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An information-processing model of three cortical regions: evidence in episodic memory retrieval

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ACT-R (Anderson, J.R., et al., 2003. An information-processing model of the BOLD response in symbol manipulation tasks. Psychon. Bull. Rev. 10, 241–261) relates the inferior dorso-lateral prefrontal cortex to a retrieval buffer that holds information retrieved from memory and the posterior parietal cortex to an imaginal buffer that holds problem representations. Because the number of changes in a problem representation is not necessarily correlated with retrieval difficulties, it is possible to dissociate prefrontal–parietal activations. In two fMRI experiments, we examined this dissociation using the fan effect paradigm. Experiment 1 compared a recognition task, in which representation requirement remains the same regardless of retrieval difficulty, with a recall task, in which both representation and retrieval loads increase with retrieval difficulty. In the recognition task, the prefrontal activation revealed a fan effect but not the parietal activation. In the recall task, both regions revealed fan effects. In Experiment 2, we compared visually presented stimuli and aurally presented stimuli using the recognition task. While only the prefrontal region revealed the fan effect, the activation patterns in the prefrontal and the parietal region did not differ by stimulus presentation modality. In general, these results provide support for the prefrontal–parietal dissociation in terms of retrieval and representation and the modality-independent nature of the information processed by these regions. Using ACT-R, we also provide computational models that explain patterns of fMRI responses in these two areas during recognition and recall.

Keywords: Recognition; Recall; Memory

Introduction

In this paper, we used an information-processing model to interpret functional magnetic resonance imaging (fMRI) data. The topic we chose is the memory retrieval, which has been one of the most popular topics in cognitive neuroimaging, undoubtedly because the retrieval of information is critical for many cognitive activities. Specifically, the retrieval process addressed in the current study is episodic in nature in the sense that participants committed novel associations to memory and later their retrieval performance was tested in fMRI sessions. In cognitive neuroimaging, episodic memory has been primarily implicated in medial temporal, prefrontal, and parietal regions (Cabeza and Nyberg, 2000; Rugg and Henson, 2002). Activations in the medial temporal lobe, including hippocampus and surrounding regions, have been shown to reflect the associative encoding when new information is introduced (Davachi et al., 2003; Stark and Quire, 2001). The medial temporal lobe activations have also been found during retrieval, but these findings have been relatively inconsistent, suggesting that hippocampal activations during retrieval may be affected by the specific nature of tasks (Rugg and Henson, 2002). In contrast, the prefrontal cortex and the posterior parietal cortex have more consistently responded to retrieving information from memory (Rugg and Henson, 2002). Because human memory is an associative network in which a piece of information is associated with multiple other concepts, the associative strength between the memory probe and the target fact is critical in determining the speed of retrieval. In this paper, we will specify how associative strength should affect retrieval behavior. We will also specify how prefrontal and parietal regions should be involved during memory retrieval, using an information-processing model developed in the ACT-R architecture of cognition.

ACT-R (Anderson et al., 2004a), illustrated in Fig. 1, interacts with the external world through several modules and buffers that are specialized for processes like identifying objects in the visual field, controlling the hand, retrieving information from declarative

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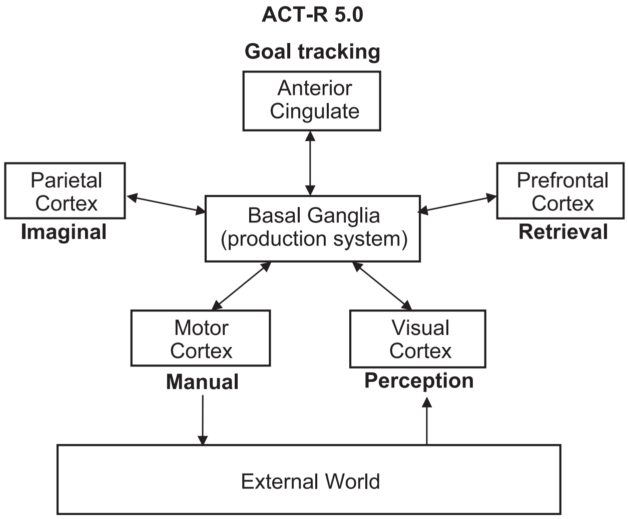

Fig. 1. The organization of information in ACT-R 5.0.

memory, or keeping track of current goals and intentions. ACT-R assumes a central production system that is sensitive to the pattern of information deposited in the buffers of these modules, and the information in a buffer changes as a result of the module activity. The significance to brain imaging is that the activity of each buffer is assumed to be reflected in cortical activity. Therefore, by specifying the buffer actions that underlie behavioral performance of a certain task, it is possible to predict the patterns of cortical activations.

Three buffers of the ACT-R architecture are of central interest to the current study. First, the imaginal buffer holds the representation of problems, such as mental images of memory probes, while other operations are being performed on these probes. The imaginal buffer is active when the problem representation changes, for example, when a new stimulus is encoded from the environment or from memory. In a previous study (Anderson et al., 2003), we defined the imaginal buffer as a region in the posterior parietal cortex, medially located in the intraparietal lobule. The imaginal-parietal mapping is consistent with findings such as the intraparietal activation during encoding of verbal items (Clark and Wagner, 2003; Davachi et al., 2001), the inferior parietal lobule activation in mental imagery tasks (Zacks et al., 2002), the superior parietal lobule activation during imagery formation of semantic content (Reichle et al., 2000), and the inferior parietal lobule activation during symbolic manipulation as opposed to verbal representation (Dehaene et al., 1999). Second, the retrieval buffer holds information retrieved from declarative memory, and it is active when there is a request for retrieval. In ACT-R, the retrieval buffer is associated with the inferior dorsolateral prefrontal cortex. Numerous brain-imaging studies have reported higher prefrontal activations during memory retrieval than during working memory maintenance (Cabeza et al., 2002; Wagner et al., 2001) or other control conditions (Thompson-Schill et al., 1997). Third, the manual buffer, which is attributed to the motor cortex, is active when a motor response is programmed and executed, reflecting the complexity of motor programming. Though not a part of the current ACT-R, it is likely that some aspects of motor programming and execution may also be associated with such regions as supplementary motor and premotor cortices.

The main goal of this paper is to describe how the prefrontal, parietal, and motor regions are involved in memory retrieval, and especially how the prefrontal and parietal regions can be functionally dissociated. Our claim is that the retrieval buffer responds to retrieval demands but the imaginal buffer responds to representational demands. In our previous event-related fMRI study (Sohn et al., 2003), we tested this hypothesis in the fan-effect paradigm (Anderson, 1974), in which participants committed arbitrary facts to memory and their recognition was tested later. In this paradigm, retrieval takes longer as elements in the probe are associated with more facts. The fan effect refers to an increase in response time and/or error rates with fan on a memory test. The explanation is that associative strength becomes weaker as more facts fan out from the memory probe. In the ACT-R architecture described earlier, the retrieval operation is directly affected by the associative strength or the fan. However, the number of items to be encoded is the same regardless of the fan in the recognition task. As evidence, Sohn et al. (2003) showed that the prefrontal activation was higher with high-fan probes than with low-fan probes, therefore, reflecting the retrieval durations of different fan conditions. In contrast, although the parietal activation did rise during the course of a recognition trial, reflecting such processes as encoding the memory probe, its activation did not vary with the fan conditions.

Sohn et al.'s (2003) study leaves two questions open. First, are there situations in which parietal activation is correlated with the associative strength? This is an important question because the parietal activation during episodic memory retrieval has been highly correlated with the prefrontal activation (for a review, see Rugg and Henson, 2002), and as a result, it has been an issue of debate how the parietal cortex is involved in episodic memory retrieval. Our hypothesis suggests that the parietal activation should not be directly related to memory retrieval but to the number of changes made to the problem representation. In the recognition paradigm, the number of representational changes does not vary with fan because the recognition task requires representation of just one probe and one retrieved trace. However, it is possible that the number of representational changes can be correlated with the associative strength. In Experiment 1, we compared a recall task with a recognition task. As will be explained, we constructed materials so that unique or stronger associations could reduce the encoding requirement in the recall task, but not in the recognition task. If the parietal cortex serves as the imaginal buffer that holds problem representations, we should observe prefrontal–parietal dissociation in the recognition task but not in the recall task.

The second question involves the specific nature of the information processed by the prefrontal and the parietal cortices. Implicitly, we have made an assumption that the information deposited in the buffers should not be modality specific. However, it is possible that these regions may be more sensitive to one modality than others. For example, evidence that the parietal cortex is associated with symbol manipulation (Dehaene et al., 1999) or with mental imagery (Reichle et al., 2000) suggests that the parietal activation may be more highly involved in representing visually presented information than information presented otherwise. Alternatively, some researchers have proposed that the parietal cortex should be the phonological store for the verbal working memory (Jonides et al., 1998). However, it is difficult to answer issues of modality-specificity on the basis of previous studies because most of them have used the visual modality for stimulus presentation. In Experiment 2, we presented fan materials visually as well as aurally for recognition tasks. By examining activations in the visual and auditory regions along with prefrontal and parietal cortices, we will be able to test whether these regions are modality specific or not.

In the following, we describe two experiments conducted in the fan effect paradigm. After reporting the behavioral results, we specify ACT-R models that explain the behavioral results. These models, constructed from component processes such as encoding, retrieval, and motor programming, specify when and how long a certain component has to be involved to produce the behavioral results. The most important purpose of this modeling effort is to acquire information about the duration of these component processes. The processing components of these models specifically tap the retrieval, imaginal, or manual buffers of the ACT-R architecture. Therefore, by estimating how long each component is in operation, we can predict the activation patterns in the brain regions corresponding to the buffers.

Experiment 1

Experiment 1 tested the proposed prefrontal–parietal distinction with recognition and recall tasks. Participants studied 25 sentences in the form of subject–verb–object such as “Programmer punches chemist”. Table 1 provides an abstract representation of these sentences. The sentences were constructed so that each subject and verb is associated with one, two, or three different object terms. After committing these sentences to memory, participants performed two episodic memory tasks. In the associative recognition task, the memory probe was a “subject–verb–object” triplet, and the task was to indicate whether the presented object term was correct for the subject–verb pair. In the cued-recall task, only the subject–verb pair was presented as a cue and the task was to indicate the correct object term.

The associative strength between the memory probe and the target fact is assumed to be less strong with increasing fan from subject–verb pairs, therefore increasing the duration of engagement of the retrieval buffer in both the recognition and the recall tasks. The encoding operation, however, does not differ with associative strength in the recognition condition because the number of items to be encoded in the memory probe is the same regardless of the fan. In the fan-1 condition of the recall task, however, the subject and the verb terms were redundant cues for the object term (see Table 1). Therefore, it is not necessary to encode both to retrieve the corresponding object term. In contrast, in the fan-2 and fan-3 conditions of the recall task, both subject and verb terms have to be encoded because only as a pair they could indicate a unique object term. Therefore, the encoding operation differs with fan in the recall task but not in the recognition task. We have two predictions to test. First, in the recognition task, only the prefrontal activation should reveal the fan effect (increased activation with high fan) but not the parietal activation. Second, in the recall task, both the prefrontal and the parietal activations should reveal the fan effect.

Materials and methods

Research participants

Nine right-handed participants (4 female, 18–22 years of age range with average of 20.6 years) were recruited locally. Participants received a monetary fee for participating. Prior to the test, participants provided written informed consent in accordance with the Institutional Review Board of the University of Pittsburgh.

Procedure

The design of the current study followed the original fan study (Anderson, 1974) and our previous fMRI study with the fan effect paradigm (Sohn et al., 2003). The E-Prime software package was used to present stimuli and to collect behavioral performance. On the acquisition day, participants memorized 25 sentences in the form of subject–verb–object (e.g., “Programmer punches chemist”). For each participant, five object terms were selected and each term was assigned to five different subject–verb pairs. Each subject and verb was associated with one, two, or three different object terms (see Table 1). Participants were first exposed to 25 sentences presented in five groups of five sentences that shared the same object term. To help memorization, participants were asked to construct and write down a story that would involve the presented object. Participants’ memory of these sentences was perfected through a triple-pass dropout cued-recall procedure. In each pass, participants were given an object term, and were asked to type all five subject–verb pairs associated with it. If they produced all the correct answers to a given object term, then this term was dropped out of the pass. If they failed, the correct answers were provided and the object term was repeated after all the other object terms had been asked. This continued until all questions had been answered correctly three times.

Table 1
Examples of subject–verb–object triplets

Fan-1			Fan-2			Fan-3		
Subject	Verb	Object	Subject	Verb	Object	Subject	Verb	Object
S1	V1	O1	S9	V9	O2	S13	V13	O4
S2	V2	O4	S9	V10	O5	S13	V14	O1
S3	V3	O5	S10	V11	O3	S13	V15	O3
S4	V4	O3	S10	V12	O4	S14	V13	O5
S5	V5	O4	S11	V11	O4	S14	V14	O2
S6	V6	O3	S11	V12	O1	S14	V15	O1
S7	V7	O2	S12	V9	O5	S15	V13	O2
S8	V8	O2	S12	V10	O1	S15	V14	O3
						S15	V15	O5

After the question–answering phase, participants received 50 recognition (25 targets and 25 foils) and 50 recall tasks. In the recognition test, a probe was in the form of a subject–verb–object triplet (e.g., “programmer-punches-chemist”). Participants made a judgment whether they had studied the probe or not. The foils were created by swapping object terms from the same condition. The “yes” and “no” responses were assigned to the second and the third buttons of a five-button response unit that is similar to the one used in a scanning session. In the recall test, a probe was in the form of a subject–verb pair (e.g., “programmer-punches-?”), and the task was to indicate which object was associated with the pair. The five object words were selected so that each one began with A, B, C, D, and E (e.g., Archer, Beautician, Chemist, Dentist, and Engineer) mapped to five buttons of the response unit.

A trial began with a warning signal (*) that stayed on the screen for 2.4 s, and the memory probe followed for 4.8 s. Participants were told to make a response while the memory probe was on the screen with emphasis both on accuracy and speed. After the memory probe, 10.8 s of resting period followed, in which feedback on accuracy and speed was provided.

On the scanning day, immediately following the acquisition day, participants received 25 recognition and 25 recall trials as “warm-up” trials before the actual scans. Feedback was provided for warm-up trials. During an fMRI scanning, there were 4 recognition blocks and 4 recall blocks with 25 trials in each block. Each sentence was used twice as a target for recognition, twice as a foil for recognition, and four times for recall. Because trial-by-trial feedback was not provided in the scanning session, participants were allowed to ask questions regarding materials between blocks so that they could correct their memories if necessary. At the end of each block, average accuracy and latency were provided as feedback.

In total, there were three tests of materials: first immediately after acquisition, second as a warm up before functional scanning, and third during the actual functional scanning.

Imaging procedures

To collect event-related fMRI data, we used a single-shot forward spiral sequence acquisition on a GE 3T scanner, with 1200 ms TR, 18 ms TE, 70° flip angle, 20 cm FOV, 21 axial slices/scan with 3.2 mm thickness, 64 × 64 matrix, and with AC-PC at the bottom slice. For each trial, 15 scans were acquired. Images were motion corrected using the 12-parameter rigid body model of the AIR (Woods et al., 1998) program and then cross-registered to a common reference brain by minimizing signal intensity differences. Then, functional images were set to a standard mean intensity, smoothed (6 mm full-width half-maximum 3D Gaussian kernel), and pooled across participants to improve signal-to-noise ratio.

Results

Behavioral results and modeling

Both accuracy and latency were subjected to two-way analysis of variance (ANOVA) with fan and task as variables. For latency, only the correct trials were analyzed. For the recognition trials, the correct trials included both hits and correct rejections. Mean accuracy and latency for each fan-by-task condition are presented in Table 2. Accuracy was higher in the fan-1 condition than in other fan conditions (F (2, 16) = 8.84, MSE = 0.002, $P < 0.01$, Newman–Keuls, $P < 0.05$). The main effect of task and its interaction with fan on accuracy were not significant (P’s > 0.09). As Table 2 shows, overall accuracy is fairly high suggesting that participants memorized materials quite well.

When considering only the recognition task, rejecting foils took significantly longer than accepting targets by 145 ms ($F(1, 8) =$ 13.39, MSE = 21146, $P < 0.01$. However, the target-foil effect did not interact with the fan effect (P’s > 0.10). To simplify analysis, we collapsed target and foil trials of recognition and compared recognition and recall tasks as a function of fan. Latency was faster with recognition than with recall ($F(1, 8) = 8.57$, MSE = 21373, $P < 0.05$). Also, latency was fastest in the fan-1 condition, intermediate in the fan-2 condition, and slowest in the fan-3 condition ($F(2, 16) = 69.72$, MSE = 41891, $P < 0.0001$; Newman–Keuls, $P < 0.05$). The interaction between task and fan was also significant ($F(2, 16) = 13.31$, MSE = 14389, $P <$ 0.0001). As shown in Table 2, the fan effect (defined as the average increase between fan-1 and fan-2 conditions and between fan-2 and fan-3 conditions) was greater on the recall task than on the recognition task (504 ms for the recall task and 270 ms for the recognition task; t (8) = 5.00, $P < 0.01$).

Both recall and recognition latencies showed the fan effect and the fan effect was greater for the recall task than for the recognition task. In this section, we describe ACT-R models that simulate the fan effect and the interaction between the fan and the task. Fig. 2 shows schematics of the models for the recognition and recall tasks. The purpose of this model construction is to have good estimates of the timing of model components. Once we achieve this goal, we will be committed to the temporal parameters provided by these models in predicting the BOLD functions in the brain regions associated with the model components.

In the recognition model, it is assumed that all three terms (subject, verb, and object) are encoded first, and then the model proceeds to retrieve the target sentence. If the target sentence is successfully retrieved, the problem representation is updated to be associated with positive response. If not, the problem representation is updated to be associated with negative response. Then, the appropriate motor response is programmed. The model suggests that there is one source of the fan effect in the recognition task: the

Table 2
Accuracy and latency, Experiment 1 and Experiment 2

	Experiment 1				Experiment 2			
	Latency		Accuracy		Latency		Accuracy	
	Recognition	Recall	Recognition	Recall	Visual	Aural	Visual	Aural
Fan-1	1400	1254	0.93	0.90	641	653	0.96	0.97
Fan-2	1822	1997	0.90	0.82	947	1003	0.88	0.87
Fan-3	1940	2261	0.91	0.80	1099	1176	0.89	0.87

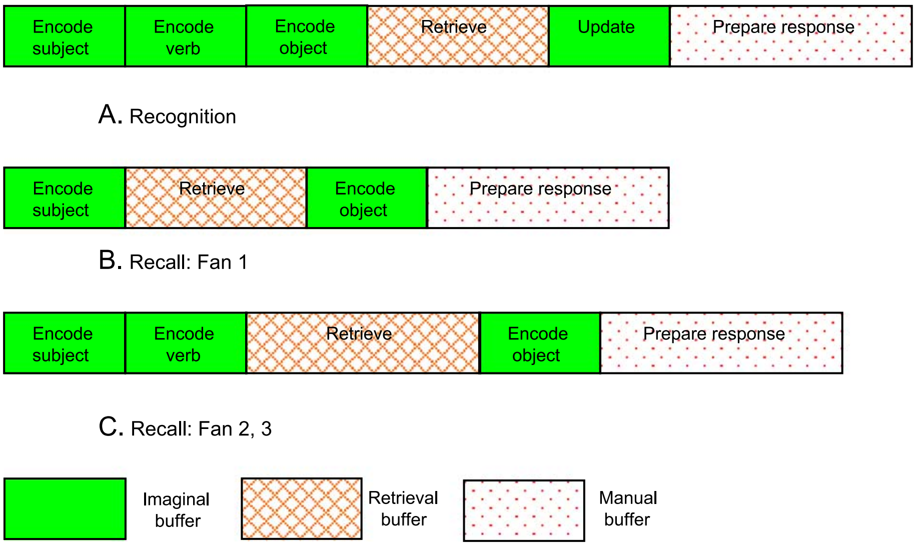

Fig. 2. ACT-R models for different conditions of Experiment 1.

retrieval takes longer for higher fan conditions because the associative strength between the memory probe and the target sentence should be relatively weak. The encoding, updating, and motor programming take the same amount of time regardless of the fan.

The memory probe for the recall task was a subject–verb pair (e.g., programmer-punches-?”), and participants indicated the missing object term. Due to the nature of material construction, the subject and the verb terms in the fan-1 condition of the recall task were redundant cues for the corresponding object. The subject–verb pairs used for the fan 1 condition were unique and not used for the fan-2 and the fan-3 conditions. Moreover, participants memorized all the materials near perfection before the test was administered. Therefore, it was an assumption of our model that participants realized it is redundant to encode both subject and verb terms when a particular subject term or a verb term is encoded. Therefore, in the fan-1 condition, the retrieval process can be initiated by encoding only one of them. In the fan-2 and fan-3 conditions, however, both the subject and the verb terms should be encoded before proceeding to retrieve. This extra encoding component provides one source of fan effect in the recall condition, which is different from recognition. Another source of the fan condition is the retrieval duration, which is also the case for recognition. After retrieval, the object term is encoded from memory, and then the appropriate motor response is programmed. These models explain the fan effect in both recognition and recall tasks by assuming that the retrieval time takes longer for high fan trials than for low fan trials. The interaction between fan and task is explained by assuming extra encoding requirement on the high fan trials of the recall task. Next, we will describe how ACT-R implements the retrieval process in these models.

In ACT-R (Anderson and Lebiere, 1998), activation spreads from presented terms to the connected nodes that represent various facts, and the latency to retrieve any fact from memory is determined by activation level of that fact. Most important, the activation level of a fact is a direct reflection of the associative strength between the presented term and the fact: the more unique the association, the higher the activation. The activation, A_i, of a particular fact i is determined by the following activation equation

$$A_i = B_i + \sum_j W_j S_{ji} \qquad \text{Activation equation}$$

where B_i is the base-level activation of the fact, reflecting its recency and frequency of study. We will simply assume $B_i = 0$ in these experiments because all the sentences are novel associations. The summation is over the concepts, j, which are the activation sources. In the current study, these sources can be subject, verb, and object terms for the recognition task and subject and verb terms for the recall task. The multiplier, W_j, is the amount of attention given to a particular dimension that a source j belongs to. The total amount of W is set to 1, and it is distributed evenly among the dimensions. S_{ji} reflects the associative strength between the concept j and the fact i, and the fan effect depends on this associative strength. As more facts are associated with a concept, the strength of association to a particular fact is weakened, because there is more competition for the limited activation. The associative strength (S_{ji}) depends on the total associative strength (S) and the number of associations from the concept, and is expressed as $S\text{-}ln(n)$, where n is the number of associations. In this paper, we used the value of S inherited from another study (1.25, Sohn et al., 2003). Therefore, none of the parameters determining activation were estimated to fit the data. The parameter that is estimated is the scale factor, F, of the latency equation of ACT-R that determines the retrieval time on the basis of activation level:

$$T = Fe^{-A} \qquad \text{Latency equation}$$

where A is the activation level.

In the models described above, the imaginal buffer actions (i.e., encoding and updating) are constrained by the ACT-R architecture to take 200 ms each. Also ACT-R constrains the motor programming time with binary options to take 400 ms, which is the case for the recognition task. To fit behavioral results, we estimated three parameters. As mentioned, the best fitting latency factor F was estimated for the retrieval time, separately for the recognition and the recall tasks. The other estimated parameter was the motor programming time for the recall task. Because there were five response alternatives, this time should be greater than the 400 ms of the recognition task. These parameters were estimated, while minimizing the χ^2 deviation of the fit to the data defined as

$$\sum_i (\hat{X}_i - \bar{X}_i)^2 / S\bar{x}^2$$

which is the ratio of the actual deviation (sum of the squared deviations of the predicted means from the actual means) to the estimated variance of the means (squared standard errors obtained from the participant-by-condition interaction). This is a statistic whose degrees of freedom is the number of observations (6 in total) minus the number of parameters (3). The model fit is presented in Fig. 3A, along with data. The latency factor was 709 ms for the recognition and 1408 ms for the recall task. The retrieval times for all conditions estimated by the best fitting model are presented in Table 3. The estimated motor programming time for the recall task was 497 ms.

The model's prediction shows a significant deviation from the data (χ^2 = 13.34, *df* = 3, critical value = 7.82 at *P* = 0.05). Inspection of Fig. 3 reveals that the misfit is largely because the model predicts participants should be taking longer in the fan-1 recognition condition. We think in this condition because the subject and verb are redundant, participants may have begun their retrieval early overlapping encoding and retrieval. However, we did not want to complicate our model to incorporate this possibility. This alternative model would not change the estimates of retrieval time or encoding time for purposes of the fitting of the fMRI data. We are only fitting the latency as a step to accounting for the fMRI data and so we were satisfied with this simpler, slightly approximate model.

Imaging results and modeling

In this section, we describe how to predict the fMRI responses in three cortical regions on the basis of the timing information from the behavioral models. The prefrontal, parietal, and motor regions in the left hemisphere were pre-defined as schematically illustrated in Fig. 4. These are the same regions investigated by several studies on retrieval, encoding, and motor programming (Anderson et al., 2004b; Qin et al., 2003; Sohn et al., 2003). Therefore, the current confirmatory analysis will provide a generalization to different tasks and materials. Each ROI was 5 voxels wide, 5 long, and 4 high for a total of 100 voxels per region (voxel size is 3.125 × 3.125 × 3.2 mm^3). The majority of the left prefrontal ROI was in the inferior dorso-lateral prefrontal cortex with its central voxel located at −44, 21, 21 in Talairach coordinates. The voxels in the prefrontal ROI are located in BA 9, 44, 45, and 46. The left posterior parietal ROI was in the intra-parietal lobule (BA 39/40), with its central voxel located at −24, −64, 34 in Talairach coordinates. The left motor ROI was in left BA 1/2/3/4, including both motor and somatosensory regions, with its central voxel located at −37, −24, 47 in Talairach coordinates.

Table 3
Retrieval times of the best-fitting ACT-R models for each condition

	Experiment 1		Experiment 2	
	Recognition (ms)	Recall (ms)	Visual (ms)	Aural (ms)
Fan-1	347	404	258	258
Fan-2	552	807	516	516
Fan-3	723	1211	773	773

To specify fMRI responses for different fan conditions that we tested, we decomposed the models into three types of buffer actions. In our models, encoding and updating operations are imaginal buffer actions and attributed to the parietal functions. The retrieval operation is a prefrontal function, and the motor programming is a motor function. In Anderson et al. (2003, in press b), a proposal has been developed for how the duration of a buffer action maps onto the predicted fMRI response. This proposal starts with the common assumption by a number of researchers (Boyton et al., 1996; Cohen, 1997; Dale and Buckner, 1997) that the blood oxygenation level dependent (BOLD) response to an event varies according to the following function of the time, *t*, since the event:

$$B(t) = (t/s)^a e^{-(t/s)}$$

where estimates of the exponent, *a*, vary between 2 and 10, and *s* is the latency scale. This is essentially a gamma function that will reach maximum at roughly $t = a \times s$ seconds. It was proposed that while a region is active it is constantly producing a change that will result in BOLD responses according to the above function. The observed fMRI response is integrated over the time that the region is active. Therefore, the observed response will vary with time as

$$CB(t) = M \int_0^t i(x)B(t-x)\mathrm{d}x$$

where *M* is the magnitude scale for response. In the above equation, *i*(*x*) is 1 if the region is active at time *x* and 0 otherwise. For instance, in the fan-1 condition of the recognition task, Fig. 2A, the parietal region is active between 0 and 600 ms and between 1060 and 1260 ms, while the prefrontal region is active between 600 and 1060 ms.

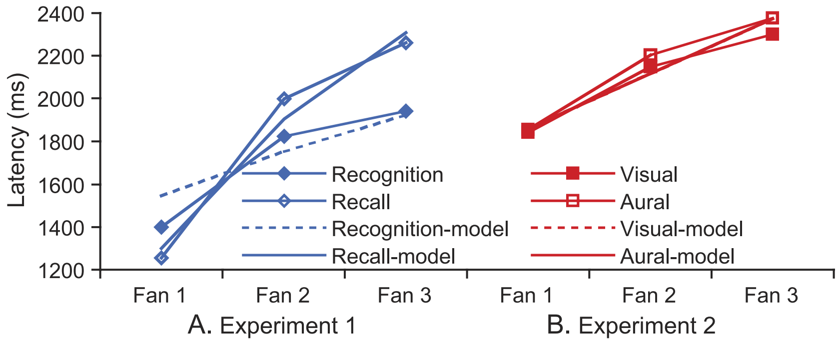

Fig. 3. Model fit to behavioral data in Experiment 1, panel (A), and in Experiment 2, panel (B).

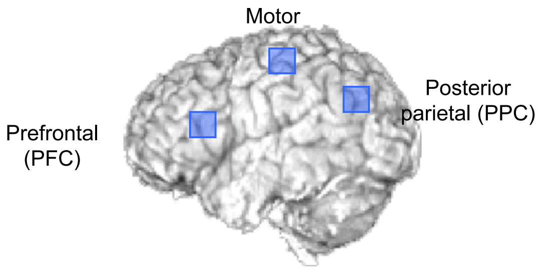

Fig. 4. Three prescribed cortical regions.

The magnitude parameter reflects the sensitivity of the region to the event, and the scale factor and the exponent determine how fast the BOLD functions will rise and fall. When multiple buffer activities are spaced out, each BOLD response to a specific buffer action will be aggregated. If a buffer is active for a total period of time T, the area under the BOLD response will be $Ms\Gamma(a+1)T$ where Γ is the gamma function (in the case of integer a, note that $\Gamma(a+1) = a!$). The implication of the above two equations is that the total area under the curve will be precisely proportional to the total time that the buffer is active. The area difference due to a particular experimental variable (e.g., fan in this study) will be realized as an interaction involving that variable and scan.

We can use the durations of the buffer activities in Fig. 2 to generate predictions for the BOLD responses in each of the prespecified ROIs for each experimental condition. In making these predictions, we have to estimate two parameters that determine exact shape of the BOLD response—the latency scale (s) and the magnitude (M). The exponent (a) is fixed at 7 across the regions. These parameters are estimated to minimize the squared deviations between the observed and predicted BOLD functions, as measured by χ^2 deviation of the fit to the data. While these parameters determine the exact shape of the BOLD response, estimating them is not bound to the ACT-R theory. As the timing of the buffer actions is set to fit the behavioral data, what ACT-R predicts is

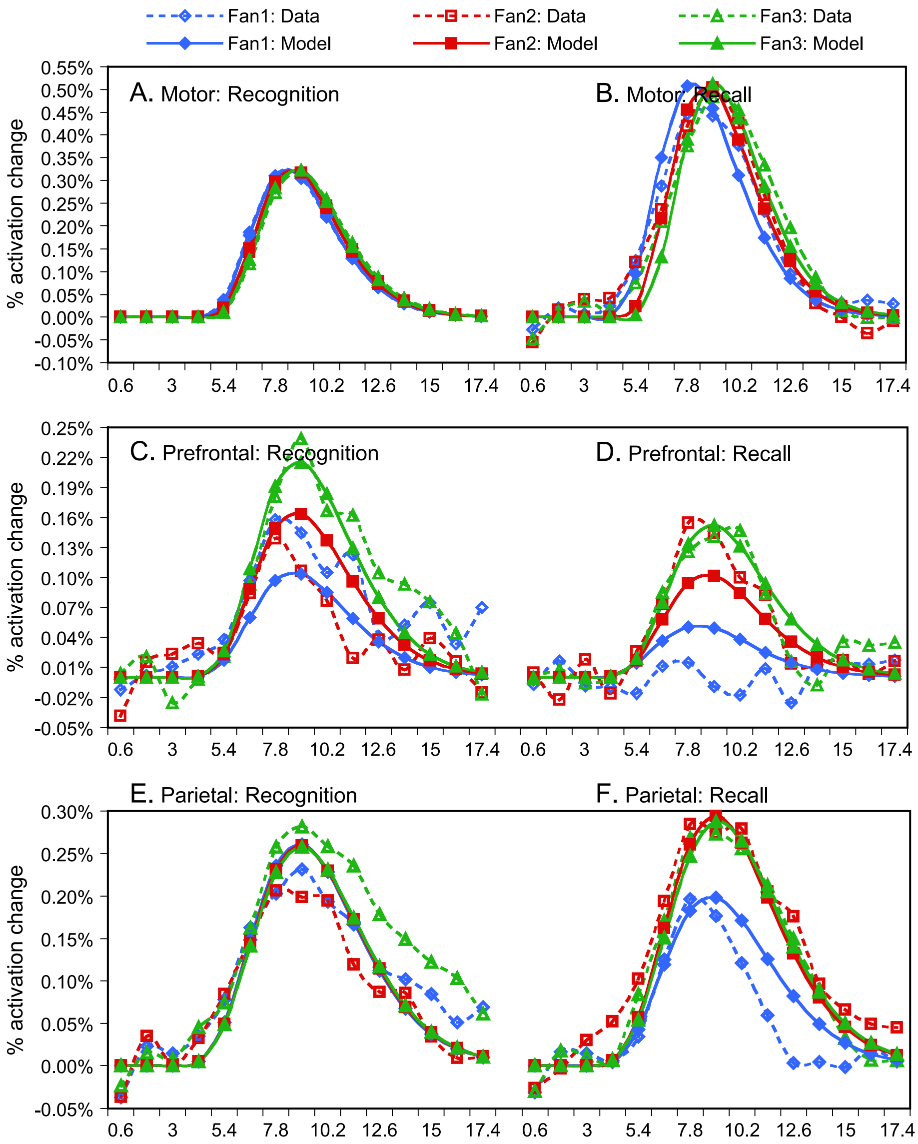

Fig. 5. Observed BOLD functions of three cortical regions and model predictions in Experiment 1. The x axis in each panel represents the time within a trial in second.

whether or not the relative areas under the BOLD functions for the different conditions should be different for a particular brain region.

We have specific predictions for each cortical region. First, because the number of imaginal operations does not differ depending on the fan for the recognition task, there should be no fan effect on the parietal activation in the recognition condition. However, the recall task should reveal a fan effect on the parietal activation, because the number of imaginal operations does differ with fan: in the fan-2 and fan-3 conditions, extra encoding is required compared with the fan-1 condition. Second, the fan effect on the prefrontal activation should be obtained for both recognition and recall tasks because the retrieval time differs with fan for both tasks. Third, the fan of a fact to be retrieved would not have effect on the motor programming time. However, activation in the motor region should reflect the complexity of motor programming. In the recognition condition, a binary response is made between "yes" and "no", while there are five alternatives to choose from in the recall condition. Therefore, the recall task should result in greater activation in the motor region than the recognition task.

In terms of parameter estimation, the scale factor and the exponent were common for the recognition and the recall tasks. Different magnitudes were estimated for recognition and recall tasks, as these tasks were administered in blocks. Further, as described below, these two tasks significantly interacted with other variables. In Experiment 1, there are 90 data points to fit (3 fan conditions × 2 memory tasks × 15 scans) with 3 parameters for each region, resulting in 87 degrees of freedom. These estimated BOLD functions are displayed along with the data in Fig. 5, and the parameter values are presented in Table 4. We conducted separate ANOVAs on motor, parietal, and prefrontal regions with task, fan, and scan as variables. Fig. 5 shows within-trial percent activation changes in these regions. For the motor region, there was a significant main effect of task ($F(1, 8) = 24.10$, $MSE = 0.017$, $P < 0.001$), a significant fan-by-scan interaction ($F(28, 224) = 2.24$, $\mathrm{MSE} = 0.003$, $P < 0.001$), and a significant task-by-scan interaction ($F(14, 112) = 10.13$, $\mathrm{MSE} = 0.004$, $P < 0.0001$). Our model attributes the task-related effects to the difficulty of motor programming for the recall task (five response alternatives) in comparison with the recognition task (two response alternatives). The model attributes the fan-by-scan interaction to the fact that the peak of the BOLD function is delayed in high fan conditions because of the delayed response. The model captures the task effect quite well and does not deviate from the data significantly ($\chi^2 = 90.22$, $df = 87$, critical $\chi^2 = 109.77$ at $P = 0.05$).

Table 4
Parameters of the best-fitting BOLD functions

		Manual to motor	Retrieval to prefrontal	Imaginal to parietal
Experiment 1	Magnitude: recognition[a]	0.039	0.017	0.020
	Magnitude: recall	0.049	0.007	0.031
	Scale (s)	0.767	0.910	0.990
	Exponent (a)	7.00	7.00	7.00
Experiment 2	Magnitude	0.22	0.14	0.056
	Scale (s)	0.625	0.929	0.817
	Exponent (a)	7.00	7.00	7.00

[a] $M' = Ms\Gamma(a + 1)$. This is a more meaningful measure since the height of the function is determined by the exponent as well as M.

For the prefrontal region, the task-by-fan-by-scan interaction was significant ($F(28, 224) = 1.86$, $\mathrm{MSE} = 0.0043$ $P < 0.01$), indicating that the fan effect differed depending on tasks. To investigate this interaction, we examined the fan-by-scan interaction in each task. This interaction was significant in both tasks ($F(28, 224) = 1.17$, $\mathrm{MSE} = 0.004$, $P < 0.05$ in recognition; $F(28, 224) = 2.95$, $\mathrm{MSE} = 0.003$, $P < 0.0001$ in recall). As indicated by Figs. 5C and D, the fan effect in the prefrontal activation seems to be greater in the recall task than in the recognition task. This interaction is primarily due to the larger fan effect in latency that we observed in the behavioral data. Looking at Table 3, which gives the estimated retrieval times for the conditions, we see a larger fan effect on retrieval time in the recall condition than in the recognition condition. Thus, the fan-by-condition interaction in the prefrontal cortex basically reflected the interaction in retrieval times predicted by the ACT-R theory. The model fits the data quite well ($\chi^2 = 84.54$, $df = 87$).

For the parietal region, the task-by-fan-by-scan interaction was significant ($F(28, 224) = 1.51$, $\mathrm{MSE} = 0.002$, $P < 0.01$). In the recognition task, neither the main effect of fan nor its interaction with scan was significant (P's > 0.09). In the recall task, the fan-by-scan interaction was significant ($F(2, 16) = 2.68$, $\mathrm{MSE} = 0.002$, $P < 0.0001$). Further, we tested whether peak responses differ as a function of fan in the recognition and recall conditions. The peak was defined by the sum of activation changes associated with the scans 7, 8, and 9. The peak responses were significantly different depending on fan in the recall condition ($F(2, 16) = 6.20$, $\mathrm{MSE} = 0.085$, $P < 0.01$). However, the peak responses were not different depending on fan in the recognition condition, $P > 0.16$. These results show that the fan effect had an impact on the parietal activation during the recall task but not during the recognition task. Our model predicts no fan effect in the recognition condition but predicts the fan effect in the recall condition because of the extra encoding requirement for the recall task. The data are well captured by the model ($\chi^2 = 91.00$, $df = 87$).

For both prefrontal and parietal regions, model predictions on the basis of behavioral data were quite consistent with the imaging data: the fan effects were significant for the prefrontal activation in both recognition and recall tasks. For the parietal activation, the fan effect was significant for the recall task, but not for the recognition task. However, close examination of models reveals that not only the fan effects within each region should differ by tasks, but also that the fan effect within each task should differ by regions.

To examine the cortical dissociation within each task, we conducted a three-way ANOVA with brain region (prefrontal and parietal regions), fan, and scan as variables separately for recognition and recall tasks. For the recognition task, as reported earlier, the fan-by-scan interaction was significant only for the prefrontal activation but not for the parietal activation. However, this difference in the two-way interaction did not enter into a significant three-way interaction involving region, $P > 0.70$. For the recall task on the other hand, both the prefrontal and parietal regions revealed significant fan-by-scan interactions, and the patterns of these interactions were significantly different by regions, $F(28, 224) = 1.67$, $\mathrm{MSE} = 0.002$, $P < 0.05$. The fact that the regional dissociation was significant only in the recall but not in the recognition task certainly raises a concern regarding the functional distinction that we proposed between these regions. However, it is important that the fan effect predictions made by the models were all consistent with the data in each combination of the task and region. The only prediction that was not supported was the one regarding the cortical difference in the fan effect for the recognition condition, though the pattern of the fan effect within each region in this task was consistent with the prediction.

Alternative explanation is available regarding the task differences in both prefrontal and parietal regions. One may think that these differences may lie in the fact that there are two types of trials in the recognition task, targets and foils. Because foil trials require rejection of the presented probe, it is possible that these trials may contribute differently than the target trials. To examine this possibility, we took only the recognition trials and examined whether the trial type (target or foil) had any different effects on the activation change. We conducted a three-way ANOVA with fan, trial type, and scan as variables. In both prefrontal and parietal region, the trial type did not have any significant main effects nor interactions with other variables, $P > 0.10$. The trial type effect on behavioral result was 145 ms, which is quite small compared with the fan effect. Considering that the temporal resolution of fMRI is pretty coarse, perhaps the 145 ms of target-foil effect may not have been large enough to produce significant activation changes. Nonetheless, the recognition-recall differences in the parietal and prefrontal region cannot be attributed to the target-foil differences in the recognition task.

Exploratory ROI analyses

To examine whether our confirmatory analyses missed any important regions, we conducted two exploratory analyses. First, we conducted voxelwise fan-by-scan ANOVAs and searched for clusters of more than 6 contiguous voxels (Forman et al., 1995) showing significant fan-by-scan interactions ($F(2, 16) = 3.63$, $P < 0.05$). To have a conservative test that deals with non-independence of successive scans, we adjusted the degrees of freedom by not assigning those from the scan to the numerator in the F-statistic for the interaction term (equivalent to the Greenhouse–Geisser correction for non-independence of conditions). Note that the fan-by-scan interaction is only significant when the fan conditions result in different BOLD functions over scans. The regions that showed greater activation change in the high fan condition included the left anterior cingulate cortex (BA 32, $F = 4.2$, −3, 16, 43), the precuneus (BA 31, $F = 4.3$, −3, −62, 25), and the left posterior cingulate cortex (BA 23/30, $F = 4.48$, −9, −54, 14). The left angular gyrus (BA 40, $F = 5.83$, −53, −52, 34) showed a negative percent activation change and the amount of change was greater for the high fan condition. The fact that we did find a strong effect in our a priori prefrontal region but did not identify this region in the exploratory analysis shows that one advantage of a confirmatory analysis is to identify meaningful patterns of activation that may not pass a conservative test of an exploratory analysis.

Second, voxelwise task-by-scan ANOVAs were conducted ($F(1, 8) = 5.31$, $P < 0.05$), and the bilateral central gyri, (BA 1/2/3/4, $F = 11.05$, −39, −24, 57 and BA 1/2/3/4, $F = 8.06$, 46, −28, 48) showed greater activation change for the recall task than for the recognition task. The greater activation change in the left central gyrus is in line with the confirmatory analysis in which the motor region showed greater activation change in the recall task than in the recognition task.

Experiment 2

Experiment 2 tested whether the proposed prefrontal–parietal dissociation depends on the modality of stimulus presentation. We used the same fan-effect paradigm of Experiment 1 with the recognition task only. The acquisition phase was essentially the same as in Experiment 1. In the scanning session, the probes were presented visually in half of the testing blocks, and aurally in the other half of the blocks. If information processed by the prefrontal and parietal cortices is modality specific, we would observe different results depending on stimulus presentation modality.

Method

Behavioral protocol

Twelve right-handed participants (4 female, 18–22 years of age range with average of 20.7 years) were recruited locally and they provided written informed consent in accordance with the guidelines of the University of Pittsburgh. The behavioral protocol was the same as in Experiment 1, except that only the recognition task was used and half of trials involved visually presented memory probes and the other half involved aurally presented memory probes. Because aural presentation inevitably involved serial presentation, we presented each element of a probe serially in both visual and aural presentation conditions for 500 ms. During fMRI scanning, there were 4 blocks of visual recognition and 4 blocks of auditory recognition with 25 trials in each block.

Imaging procedures

Due to the change of scanners between experiments, slightly different scanning parameters were used. Event-related fMRI data were collected with echo-planar imaging sequence on a Siemens 3T scanner, 1500 ms TR, 50 ms TE, 70° flip angle, 21 cm FOV, 26 axial slices/scan with 3.2 mm thickness, 64 × 64 matrix, and with AC-PC at the 21st slice from the top. For each trial, 10 scans were acquired. Images were motion corrected using the 12-parameter rigid body model of the AIR (Woods et al., 1998) program and then cross-registered to a common reference brain by minimizing signal intensity differences. Then, functional images were set to a standard mean intensity, smoothed (6 mm full-width half-maximum 3D Gaussian kernel), and pooled across participants to improve signal-to-noise ratio.

Behavioral results and modeling

Accuracy and latency were analyzed in terms of fan, trial type (target and foil), and modality of stimulus presentation. For latency, only the correct trials (hits and correct rejections) were analyzed. Mean accuracy and latency for each fan-by-modality condition are presented in Table 2. Note that in general the latency in Experiment 2 is much faster than in Experiment 1 because it was measured from the onset of the third component of the probe due to serial presentation. Though not precise, adding 1000 ms, which is the presentation time for the first two components of a probe, the latency becomes comparable to Experiment 1.

Accuracy was higher in the fan-1 condition than in other fan conditions ($F(2, 22) = 8.62$, MSE = 0.012, $P < 0.01$, Newman–Keuls, $P < 0.05$). The modality-by-trial type interaction was also significant ($F(2,22)-8.62$, MSE = 0.012, $P < 0.05$). In the aural condition, accuracy was higher when rejecting foils than accepting targets (0.94 and 0.88, $t(11) = 2.37$, $P < 0.05$), while there was no difference in the visual condition (.91 each, $P > 0.70$). No other main effects or interactions were significant (P's > 0.10).

Latency was fastest in the fan-1 condition, intermediate in the fan-2 condition, and slowest in the fan-3 condition ($F(2, 22) = 57.65$, MSE = 51870, $P < 0.0001$, Newman–Keuls, $P < 0.05$). The target trials were faster than foil trials by 72 ms ($F(2, 22) = 14.16$, MSE = 13058, $P < 0.01$). No other main effects or interactions were significant (P's > 0.10). The behavioral results indicate that there is generally no effect of presentation mode.

We used the same model as for Experiment 1 except for some modifications to deal with fact that the elements were presented one at a time. Our Experiment 2 model encoded each item as it was presented. It also initiated retrieval after the second element. Even though it had to encode the third when it was presented, the first two elements were enough to direct retrieval. We estimated a single latency factor for the visual and aural presentation. The modeling result is presented in Fig. 3, along with the data. The retrieval times for all conditions estimated by the best fitting model are presented in Table 3. The latency factor was 900 ms. The performance was quite good and did not significantly deviate from data ($\chi^2 = 8.14$, $df = 5$, critical value = 11.07, $P < 0.05$).

Imaging results and modeling

In Experiment 2, the field of view was greater (210 mm) than in Experiment 1 (200 mm). Our reference brain in which we defined the three cortical regions was initially prepared in 200 mm field of view. Expanding the reference brain within the new field of view resulted in larger voxel dimensions, and as a consequence, the reported coordinates of three regions are slightly different from Experiment 1. However, these differences are less than a size of a voxel. The center of the left prefrontal region was at −45, 24, 21 in Talairach coordinates. The center of the left posterior parietal region was at −24, −64, 34 in Talairach coordinates. The center of the left motor region was at −41, −25, 47 in Talairach coordinates.

The three-way ANOVAs were performed on the motor, parietal, and prefrontal regions with modality, fan, and scan as factors. Fig. 6 shows within-trial percent activation changes in these regions. Table 4 presents the parameters of the best-fitting BOLD signal estimations. Because we assume that the activation in these regions is not modality-specific, we estimated the same exponent, scale factor, and magnitude between the visual and the aural presentations. For the motor region, there was a significant fan-by-scan interaction ($F(18, 198) = 2.31$, MSE = 0.1469, $P < 0.01$). The fan-1 condition seems to fall back to baseline slightly earlier than other conditions, because the response is given earlier. The model fit was good ($\chi^2 = 67.04$, $df = 58$, critical $\chi^2 = 76.78$ at $P = 0.05$).

For the prefrontal region, the main effect of fan was significant ($F(2, 22) = 5.74$, MSE = 0.77, $P < 0.05$). Also, the fan-by-scan interaction was significant ($F(18, 198) = 2.93$, MSE = 0.168, $P < 0.0001$). As expected by the model ($\chi^2 = 36.48$, $df = 58$), the fan effect was significant in both presentation modes, and did not depend on modalities.

For the parietal region, the fan-by-scan interaction was not significant ($P > 0.40$). In this region, the modality-by-scan interaction was marginally significant ($F(9, 99) = 1.92$, MSE = 0.103, $P < 0.06$). It seems that the activation change reach higher peak in the visual presentation condition. Although it appears that there is a fan effect in the aural presentation condition, the fan-by-mode-by-scan interaction was not significant ($P > 0.10$) and when considered only the aural presentation condition, the fan-by-scan interaction was still not significant ($P > 0.20$). Despite the apparent differences between two modality conditions, we used a model that did not assume any differences between presentation modes, and the fit was quite good ($\chi^2 = 37.03$, $df = 58$).

The apparent fan effect in the parietal region for the aural condition raises a question regarding the reliability of the proposed prefrontal–parietal distinction. One possibility is that the good model fit may be primarily due to the visual presentation condition in which fan did not seem to have much impact. We examined how well ACT-R predictions described above can explain data from each presentation condition. The parameters mentioned above fit each data set quite well. For the visual presentation condition, χ^2 deviation was 22.35, and for the aural presentation, it was 20.41 condition. Each did not deviate from data significantly (critical value = 41.34, $df = 28$). One might argue that the data from the aural condition might have been quite noisy, which could have prevented a significant fan effect from being detected. Extreme noise in the data could allow any model to fit the data decently. However, the standard error that we estimated for fitting the parietal region (0.18%) was smaller than for the prefrontal region (0.60%).

Our modeling effort is focused on the fan effect and ignored the target-foil difference. Just to make sure that the results reported here are not different depending on the trial type, we conducted a four-way ANOVA with trial type, fan, modality, and scan in each region. The only significant result involving trial type was a trial type-by-scan interaction in the prefrontal region. Foil trials produced greater activation change than target trials, ($F(9, 99) = 4.44$, MSE = 0.199, $P < 0.0001$), perhaps reflecting their greater latency. However, trial type did not significantly modulate the fan-by-scan interaction in any region.

Exploratory ROI analysis

As in Experiment 1, we conducted two exploratory analyses. First we conducted voxelwise fan-by-scan ANOVAs, and searched for clusters of more than 6 contiguous voxels showing significant fan-by-scan interactions ($F(2, 22) = 3.44$, $P < 0.05$). Consistent with the confirmatory analysis, two left prefrontal regions showed greater activation changes for high fan conditions than for low fan conditions (BA 9/44, $F = 5.13$; −51, 14, 29; BA 45, $F = 5.10$; −31, 17, 4). In addition, the posterior cingulate cortex (BA 23/30, $F = 4.92$; −11, −53, 4), showed higher activation change for the high fan condition. However, the parietal region was not identified, which is also consistent with the confirmatory analysis. Second, voxelwise mode-by-scan ANOVAs were conducted ($F(1, 11) = 4.84$, $P < 0.05$). As would be expected, bilateral occipital activation favoring the visual presentation condition (BA 19, $F = 11.48$; −41, −70, −7 and BA 19, $F = 8.07$; 42, −63, −6) and bilateral temporal activation favoring the aural presentation (BA 21/22/41/42, $F = 23.69$; −50, −26, −1 and BA 21/22/41/42, $F = 24.97$; 52, −18, 11) were identified. The pattern of activation changes in Fig. 7 suggests that modality manipulation did affect the corresponding cortical regions.

Discussion

The most important premise of the current study is the proposed mapping between ACT-R buffers and cortical regions. In general, the current imaging results and computational modeling seem to support the prefrontal–parietal distinction in terms of retrieval and representation. In addition to the prefrontal–parietal distinction, the current study also showed that our prescribed motor region is sensitive to the manual buffer activity as reflected in the recognition–recall difference in Experiment 1. This task effect was modeled on the basis of the differential complexity in the motor programming during the recall and during the recognition task.

The prefrontal activation reflected the retrieval difficulty in both recognition and recall tasks (Experiment 1) and was independent of

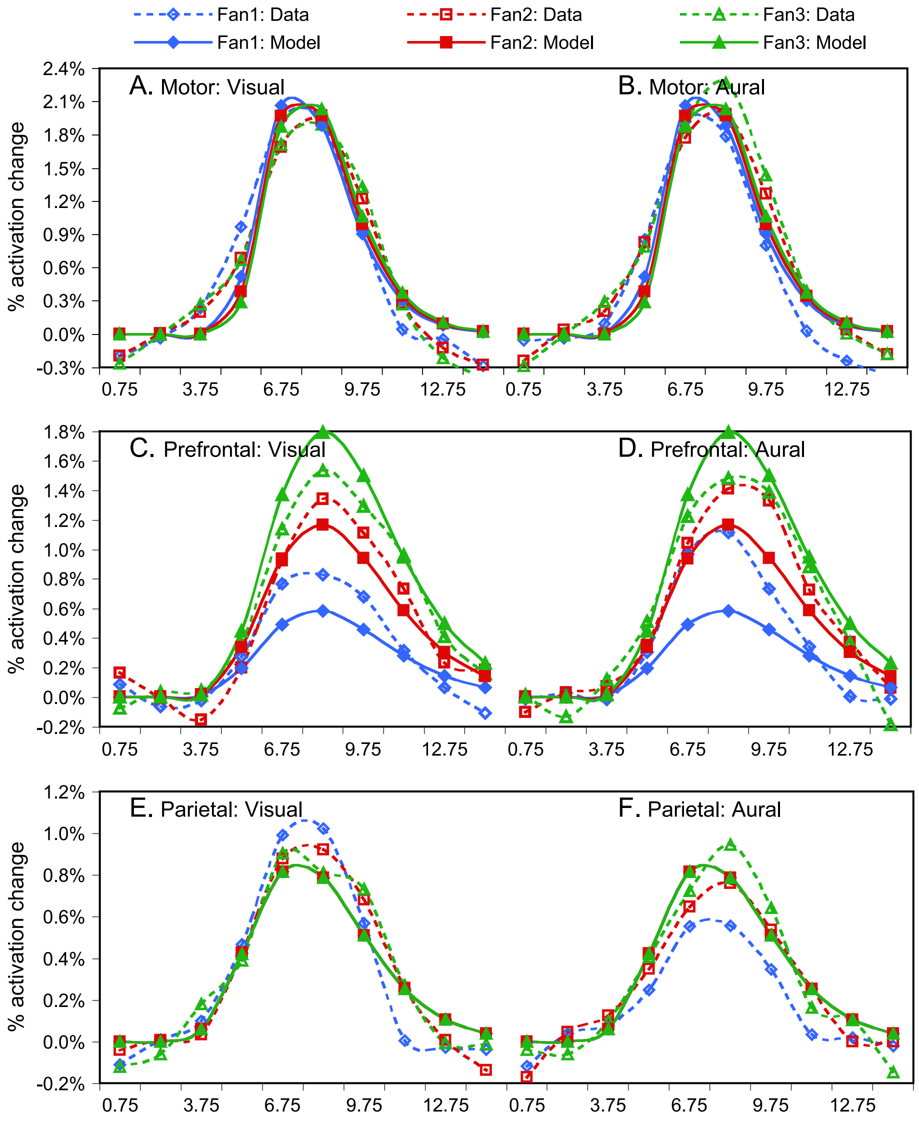

Fig. 6. Observed BOLD functions of three cortical regions and model predictions in Experiment 2. The *x* axis in each panel represents the time within a trial in second.

the modality of stimulus presentation (Experiment 2). The retrieval difficulty had a greater impact on the recall performance than on the recognition performance, which was reflected in both latency and the prefrontal activation. These patterns of results in the prefrontal activation matched the predictions of the retrieval component of the ACT-R model. It should be noted that in the Experiment 1 results, the percent activation change of the prefrontal cortex is greater for the recognition task than for the recall task. Considering that normally the recall task takes longer than the recognition task, this result may seem counterintuitive. However, because these two tasks were administered in a blocked manner, it is possible that the baseline activation level of the prefrontal cortex might have been different for each task. Participants might have been more alert for the recall task, which may well increase the activation level of the prefrontal cortex in general, resulting in less increase of percent activation change.

The posterior parietal activation was explained by the imaginal buffer activity. In Experiment 1, the parietal activation reflected the fan effect in the recall task but not in the recognition task. However, this interaction does not seem to be an indication of direct relationship between the parietal cortex and the retrieval buffer. Rather, ACT-R models of behavioral results suggest that the number of representational changes, which are the processes that the imaginal buffer is sensitive to, coincidentally increases with the retrieval difficulty in the recall task but not in the recognition task. There has been evidence that the parietal cortex responds to the existing level of competition (Bunge et al., 2002; Schumacher and D'Esposito, 2002). These studies used a stimulus-response compatibility paradigm, in which participants respond to the target in the face of a distractor that affords either a compatible or incompatible response with the one associated with the target. Results showed that parietal activation was higher when the distractor was associated with a potential response that is incompatible with the target response than when it was compatible. That is, the parietal cortex responds to the presence of competition even though the number of stimulus elements was controlled. We suggest that this result occurred because the stimulus-response compatibility task may require retrieval processes that are similar to the recall task. In the

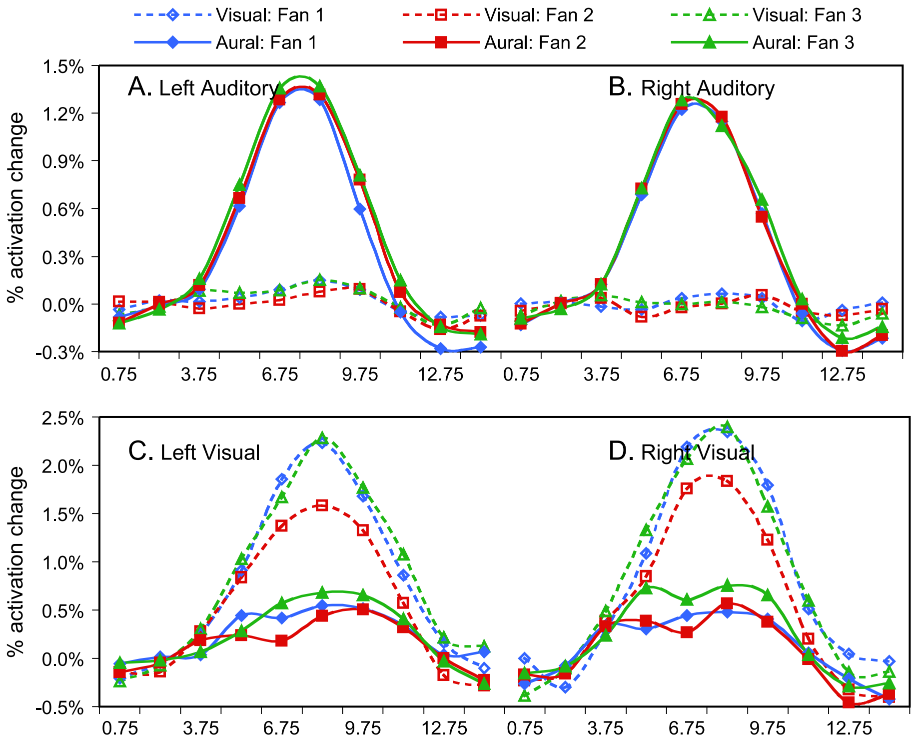

Fig. 7. BOLD functions in the auditory and the visual cortices in Experiment 2. The *x* axis in each panel represents the time within a trial in second.

stimulus-response compatibility task, the response as a part of a stimulus-response association has to be recovered through a recall process, which results in updating the problem representation, tapping the imaginal buffer. According to our analyses, greater parietal activation will occur when the task-irrelevant information (i.e., distractor-response mapping) is retrieved before the task-relevant information (i.e., target-response mapping).

In Experiment 2, the prefrontal and parietal regions responded well to the task regardless of stimulus presentation modalities. Interestingly, the parietal activation was higher with visual stimuli than with auditory stimuli. It is not clear to us why our left parietal region was more sensitive to visual presentation than to auditory presentation. However, as our modeling showed, even when we assumed no difference between modalities, the parietal activation could well be explained by the imaginal buffer activities, suggesting that the parietal activation may not be entirely modality specific. Our tentative conclusion is that, although the parietal region generally deals with modality-independent representations, it may be possible that different modalities may result in different strategies that may tap into the imaginal buffer differentially.

Although our models generated relatively good fits to fMRI data, it should be also noted that there were some inconsistencies. One prominent misfit is that while the model predicts gradual increase of fMRI responses in the prefrontal activation, in some conditions the fan-2 and the fan-3 curves are not really separated from each other (see Fig. 6). One reason for this misfit may be that the latency difference between these two conditions resides in other processes that we did not consider in the current models. We take this as a challenge for further investigation to elaborate the model and to specify the functions associated with other brain regions that we left out in the current study. Another apparent misfit is related to the fan effect in the parietal activation for the aural presentation condition of Experiment 2. While this fan effect was not statistically significant, it needs to be further investigated in studies that manipulate presentation modality.

These misfits raise a question how much the success of our model fitting is actually due to the ACT-R mappings of retrieval-imaginal buffers to prefrontal–parietal cortices, and not to the gamma function assumption for BOLD responses. One way to address this issue is an alternative model fitting. We fitted the prefrontal activation using the imaginal buffer action and the parietal activation using the retrieval buffer action. If the goodness of model fitting that we achieved is primarily due to the gamma function assumption, this alternative model fitting may result in as good fit as we reported earlier. In Experiment 1, the parietal predictions generated from the retrieval buffer action fit the data quite poorly (χ^2 = 148.54, df = 87, critical χ^2 = 109.77 at P = 0.05). The prefrontal predictions from the imaginal buffer action did not provide a statistically deviant misfit (χ^2 = 99.32), but this fit is worse than the one with the prefrontal predictions from the retrieval buffer action (χ^2 = 84.54). If we take the χ^2 difference (D) between two models fitting the same data, it is the relative likelihood of the data under the two models. It can be seen that data for both the prefrontal and the parietal activations are at least 1000 times more likely under the proposed models than the alternative models. In Experiment 2, the parietal predictions generated from the retrieval buffer action fit the data quite poorly (χ^2 = 85.27, df = 58, critical χ^2 = 76.78 at P = 0.05). The prefrontal predictions from the imaginal buffer action did not provide a statistically deviant misfit (χ^2 = 40.93), but this fit is worse than the one with the prefrontal predictions from the retrieval buffer action (χ^2 = 36.48). It is at least 10 times more likely that the prefrontal activations are under the proposed models than the alternative models.

An alternative to our modeling effort that involves magnitude, exponent, and scale factor would be to extract a single magnitude measure to fit the area above baseline. Here, the prediction is that these magnitudes should be proportional to the buffer time. Certainly, this is a much simpler way of modeling because it does not require exponent and scale factors. However, this modeling will not allow the test of whether the responses are really hemodynamic in nature. It is possible that in some regions of the brain, non-hemodynamic responses may result in significant conditions effects.

One aspect of episodic memory that we have downplayed in the current study is the difference between accepting the correct memory trace and rejecting the foils. In the current study, foils were created by rearranging the elements of targets. Therefore, it must have been more difficult to reject foils than to accept targets and both behavioral latency and prefrontal activity in Experiment 2 supported this. For simplicity, we have treated the target and foils the same way but more elaborate models (e.g., Anderson and Reder, 1999) would predict this difference. Another aspect of memory in general that is missing in the current model is how people initially form associations. Instead, our model is mainly concerned with how people retrieve already stored information. Forming new associations has been primarily associated with the hippocampus rather than the three cortical regions that we focused on in this paper. For example, the hippocampus activation during acquisition of new associations was positively correlated with success in subsequent memory tests (Davachi et al., 2001). Also, amnesic patients with hippocampal damages could not explicitly recognize learning episodes while their brain damages were not particularly associated with the regions of the current interest (Knowlton et al., 1996).

The current study examined the roles of the prefrontal and parietal cortices during episodic retrieval. We began by constructing ACT-R models that simulate behavioral results. These models were decomposed into different buffer activities as suggested by ACT-R, and then these components were used to predict BOLD functions of prefrontal, parietal, and motor cortices. As the confirmatory analyses showed, the proposed buffer-cortex mappings were supported in general: The prefrontal cortex is directly related to retrieval load and the parietal activation is sensitive to the number of changes in a problem representation. Admittedly, this paper is based on a tentative mapping from ACT-R buffers to cortical region, which may have to be revised with further evidence. However, the most important contribution of this paper is the conception that the detailed processing of an information-processing theory like ACT-R can make predictions about the fMRI response. In fact, it is our belief that this same conception can be incorporated into other information-processing theories.

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