneus (BA 19) for the second implied contrast.

A factor potentially confounding this analysis is the delay between encode and probe phases (3 s separated the presentation of the last list pair and the probe pair). Activity during the recognition phase could be confounded with activity during the encoding phase owing to the lag in the hemodynamic response. However, with regard to the number of incidental associates, this factor only affects contrasts between different lists. For example, distractor versus target for u6 lists contrasts the same number of incidental associates during the encoding phase (i.e., zero). But, a contrast of b4 versus u4 and u6 distractors confounds two versus two incidental associates in the probe phase with two versus zero in the encode phase. And a contrast of b4 versus u4 and u6 targets confounds two versus zero associates in the probe phase with two versus zero in the encode phase. Thus, the effects attributed to differences in the number of incidental associates in the probe phase could be due to differences in the number of associates in the encode phase. However, if this were the case, then activity observed in the b4 versus u4 and u6 targets implies activity for b4 versus u4 and u6 distractors (since in both contrasts b4 has more incidental associates during encoding), but none was observed. Therefore, activity was more likely the result of differences during recognition, rather than study. The same reasoning also applies to the b4 distractor versus unary target and b4 target versus unary distractor contrasts.

Further support for this view is found in a closer analysis of response times. Although no significant difference was found between b4 and u6 lists, a difference is more likely to occur between b4 and u6 targets, but not distractors. Accordingly, within each experiment, mean response times were longer for b4 than u6 targets, but b4 distractors were not consistently longer than u6 distractors. A planned comparison of u6 and b4 targets for all experiments showed that the effect was marginally significant $F(1,3) = 6.71$; $P = 0.081$, but not

for distractors $F(1,3) = 0.54$; $P > 0.5$. Interestingly, Prabhakaran *et al.* (2000) reported longer response times for incongruent than congruent positive trials. For incongruent positive trials, the test letter–position had two incidental associates, because the test letter appeared in a different position, and the test position had a different letter in the study display. For congruent positive trials, the test letter–position had no incidental associates, because the same letter appeared in the same position in the study display. In relational terms, their incongruent and congruent trials correspond, respectively, to distractor and target probes of u8 lists having four letter–position pairs, which means that their result is also consistent with relation (2) above.

Closely related to this issue of recognition processes is a study by Mewhort and Johns (2000). Their account for the rejection of distractors in item recognition was based on the number of probe features not appearing in the study list. Given the feature list Aa, Ab, Bc, Cc, rejection of a 1:1 distractor (i.e., both distractor features appeared once in the list, e.g., Bb) was significantly worse than a 1:0 distractor (i.e., one feature in the list, e.g., Bx) and a 2:0 distractor (i.e., one repeated feature, e.g., Ax). There was no significant difference between 1:0 and 2:0 distractors (Experiments 1–3). Our account suggests no difference between 1:1 and 2:0 distractors, which have the same number of incidental associates (e.g., Bb has incidental associates A and c; Ax has associates a and b), but better performance for 1:0 distractors, which have fewer associates (e.g., Bx has associate c). However, the difference between these two accounts may be specific to (extralist) features not appearing in the study list. A contrast of distractors without extralist features for three-feature lists of the form Aa α , Ab β , Bb α showed significantly better performance on 1:1:1 distractors Ba β (having associates A, b, and α) than 2:2:2 distractors Ab α , which have more incidental associates (A, B, a, b, α , β) (Experiment 4).

Attention or retention? This analysis suggests that retrieval of incidental associates also plays a role during explicit recognition. However, several complications to this analysis make it difficult to infer whether the incidental associates during study impacted upon memory-related attentional or retentional processes. Our more conservative approach of masking by material-specific contrasts did not reveal common voxels of increased activity for some masks. Furthermore, the effects were left dominant for recognition, but right dominant for study. Recognition in the binary condition was also complicated by possible alternative strategies. For example, instead of simply comparing the probe to each list pair, subjects could use a count of the number of times each probe item appeared in the study list. Since CD was the only possible distractor with items in their original list positions, it could be rejected

by recognizing that both of its items appeared only once. (This may explain why subjects were more accurate on b4 lists for shapes, although only one subject reported using such a strategy.) Focusing on the encoding phase obviated these alternatives, allowing us to isolate relational effects without unduly complicating the experimental design. The short delay to probe presentation allowed us to generate sufficient trials within the maximum scan time available. But, the short delay made it difficult to determine whether the observed effects were due to attention, encoding, retention, or retrieval processes. A likely cause for right temporoparietal and frontal activity was memory-driven shifts of attention. There are two reasons to suspect shifts of attention. First, as discussed earlier, others have implicated right parietal regions in shifts of attention. Second, the effects were strongest for kanji and shape, which span both verbal and visual domains; whereas in the probe phase the left inferior frontal gyrus, often implicated in rehearsal of verbal information, was strongly activated for kanji, hiragana, and number, but not shape. A further experiment, reported in the next section, was conducted to isolate retention effects in the absence of visual stimuli by using a longer delay between study and probe.

Chunking of Item Pairs

The domain-specific effects suggest an interesting possible link to the purported mechanism of chunking in working memory processes. Chunking is supposed to explain the extraordinary memory capacity of experts compared to novices in their field of expertise, yet their mediocre level outside that field—through experience, experts learn to recode *apparently* unrelated groups of items into a smaller number so as not to exceed normal capacity limits (e.g., Ericsson *et al.*, 1980; Ericsson and Kintsch, 1995). But, pinning down the nature of the chunking mechanism has proven illusive. The cost of chunking is that it requires training, and relations between chunked items become temporarily inaccessible (Halford *et al.*, 1998b). But, recoding has a beneficial effect: combinations of apparently similar items may become dissimilar after recoding (e.g., *blackball* and *blackmail*). (In database terms, for example, each employee record is given a unique number for easy retrieval of otherwise overlapping information, but the employee number may bear no other relation to the employee's record.) Kanji pairs were constructed so as not to form words. Shape pairs were entirely novel items. In both cases, experience with such pairs is rare or nonexistent and therefore not available to processes that learn to chunk them. On the other hand, most hiragana appear together at one time or another as part of a word, even though they may not constitute words themselves. Similarly, pairs of numbers can be interpreted either individually or as single double-digit

numbers. When interpreted as single numbers, 38 and 18 do not share the same degree of overlap. Thus, chunking redefines the index length of a set from binary, as in (5 8), (2 8), (5 4) to unary (58 28 54). If the recoded items no longer overlap, less attention is needed to establish a trace. In this case, the right inferior parietal lobule and right middle frontal gyrus provide indicators of chunking in the context of otherwise overlapping complex objects. The idea that chunking explains the change from parietal to temporal activity associated with domain-specific improvements in performance gains support from observations that the right parietal cortex is involved with shifts of attention, but not binding in visual feature binding tasks (Ashbridge *et al.*, 1999), this role is reduced with training (Walsh *et al.*, 1999), and neurons in monkey anterior temporal cortex were selective to conjunctions of shapes after training, but not to the shapes when presented alone (Sakai and Miyashita, 1991).

EXPERIMENT 5: KANJI PAIRED RECOGNITION WITH LONGER DELAY

Subjects performed kanji paired recognition, as in Experiment 1, but with a longer delay between study and probe pairs.

Method

Nine Japanese subjects (four male, five female; right-handed) undertook the experiment after providing informed consent. One subject gave 14 successive *No* responses during the first half of the experiment. She reported that the noise generated by the magnet distracted her responses until she became accustomed to the MRI environment, so her data were omitted from behavioral analysis.

The experimental procedure and event timings followed Experiment 1, with the following three exceptions: (1) In order to isolate retention effects in the absence of visual information, there was a 12-s delay from the end of the third target pair event to the start of the probe event. (2) During this interstimulus delay period the screen was clear (i.e., there was no “?” event). (3) Because the longer delay greatly increased the total scan time, only u6 and b4 list types were employed. All other aspects were the same as Experiment 1. Each trial consisted of the sequence: Target Pair 1 (1170 ms), clear screen (1000 ms), Target Pair 2, clear screen, Target Pair 3, delay (12000 ms), probe (2000 ms), plus (5000 ms).

For behavioral data analysis, we used a 2 (Complexity) \times 2 (Probe) \times 10 (Trial) design. For fMRI data analysis, 2 (u6, b4) \times 2 (encode, retention) + 2 (u6, b4) \times 2 (target, distractor) + 1 (error) = 9 event types were defined. Encode events were modeled by a boxcar function (covering all target pair events, 5510 ms) con-

involved with the canonical hemodynamic response function; interstimulus retention events were modeled by a box-function function (covering the delay period, 12000 ms); and probe events were modeled by the canonical hemodynamic response function, where the onset was the start of the probe presentation event. All other aspects of fMRI data acquisition and analysis were the same as in Experiment 1.

Results

Behavior. A 2 (Complexity) \times 2 (Probe) repeated-measures ANOVA revealed no main effects for errors (Fig. 3), $F(1,7) = 1.55$; $P > 0.25$ (Complexity); $F(1,7) = 4.09$; $P > 0.08$ (Probe). A 2 (Complexity) \times 2 (Probe) \times 10 (Trial) repeated-measures ANOVA revealed a main effect of Complexity on response time, $F(1,7) = 7.88$; $P < 0.05$, but not for Probe, $F(1,7) = 1.79$; $P > 0.22$ (Fig. 4a). There were no other effects.

The data for u6 and b4 trials from Experiment 1 were combined with the data here, treating Delay as a between-groups factor. Analysis of variance revealed no main effects on error. However, on response time, there were main effects of Delay, $F(1,12) = 4.36$; $P < 0.06$; Complexity, $F(1,12) = 6.47$; $P < 0.05$; and Probe, $F(1,12) = 4.87$; $P < 0.05$. There was also an effect of Trial, $F(9,108) = 1.99$; $P < 0.05$. But, post hoc analysis (Scheffe test, $\alpha = .05$) revealed no significant differences between Trial means.

fMRI. For the purpose of isolating effects on retention processes, the contrast analyses focus on the delay period. As for the previous experiments, summary and conjunctive contrast analyses were performed over all (nine) subjects. The results of summary and conjunction contrasts for u6 versus b4 and b4 versus u6 retention events are shown in Fig. 7 and Table 6. As before, contrasts were thresholded at $P < 0.05$, corrected. No voxel in the conjunction contrasts survived this threshold. However, activity was revealed at the lower threshold of $P < 0.0001$, uncorrected.

For the u6 versus b4 summary contrast, the three largest clusters of activity appeared at the left middle frontal gyrus, right insula, and right superior frontal gyrus. However, only one of these clusters survived the conjunction contrast. That was the cluster at left middle frontal gyrus, BA 9 (−32 40 27; 8 voxels; $Z = 4.39$).

For the b4 versus u6 summary contrast, clusters appeared bilaterally at the parietal lobes, left superior temporal gyrus, and left middle frontal gyrus. Four clusters survived the conjunction contrast, all in the left hemisphere. They were at the middle frontal gyrus, BA 8 (−36 25 43; 3 voxels; $Z = 4.39$); precuneus, BA 19 (−36 −72 37; 19 voxels; $Z = 4.68$); superior temporal gyrus, BA 22 (−55 −10 −1; 20 voxels; $Z = 4.33$); and angular gyrus, BA 39 (−42 −62 36, 8 voxels, $Z = 4.01$). The corrected P values reported for the conjunctions were calculated on *small-volume* comparisons. Because

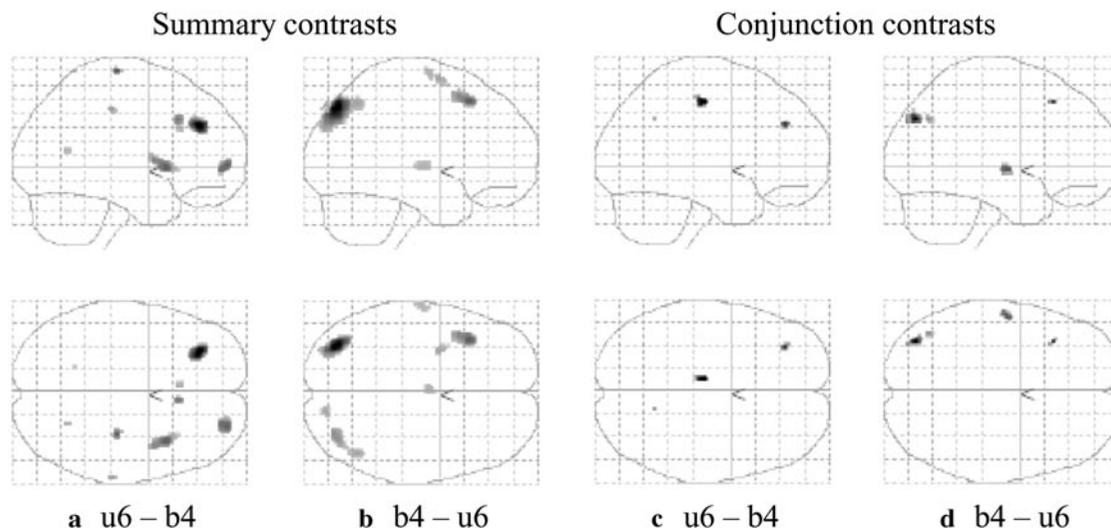


FIG. 7. Sagittal (top) and transverse (bottom) views for summary contrasts (a) u6–b4 and (b) b4–u6, and conjunction contrasts (c) u6–b4 and (d) b4–u6 of retention events for kanji paired recognition.

the earlier experiments revealed similar regions of activity, the correction for whole brain comparison was overly conservative. A more accurate estimate of the chance cooccurrence of activity across all subjects was obtained by selecting the nearest peak voxel identified in the summary analysis as the center of the smallest spherical search volume covering all voxels in the cluster identified by the conjunction. A search radius of 16 mm for the most significant cluster in the u6 versus b4 contrast resulted in a value of 0.013. A search radius of 5 mm in the b4 versus u6 contrast resulted in a value of 0.0004.

The mean subject peristimulus time histories for the four peak voxels identified by conjunction analysis in the left frontal, parietal, and temporal lobes for the b4 versus u6 contrast and the left frontal for the u6 versus b4 contrast are shown in Figs. 8a, 8b, 8c, and 8d, respectively.

Discussion

The main result from this experiment is that relational load effects were also found for the retention-only period. Consistent increased activity sustained for the duration of the retention period was observed in all subjects at three locations: left parietal lobule, middle frontal, and superior temporal gyri with increased index length. Increased activity was also observed at the more anterior and inferior region of the left middle frontal gyrus with increased items, but this effect may have resulted from an interaction with activity during the encode phase. A conjunction contrast ($P < 0.0001$, uncorrected) revealed a significant increase in activity for the opposite, b4 versus u6 contrast during encoding at an adjacent voxel ($-30\ 40\ 27$; $Z = 3.96$). For this voxel, there was an increase in the mean fitted re-

sponse during encoding for b4 trials, but a decrease for u6 trials. Conversely, during the delay period, there was an increase for u6 trials, but a decrease for b4 trials (Fig. 8d). There were no such interactions for the three significant clusters observed for b4 versus u6 retention events. The cluster at the middle frontal gyrus was superior and posterior to these (nearest) b4 versus u6 encode/u6 versus b4 retention clusters. The cluster at the left precuneus was inferior and posterior to the (nearest) cluster observed at the left superior parietal lobule, BA 7 ($-32\ -52\ 54$; 53 voxels; $Z = 3.88$) for b4 versus u6 encode events. Hence, it is more likely that the relational load effects were due to retention/rehearsal processes in the absence of visual stimuli, rather than attention/encoding related processes in the presence of visual stimuli.

Parietal and frontal activity arising from index length was left dominant here, but right dominant in the other experiments. This difference suggests some degree of lateralization between encoding and retention. However, in this experiment, activity was also left dominant during the encoding phase. Rather, the increased delay may have biased the type of retention strategy. When memorizing kanji pairs, subjects reported using either phonological or shape information, on a case-by-case basis, whichever appeared easier. The shorter delay period interrupted by the “?” event in Experiment 1 may have made phonological rehearsal more difficult and hence biased subjects toward a visual strategy inducing greater shifts of attention to overlapping spatial information, in which case there would be greater reliance on right frontoparietal regions. Although the left middle front gyrus was dominant here, it was also activated in Experiments 1–4. Activation of this region across different types of stim-

TABLE 6

Significant Voxels of Activity for Kanji (with Longer Delay) Summary/Conjunction Contrasts (a/c) u6 versus b4 and (b/d) b4 versus u6 Retention

P_{corr}	Z	Voxels	Location (mm)			Region	BA	Range
(a)								
0.000	5.72	129	-28	36	28	Middle frontal gyrus	9	1
0.002	5.24	94	38	12	-1	Insula	13	5
0.006	4.96		40	6	5	Insula	13	3
0.002	5.21	14	32	-18	67	Precentral gyrus	6	1
0.002	5.21	75	26	56	-1	Superior frontal gyrus	10	3
0.004	5.07	20	6	23	32	Cingulate gyrus	32	3
0.013	4.79	4	63	-23	42	Postcentral gyrus	1	5
0.022	4.67	1	-18	-49	69	Postcentral gyrus	7	5
0.023	4.66	8	-4	23	26	Cingulate gyrus	32	1
0.024	4.64	4	24	-57	16	Posterior cingulate	30	9
(b)								
0.000	7.50	336	-34	-72	44	Superior parietal lobule	7	1
0.000	6.31	102	-38	24	45	Middle frontal gyrus	8	3
0.000	5.55	121	34	-72	46	Superior parietal lobule	7	1
0.003	5.11		46	-56	47	Inferior parietal lobule	40	3
0.003	5.12	15	-30	3	61	Middle frontal gyrus	6	3
0.004	5.04	11	16	-79	46	Precuneus	7	3
0.008	4.90	23	-2	-5	65	Superior frontal gyrus	6	5
0.011	4.84	24	-63	-13	3	Superior temporal gyrus	22	3
0.049	4.47	1	-34	9	57	Middle frontal gyrus	6	3
(c)								
0.013	4.24	8	-32	40	27	Middle frontal gyrus	9	3
0.148	4.35	20	-8	-17	45	Paracentral lobule	31	5
0.150	3.86	1	14	-53	36	Precuneus	31	7
(d)								
0.000	4.39	3	-36	25	43	Middle frontal gyrus	8	3
0.001	4.68	29	-36	-72	37	Precuneus	19	3
0.009	4.33	20	-55	-10	-1	Superior temporal gyrus	22	1
0.040	4.01	8	-42	-62	36	Angular gyrus	39	1

Note. For definition of entries see Table 1. Estimates of P_{corr} for (c) and (d) were calculated for small-volume comparisons using the nearest peak voxel from the corresponding summary contrasts as the center of a sphere that covered all voxels in the conjunction.

uli is consistent with a recent report that the posterior superior frontal sulcus and neighboring regions, including BA 8, were activated during retention in an n -back task in spatial and verbal domains (Zurowski *et al.*, 2002).

SUMMARY AND FURTHER WORK

This work was motivated by Cowan's argument that relational complexity effects in working memory are reducible to the cost of storing items. We have provided evidence from experiments in four different domains showing that relational effects are not reducible to item effects using the concept of index length. Index length is a measure of the overlap between items in a memory set. The main result has been to show that parietal and frontal regions were sensitive to increases in index length when the number of presented items was held constant and the number of unique items decreased. Therefore, this effect cannot be explained by number of items stored.

A longer index implies greater overlap (number of shared items) between study pairs. We have suggested

that shared items cause incidental retrieval of items previously associated with items in the currently presented study pair. The binary indexed lists have two incidental associates, whereas the unary indexed lists have none. Hence, a likely role of right inferior parietal lobule in this context is to shift attention between left and right items so as to enhance encoding of overlapping pairs. The magnitude of the effect varied with materials. We have also suggested that commonly cooccurring items may be chunked so as to reduce their overlap between other pairs and the need to enhance encoding. In this case, the right inferior parietal lobule may provide an indicator of chunking in working memory tasks.

A further experiment showed that index length also resulted in increased left inferior parietal, middle frontal gyrus, and superior temporal gyrus activity during retention in the absence of visual stimuli. Thus, relational load also impacts upon retention processes.

Although the dominant effect in this series of experiments arose from changes in index length, we are not denying the existence of item effects. As noted earlier the lack of strong item effects was probably due to all

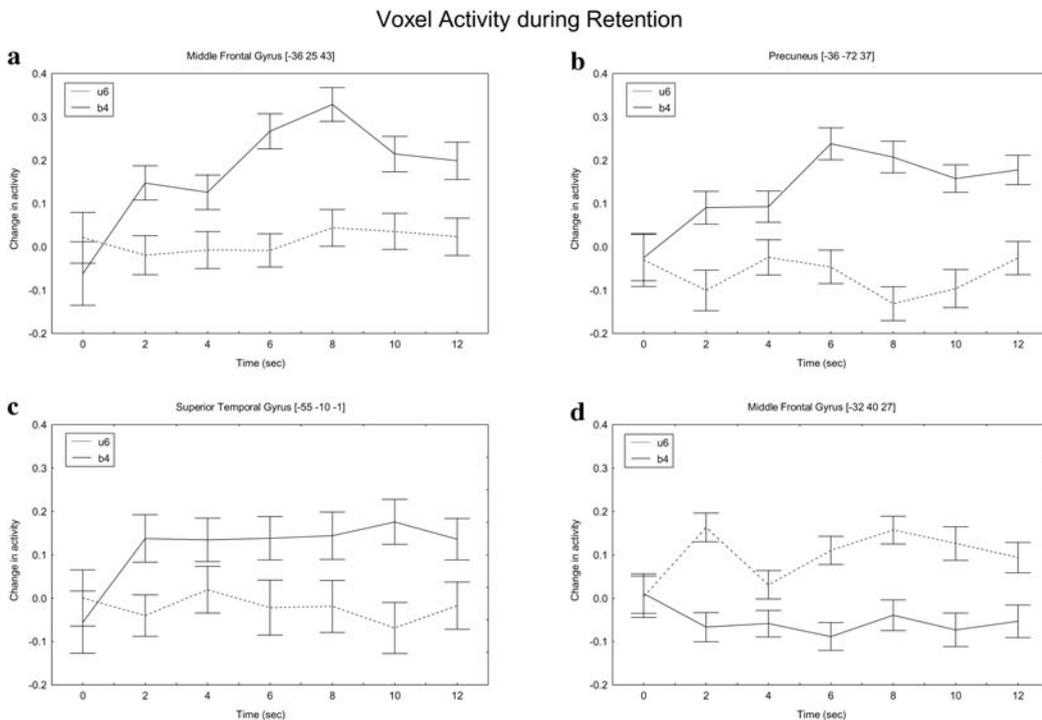


FIG. 8. Peristimulus time history during the retention period for peak voxels identified in the (a–c) b4–u6; and (d) u6–b4 conjunction contrasts averaged over all nine subjects. Error bars indicate one standard error.

list conditions being at or above the putative four-item capacity limit. Regions invoked at or above this limit would have been activated in all three conditions and so would be less evident when contrasted.

Manipulation of index length can be extended in a number of interesting ways. First, sensitivity to positional cues can be further distinguished from associate cues in AB, AC versus AB, BC lists. If the effects were due to incidental retrieval of associates by position-specific cues, characteristic of relational processes, then the implicit B cue in the second pair of an AB, BC list is less likely to invoke retrieval of associate A from the first pair. Second, chunking or recoding to reduce index length can be investigated with lists such as *black chair, black dog, white dog* (visual binary index, conceptual binary index) versus *blackball, blackmail, football* (visual binary index, conceptual unary index). Third, quaternary (4-tuple) lists permit further variation of index length from one to three. While one-shot memorization of four 4-tuples (16 items) may be beyond verbal memory capacity, it appears to be within the limits of visual memory when the items are object features (Luck and Vogel, 1997).

ACKNOWLEDGMENTS

We thank Jing Luo for many helpful discussions on an earlier version of this work. We also thank Simon Dennis, Graeme Halford, Karina Christoff, and Shigeru Kitazawa for their comments, Simon Dennis for bringing to our attention the Mewhort and Johns study,

and Kenji Kawano for suggesting the use of randomly generated shapes. We also thank two anonymous reviewers for their thoughtful comments and suggested additional analyses and references, which have helped improve the presentation of this work.

REFERENCES

- Allan, K., Dolan, R. J., Fletcher, P. C., and Rugg, M. D. 2000. The role of the right anterior prefrontal cortex in episodic retrieval. *Neuro-Image* **11**(3): 217–227.
- Andrews, G. 1997. *Relational Complexity as a Capacity Construct in Cognitive Development*. Ph.D. thesis, School of Psychology, University of Queensland, Brisbane, Australia.
- Andrews, G., and Halford, G. S. 1998. Children's ability to make transitive inferences: The importance of premise integration and structural complexity. *Cogn. Dev.* **13**(4): 479–513.
- Andrews, G., and Halford, G. S. A cognitive complexity metric applied to cognitive development. *Cogn. Psychol.*, in press.
- Ashbridge, E., Cowey, A., and Wade, D. 1999. Does parietal cortex contribute to feature binding? *Neuropsychologia* **37**: 999–1004.
- Awe, E., and Jonides, J. 2001. Overlapping mechanisms of attention and spatial working memory. *Trends Cogn. Sci.* **5**(3): 119–126.
- Baddeley, A. 2000. The episodic buffer: A new component of working memory. *Trends Cogn. Sci.* **4**(11): 417–423.
- Brett, M. 1999. *The MNI Brain and the Talairach Atlas*. (<http://www.mrc-cbu.cam.ac.uk/Imaging>)
- Cabeza, R., and Nyberg, L. 2000. Imaging cognition II: An empirical review of 275 PET and fMRI studies. *J. Cogn. Neurosci.* **12**(1): 1–47.
- Christoff, K., and Gabrieli, J. D. E. 2000. The frontopolar cortex and human cognition: Evidence for a rostrocaudal hierarchical organization within the human prefrontal cortex. *Psychobiology* **28**(2): 168–186.

- Christoff, K., Prabhakaran, V., Dorfman, J., Kroger, K. J., Zhao, Z., Holyoak, K. J., and Gabrieli, J. D. E. 2001. Rostral prefrontal cortex involvement in relational processing during reasoning. *NeuroImage* **14**(5): 1136–1149.
- Cohen, J. D., Perlstein, W. M., Braver, T. S., Nystrom, L. E., Noll, D. C., Jonides, J., and Smith, E. E. 1997. Temporal dynamics of brain activation during a working memory task. *Nature* **386**: 604–608.
- Corbetta, M., Shulman, G. L., Miezin, F. M., and Petersen, S. E. 1995. Superior parietal cortex activation during spatial attention shifts and visual feature conjunction. *Science* **270**(5237): 802–805.
- Cowan, N. 2001. The magical number 4 in short-term memory: A reconsideration of storage capacity. *Behav. Brain Sci.* **24**(1): 87–185.
- Duncan, J., Seitz, R. J., Kolodny, J., Bor, D., Herzog, H., Ahmed, A., Newell, F. N., and Emslie, H. 2000. A neural basis for general intelligence. *Science* **289**(5478): 457–460.
- Ericsson, K. A., Chase, W. G., and Faloon, S. 1980. Acquisition of a memory skill. *Science* **208**: 1181–1182.
- Ericsson, K. A., and Kintsch, W. 1995. Long-term working memory. *Psychol. Rev.* **102**: 211–245.
- Fletcher, P. C., Shallice, T., Frith, C. D., Frackowiak, R. S., and Dolan, R. J. 1998. The functional roles of prefrontal cortex in episodic memory. II. retrieval. *Brain* **121**(7): 1249–1256.
- Friston, K. J., Holmes, A. P., Price, C. J., Buchel, C., and Worsley, K. J. 1999a. Multisubject fMRI studies and conjunction analysis. *NeuroImage* **10**: 385–396.
- Friston, K. J., Holmes, A. P., and Worsley, K. J. 1999b. How many subjects constitute a study? *NeuroImage* **10**(1): 1–5.
- Halford, G. S. 1984. Can young children integrate premises in transitivity and serial order tasks? *Cogn. Psychol.* **16**(6): 65–93.
- Halford, G. S. 1993. *Children's Understanding: The Development of Mental Models*. Erlbaum, Hillsdale, NJ.
- Halford, G. S., Phillips, S., and Wilson, W. H. 2001. Processing capacity limits are not explained by storage limits. *Behav. Brain Sci.* **24**(1): 123–124.
- Halford, G. S., and Wilson, W. H. 1980. A category theory approach to cognitive development. *Cogn. Psychol.* **12**: 356–411.
- Halford, G. S., Wilson, W. H., and Phillips, S. 1998a. Author's response: Relational complexity metric is effective when assessments are based on actual cognitive processes. *Behav. Brain Sci.* **21**(6): 848–864.
- Halford, G. S., Wilson, W. H., and Phillips, S. 1998b. Processing capacity defined by relational complexity: Implications for comparative, developmental, and cognitive psychology. *Behav. Brain Sci.* **21**(6): 803–831.
- Halpin, T. A. 1995. *Conceptual Schema and Relational Database Design*, 2nd ed. Prentice Hall Australia, Sydney.
- Hunkin, N. M., Mayes, A. R., Williams, S. C., Gregory, L. J., Nunn, J. A., Nicholas, A. K., Brammer, M. J., and Bullmore, E. T. 2000. Does frontal lobe activation during retrieval reflect complexity of retrieved information? *NeuroReport* **11**(3): 557–561.
- Kessels, R. P. C., d'Alfonso, A. A. L., Postma, A., and Haan, E. H. F. de. 2000. Spatial working memory performance after high-frequency repetitive transcranial magnetic stimulation of the left and right posterior parietal cortex in humans. *Neurosci. Lett.* **287**(1): 68–70.
- Klingberg, T., and Roland, P. E. 1998. Right prefrontal activation during encoding, but not during retrieval, in a non-verbal paired-associates task. *Cereb. Cortex* **8**(1): 73–79.
- Lancaster, J. L., Woldorff, M. G., Parsons, L. M., Liotti, M., Rainey, C. S. F. L., Kochunov, P. V., Nickerson, D., Mikiten, S. A., and Fox, P. T. 2000. Automated Talairach Atlas labels for functional brain mapping. *Hum. Brain Mapping* **10**(3): 120–131.
- Losier, B. J. W., and Klein, R. M. 2001. A review of the evidence for a disengage deficit following parietal lobe damage. *Neurosci. Biobehav. Rev.* **25**: 1–13.
- Luck, S. J., and Vogel, E. K. 1997. The capacity of visual working memory for features and conjunctions. *Nature* **390**: 279–281.
- Maybery, M. T., Bain, J. D., and Halford, G. S. 1986. Information processing demands of transitive inference. *J. Exp. Psychol. Learning Memory Cogn.* **12**: 600–613.
- Mewhort, D. J. K., and Johns, E. E. 2000. The extralist-feature effect: Evidence against item matching in short-term memory. *J. Exp. Psychol. Gen.* **129**(2): 262–284.
- Miller, G. A. 1956. The magical number seven, plus or minus two: Some limits on our capacity for processing information. *Psychol. Rev.* **63**: 81–97.
- Mitchell, K. J., Johnson, M. K., Raye, C. L., and D'Esposito, M. 2000a. fMRI evidence of age-related hippocampal dysfunction in feature binding in working memory. *Brain Res. Cogn. Brain Res.* **10**(1–2): 197–206.
- Mitchell, K. J., Johnson, M. K., Raye, C. L., Mather, M., and D'Esposito, M. 2000b. Aging and reflective processes of working memory: Binding and test load deficits. *Psychol. Aging* **15**(3): 527–541.
- Nobel, P. A., and Shiffrin, R. M. 2001. Retrieval processes in recognition and cued recall. *J. Exp. Psychol. Learning Memory Cogn.* **27**(2): 384–413.
- Nyberg, L., Cabeza, R., and Tulving, E. 1996. PET studies of encoding and retrieval: The HERA model. *Psychonom. Bull. Rev.* **3**(2): 135–148.
- Phillips, S. 1997. Measuring relational complexity in oddity discrimination tasks. *Noetica* **3**(1): (<http://www2.psy.uq.edu.au/CogPsych/Noetica/Journal.html>)
- Phillips, S., Halford, G. S., and Wilson, W. H. 1995. The processing of associations versus the processing of relations and symbols: A systematic comparison. In *Proceedings of the Seventeenth Annual Conference of the Cognitive Science Society* (J. D. Moore and J. F. Lehman, Eds.), pp. 688–691. Pittsburgh, PA
- Phillips, S., Halford, G. S., and Wilson, W. H. 1998. What changes in children's drawing procedures? Relational complexity as a constraint on representational redescription. *Cogn. Stud.* **5**(2): 33–42.
- Phillips, S., Niki, K., and Luo, J. 2001. An fMRI study of relational complexity effects in a kanji pair list recognition task. *NeuroImage* **13**(6): S723. (<http://www.apnet.com/www/journal/hbm2001/10718.html>)
- Prabhakaran, V., Narayanan, K., Zhao, Z., and Gabrieli, J. D. E. 2000. Integration of diverse information in working memory within the frontal lobe. *Nat. Neurosci.* **3**(1): 85–90.
- Prabhakaran, V., Rypma, B., and Gabrieli, J. D. 2001. Neural substrates of mathematical reasoning: a functional magnetic resonance imaging study of neocortical activation during performance of the necessary arithmetic operations test. *Neuropsychology* **15**(1): 115–127.
- Prabhakaran, V., Smith, J. A., Desmond, J. E., Glover, G. H., and Gabrieli, J. D. 1997. Neural substrates of fluid reasoning: An fMRI study of neocortical activation during performance of the raven's progressive matrices test. *Cogn. Psychol.* **33**(1): 43–63.
- Robin, N., and Holyoak, K. J. 1995. Relational complexity and the functions of prefrontal cortex. In *The Cognitive Neurosciences* (M. S. Gazzaniga, Ed.), pp. 987–998. MIT Press, Cambridge, MA.
- Rugg, M. D., Fletcher, P. C., Allan, K., Frith, C. D., Frackowiak, R. S., and Dolan, R. J. 1998. Neural correlates of memory retrieval during recognition memory and cued recall. *NeuroImage* **8**(3): 262–273.
- Rugg, M. D., Fletcher, P. C., Chua, P. M., and Dolan, R. J. 1999. The role of the prefrontal cortex in recognition memory and memory for source: An fMRI study. *NeuroImage* **10**(5): 520–529.

- Rugg, M. D., and Wilding, E. L. 2000. The effect of divided attention on encoding and retrieval in episodic memory revealed by positron emission tomography. *Trends Cogn. Sci.* **4**(3): 108–115.
- Rypma, B., Prabhakaran, V., Desmond, J. E., Glover, G. H., and Gabrieli, J. D. E. 1999. Load-dependent roles of frontal brain regions in the maintenance of working memory. *NeuroImage* **9**: 216–226.
- Sakai, K., and Miyashita, Y. 1991. Neural organization for the long-term memory of paired associates. *Nature* **354**: 152–155.
- Shimamura, A. P., Jurica, P. J., Mangels, J. A., Gershberg, F. B., and Knight, R. T. 1995. Susceptibility to memory interference effects following frontal lobe damage: Findings from tests of paired-associate learning. *J. Cogn. Neurosci.* **7**(2): 144–152.
- Smith, E. E., Jonides, J., Marshuetz, C., and Koeppel, R. A. 1998. Components of verbal working memory: Evidence from neuroimaging. *Proc. Natl. Acad. Sci. USA* **95**: 876–882.
- SPM. 1999. *Statistical Parameter Mapping*. (Computer program manual)
- Statistica, I. 2000. *Statistica for Windows*. (Computer program manual)
- Sternberg, S. 1966. High-speed scanning in human memory. *Science* **153**: 652–654.
- Talairach, J., and Tournoux, P. 1988. *Co-planar Stereotaxic Atlas of the Human Brain: 3-Dimensional Proportional System: An Approach to Cerebral Imaging*. Thieme, New York.
- Thatcher, R. W. 1991. Maturation of the human frontal lobes: Physiological evidence for staging. *Dev. Neuropsychol.* **7**: 397–419.
- Walsh, V., Ellison, A., Ashbridge, E., and Cowey, A. 1999. The role of parietal cortex in visual attention—Hemispheric asymmetries and the effects of learning: A magnetic stimulation study. *Neuropsychologia* **37**: 245–251.
- Waltz, J. A., Knowlton, B. J., Holyoak, K. J., Boone, K. B., Mishkin, F. S., Santos, M., Thomas, C. R., and Miller, B. L. 2001. A system for relational reasoning in human prefrontal cortex. *Psychol. Sci.* **10**(2): 119–125.
- Waltz, J. A., Lau, A., Grewal, S. K., and Holyoak, K. J. 2000. The role of working memory in analogical mapping. *Memory Cogn.* **28**(7): 1205–1212.
- Zahn, C. T., and Roskies, R. Z. 1972. Fourier descriptors for plane closed curves. *IEEE Trans. Comput.* **21**: 269–281.
- Zurowski, B., Gostomzyk, J., Gron, G., Weller, R., Schirrmeyer, H., Neumeier, B., Spitzer, M., Reske, S. N., and Walter, H. 2002. Dissociating a common working memory network from different neural substrates of phonological and spatial stimulus processing. *NeuroImage* **15**: 45–57.