

Research report

Functional comparison of primacy, middle and recency retrieval in human auditory short-term memory: an event-related fMRI study

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Abstract

Primacy and recency effects refer to the better performance or shorter response time on the first and last items than the middle ones of a memory list. In order to investigate its neural basis in auditory short-term memory, event-related fMRI was used to measure brain activities when subject was recalling the first, the last, or the middle items. Recalling the middle item was associated with more extensive activation in the left parietal and visual cortex, basal ganglia, and dorsal cerebellum. Recalling items from different serial positions also resulted in different activation time courses in the bilateral primary auditory cortex, left prefrontal cortex and left premotor cortex. These data indicate that the auditory cortex may serve as a transient storage or the auditory input buffer, which seems to play an important role in the primacy and recency effects.

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1. Introduction

Shortly after learning a list of items, subjects' recall or recognition performance usually depends on the serial position of the item in a predictable way: items in the first and the last positions are often better remembered than the ones in the middle of the list as indicated by either higher accuracies or shorter reaction times. The superior memory for the first item has been termed the primacy effect, and for the last item, the recency effect.

The short-term memory of items in a list is one of the most extensively studied topics in cognitive psychology.

Although many models were introduced on the basis of a large body of experimental evidence [4,10,13,20,27], all of them treated the brain as a black box, with the components in the models assumed without considering the actual neural structures in the brain. Despite the theoretical importance of these models, and given the large number of functional imaging studies on human memory, it is rather surprising to see the lack of neuroimaging studies conducted to determine their neural basis.

In the work reported here, we used event-related fMRI to measure hemodynamic responses in the brain when subjects were recalling the first (Primacy, P), the last (Recency, R), or the middle (M) digit presented to them in a sequence. Compared to traditional block designs, event-related (or single trial) design allowed us to (1) randomize the presentation of behaviorally distinct trial types in a single run, (2) examine the functional correlates of individual behavioral trials, and (3) study temporally sepa-

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rated behavioral subcomponents within trials [3,19,30]. Combining behavioral measures with single trial fMRI, the aims of the present study are: (i) mapping the activated brain regions for the primacy, middle and recency conditions and identifying the differences between them, and (ii) by quantitatively comparing the detailed properties of the activation time courses in different areas among different conditions (covered area, amplitude, time to peak, and width), to make inferences about the neural mechanisms of the behavioral models.

2. Methods

2.1. Subjects

Eleven (five females, six males, age range 20–25) healthy right-handed students at the University of Science & Technology of China (USTC) participated in, first the behavioral, and then the fMRI study. They volunteered to take part in this experiment with informed consent and received monetary compensation for their time.

2.2. Behavioral experiment

Each subject finished 80 trials in four sessions, with 20 trials in each. There was 5 min rest time between sessions. In each trial, an eight-digit string was presented aurally at a speed of two digits/s. One second after the end of the presentation, an aural cue was presented instructing the subject to report the digit at a certain position in the string. They were told to report the digit as accurately and quickly as possible at the beginning of the experiment. The subject's response and the corresponding reaction time (RT) were recorded. To avoid the interaction between the serial cue and digit, the answer of trial probing position 'n' was never 'n'. Of the 80 trials, 32 trials were for positions 3, 4, 5, and 6 (eight trials each), and 48 trials were for positions 1, 2, 7, and 8 (12 trials each). The probing position of each trial was counterbalanced and pseudo-randomized across trials and sessions.

2.3. fMRI experiment

Averaged single trial design was used in this study. There were a total of 72 trials for each subject. The

presentation of digits and instruction cue was identical to the behavioral experiment: an eight-digit string followed by a 1-s gap, and then an instruction cue. After that, subjects had 18 s to report the digit by finger gestures with their dominant hand and rest. Before scanning, all subjects were trained to give adroit gesture report and they were only allowed to move their fingers during scan. For each subject, the time needed to give a motor response was no more than 3 s, so there was at least 15 s left for hemodynamic recovery (Fig. 1). The gesture reports were inspected and recorded by one of the authors. The 72 trials were distributed into eight scans with nine trials/scan. The inter scan interval was 1 min. Among the 72 trials, there were 12 trials probing the first and last positions, respectively, and eight trials for each of the six middle positions. The order of the probing positions was pseudo-randomized across trials and scans.

2.4. Imaging data acquisition

Imaging data were collected on a GE 1.5T MR scanner. Headphones equipped to the scanner were used to reduce noise and to present auditory stimuli. A total of 144 T_2^* -weighted EPI images per slice (TR=1500 ms, TE=55 ms, 10 sagittal 12-mm slices, gap=2 mm, FOV=24 cm) were obtained in each of eight scans at an in-plane resolution of 64×64 pixels. During these scans, the subject was performing the tasks described above. Corresponding high resolution (256×256 pixels) sagittal T1-weighted S.E. (for anatomical overlay) and SPGR (for stereotaxic transformation) images were also collected.

2.5. fMRI data analysis

The software package AFNI (Analysis of Functional NeuroImages: Robert W. Cox, Medical college of Wisconsin) was used for data processing. Images were first realigned, corrected for motion and normalized to stereotaxic Talairach coordinates systems. Based on the result of our behavior data, trials probing the first position (primacy condition), the last position (recency condition), and positions 3 and 6 (middle condition) were separately averaged (positions 3 and 6 had the longest RTs and were averaged together as middle condition). In each condition, a statistical parametric map was generated by correlating the fMRI signal with a template designed by considering both the

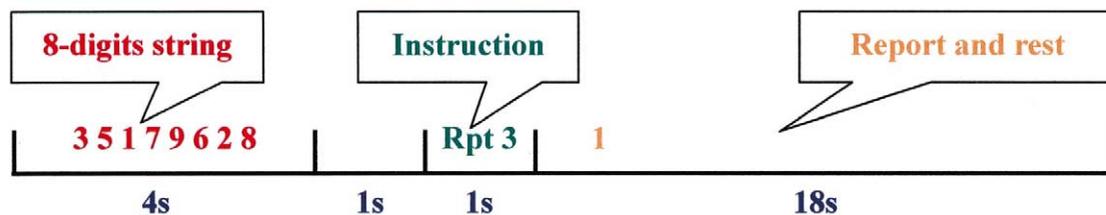


Fig. 1. Schematic diagram of one trial in the fMRI experiment. Stimuli were presented aurally, and subjects reported the cued item with finger gestures.

stimulus function and the hemodynamic response. Those voxels activated (correlation $P < 0.05$ and within a cluster of at least three conjoined voxels) in all three conditions, and in at least eight out of the 11 subjects, were designated as the ROIs for further analysis. The time course of each ROI was fitted with a ‘Gamma’ function and then quantitatively compared across the three conditions.

3. Results

3.1. Behavioral experiment

Since eight digits was within the digit span of all the subjects, their recall accuracies were all nearly perfect (Mean 94.8%, S.D. 3.4%). But the primacy and recency effects can be seen clearly when subject’s reaction time is plotted as a function of the serial position (Fig. 2). The RT of both position 8 and position 1 are shorter than any other positions. (MANOVA analysis (DF=7) P value: 1 vs. 2=0.007; 1 vs. 3<0.001; 1 vs. 4=0.002; 1 vs. 5=0.142; 1 vs. 6=0.001; 1 vs. 7=0.003; 1 vs. 8=0.189; 2 vs. 8=0.022; 3 vs. 8<0.001; 4 vs. 8<0.001; 5 vs. 8=0.040; 6 vs. 8<0.001; 7 vs. 8<0.001.) The longest RT appeared at positions 3 and 6, with little difference between them (3 vs. 6 $P=0.688$). This was the basis of our subsequent fMRI data processing: averaging the trials probing the first and last position, respectively, as primacy and recency condition; averaging the trials probing the positions 3 and 6 together as middle condition.

3.2. fMRI experiment

Consistent with most other fMRI studies of short-term memory using auditory stimuli, the activated areas com-

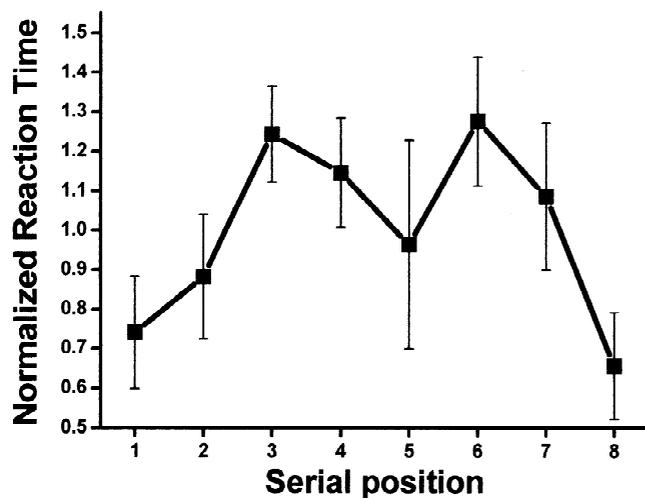


Fig. 2. Average RT of all subjects plotted as a function of serial position. The error bars are ± 1 standard deviations. RT values were normalized by treating the mean RT as 1 within subjects.

prised bilateral superior temporal gyrus (BA 42), inferior frontal gyrus (BA 45/47), left middle frontal gyrus (BA 9), left supplementary motor area (BA 6), left supramarginal and precuneus cortex (BA 40/7). Besides these commonly activated areas during auditory working memory tasks, basal ganglia, dorsal cerebellum and visual cortex were also activated in the present study. Looking at the activation maps (Fig. 3) across the three conditions, it is evident that there were more brain areas activated in middle condition than the primacy and recency conditions. Furthermore, in basal ganglia, dorsal cerebellum, left parietal cortex and visual cortex, the activated volume (measured as number of voxels of unit size: $3.75 \times 3.75 \times 12 \text{ mm}^3$) in middle condition was larger than both primacy and recency conditions. However, there was no significant difference between the primacy and recency conditions in activated volumes. Quantitative results across subjects are listed in Table 1.

The result that the volumes activated in these four regions was significantly larger (except P versus M in basal ganglia, which was nearly significant) in the M than the P and R conditions are informative. The volume data indicated the extensiveness of the involvement of particular brain regions in different tasks, the activation time courses across the three conditions can give us additional information on the dynamics of their involvement. Both the spatial and temporal information will help us to gain more insights on the neural mechanisms in serial item retrieval.

When comparing the activation time course curves across the three experimental conditions, in bilateral BA42 area, the BOLD responses in both primacy and recency conditions were significantly (except P versus M in right BA42, which was nearly significant) higher than that in the middle condition. In left BA6 and BA9, response for primacy and recency conditions peaked before the middle condition and the time from onset to peak was longer in middle condition. Table 2 and Fig. 4 show the result of time course comparison quantitatively and graphically.

The activation time course curves in left BA40/7, left IFG, visual cortex, basal ganglia and dorsal cerebellum were not significantly different across the three experimental conditions.

4. Discussion

In this study, guided by the behavioral data, event-related fMRI was used to investigate the neural basis of the position effect in list retrieval in human auditory short-term memory. In behavioral experiments, the middle items had longer reaction time, correspondingly, their retrieval activated more voxels in four brain regions. In addition, there were different patterns of activation in regions that were not apparently different in the volume of activated voxels.

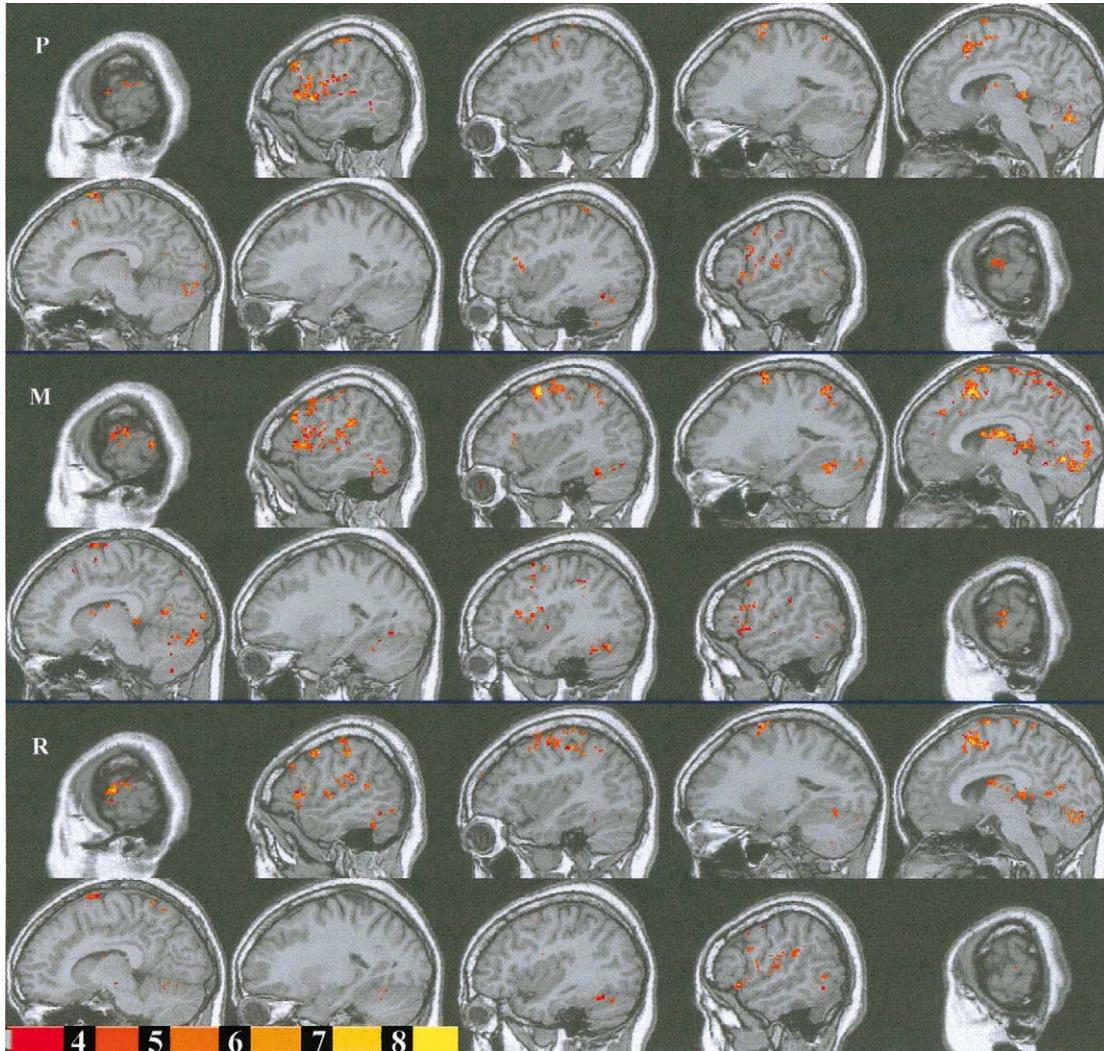


Fig. 3. Average of activation voxels of 11 subjects overlaid on one subject's structure image. The 'P', 'M' and 'R' represent the three retrieval conditions (Primacy, Middle and Recency). The upper five images in each condition are slices of left hemisphere and the lower five images, right hemisphere. The colors in the scale bar indicate how many subjects out of 11 activated in the region. Voxels active in at least eight subjects and were part of a minimum 3-voxel cluster were included in ROIs for further detailed analysis and comparison across conditions.

4.1. Bilateral auditory cortex

According to Alan Baddeley's working memory model,

in phonological loop, there is a phonological buffer that temporarily stores phonological information. Memory traces in it will decay rapidly and become unretrievable in

Table 1
MANOVA analysis of serial position effect on number of activated voxels (n=11)

Brain area (Centroid)	Serial position effect		P vs. M			P vs. R			M vs. R		
	F	P	Voxel no.	F	P	Voxel num	F	P	Voxel num	F	P
BG (3.2 11.6 15.3)	2.59	0.100	7.5:10.5	2.95	0.117	7.5:6.5	0.17	0.692	10.5:6.5	9.09	0.013
CB (12.6 54.0 -14.3)	8.19	0.003	6.2:11.6	10.96	0.008	6.2:6.8	0.65	0.439	11.6:6.8	7.30	0.022
Sup and Pre (34.0 48.2 47.1)	10.76	0.001	15.5:24.2	19.23	0.001	15.5:14.9	0.09	0.776	24.2:14.9	13.55	0.004
Vis (2.2 78.9 9.7)	3.16	0.064	23.5:32.0	4.91	0.051	23.5:22.2	0.07	0.792	32.0:22.2	4.64	0.057

P, primacy; M, middle; R, recency; BG, basal ganglia; CB, cerebellum; Sup&Pre, supramarginal and precuneus cortex; Vis, visual cortex.

Table 2
MANOVA analysis of serial position effect on parameters of activation curves

Brain area (Centroid)	Parameter	P	M	R	Serial position effect		P vs. M		P vs. R		M vs. R	
					F	P	F	P	F	P	F	P
Left BA42 (49.3 16.0 9.9)	Amplitude	0.031	0.028	0.033	3.98	0.039	8.35	0.020	0.73	0.418	5.91	0.041
Right BA42 (-51.0 24.7 12.2)	Amplitude	0.035	0.030	0.036	4.28	0.035	4.36	0.075	0.19	0.678	15.83	0.005
Left BA9 (45.3 -29.7 30.8)	PT	4.6	5.6	5.0	5.08	0.020	6.44	0.035	1.85	0.211	5.89	0.041
	PT-OT	2.7	3.4	3.0	3.92	0.041	4.61	0.064	2.09	0.186	3.74	0.089
Left BA6 (22.4 -0.4 61.8)	PT	5.2	5.6	5.4	6.66	0.007	12.93	0.006	2.70	0.135	4.52	0.062
	PT-OT	3.2	3.5	3.3	8.28	0.003	10.35	0.011	5.83	0.039	6.08	0.036

For left BA42 and left BA9, n=9; for right BA42, n=8; for left BA6, n=10.

PT, peak time; OT, onset time; values for amplitude is signal change relative to base line, unit for PT and PT-OT is TR (1 TR=1.5 s).

about 2 s. When external speech enters this buffer, in order to keep it for longer time, subvocal rehearsal can be used to refresh it [2]. Many previous studies have also suggested that there was an acoustic input buffer for auditory stimuli. Acoustic inputs arrived via the auditory input buffer and were maintained there until the arrival of next item. The primary auditory cortex, the bilateral superior temporal gyri (BA42) have been associated with this transitory storage function [4,12,25,26,28]. Auditory sensory memories are predominantly stored in auditory cortex contralateral to the ear of presentation [1] and decays exponentially with time [17]. In the present study, BOLD response in the recency and primacy conditions was significantly higher than the middle condition in the

bilateral BA42, presumed auditory input buffer. If we take the simplistic view (as most people do) that more activation of an area in a task means more involvement of that area in the task, then this result suggests that the faster recall of the first and the last item may be partly supported by retrieval from this buffer. Possibly the last item did not vanish yet from the auditory input buffer when the cue was presented, so we can retrieve it directly from this buffer and hence the fast recall process. But for the middle items, which were presented earlier, the rapid decay of their memory traces made the retrieval more difficult and the reaction time longer. This explanation is also corroborated by a previous ERP study of serial position effect in which larger ERPs and faster RTs were recorded for probe items

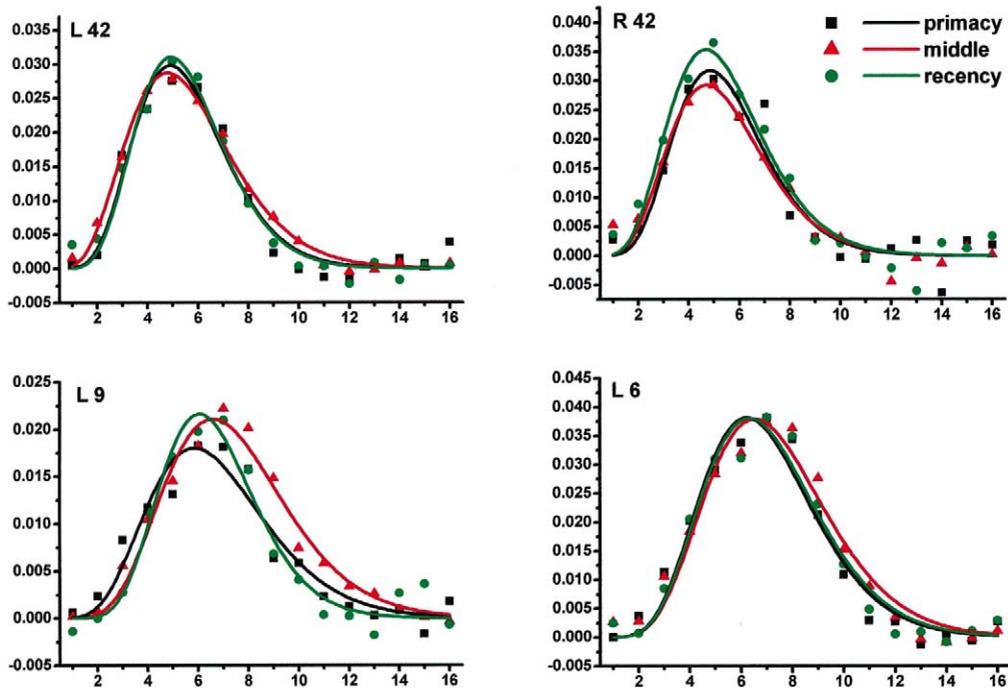


Fig. 4. Response time courses for the three experimental conditions. Horizontal axis is in units of TR (1 TR=1500 ms) and vertical axis represents signal change relative to base line. In bilateral BA42, P and R have higher response amplitude. In left BA6 and BA9, M curve peaked later and the time from onset to peak was longer.

presented in the recency portion of the list suggesting that stronger memory traces were associated with the more recently presented items [21]. Admittedly, the interpretation for involvement of BA42 in the retrieval of the first item is less straightforward. BA42 may contribute to the retrieval of primacy item in two ways. On the one hand it may help transferring primacy item to more long-term memory store. On the other hand, presumably memory trace in auditory input buffer can be refreshed at each time of rehearsal, so primacy item can still keep a relatively high fidelity in acoustic input buffer by receiving more rehearsal than other items in the list [27]. Primacy effect was traditionally explained in line of rehearsal-LTM. This was based on extensive behavioral experiments [11]. Our fMRI result here added feasibility to the idea that rehearsal-acoustic buffer could be involved in primacy item retrieval. The evidence that inner voice can activate auditory cortex [5] and this brain area was recruited by vivid memory retrieval [29] also lend support to this view.

4.2. *Left parietal cortex*

The better retrieval of primacy and recency items may be partly explained by the higher contributions from the sensory auditory input buffer. What about the middle items? The present study suggests that the left parietal cortex may be important for retrieval of the middle items. Left parietal cortex has been implicated for phonological storage or active maintenance of verbal information [14,23,25]. Honey and colleagues have previously demonstrated that prolonged reaction time in a verbal working memory task was significantly associated with increased power of functional response in bilateral posterior parietal cortex [14]. Consistent with their result, in the present study a significantly larger volume in left BA40/7 was activated in retrieving the middle items. Comparing to retrieval of the first and last items, which may benefit more from acoustic input buffer, retrieving the middle items depends more strongly on the left parietal cortex.

4.3. *Left PFC*

Although the first/last and middle items may be retrieved from different memory storage, they share an important common process of executive control. The executive control of memory scanning most likely requires the participation of the dorsal lateral prefrontal cortex (DLPFC). D'Esposito and colleagues have found that DLPFC represented an important substrate of memory scanning, a retrieval process initiated with the onset of probe stimulus [8]. Retrieving middle items probably required more scanning resulting in longer retrieval times. Correspondingly, the BOLD response in middle condition peaked later in left BA9 and the time from onset to peak was also longer. In left BA9, it was a bit puzzling to see that the BOLD signal amplitude in the recency condition

was higher than primacy response (nearly significantly, $P=0.08$). But this was not the only case that higher prefrontal activation appeared in relatively easier tasks. For example, in a functional imaging study of working memory, Prabhakaran and colleagues also found that greater prefrontal activation occurred in the easier condition [23]. In an ERP study of list memory, Patterson and colleagues found the highest P300 amplitude associated with probing recency portion of the list, and the amplitude of P300 was associated with the amount of attention allocated to a task [21]. In light of these results, the high amplitude of BOLD response in the recency condition in left BA9 found in the present study may indicate that recently presented items receive more attention or processing capacity.

4.4. *Visual cortex*

We believe that the visual area was involved in memory scanning through visual imagery [6,16]. Since subjects were instructed to close their eyes and the room was dark throughout the experiment, the activation of visual area could not be due to physical visual stimulation. The activated area in visual cortex was larger under middle condition than primacy ($P=0.051$) and recency ($P=0.057$) conditions, and response in the middle condition also lasted a little longer than the responses in the primacy and recency conditions ($P=0.1$). This data were consistent with reports of most of our subjects on their retrieval strategies, both suggest that visual imagery was involved more in the middle items retrieval. Subjects' strategy can be described as mentally moving a 'jumping arrow', making the arrow pointing to one item and then next until the target item was found. Part of the activation in the visual cortex could be related to the need of keeping track of (or counting/subitizing) how many items have been scanned in the memory for the middle items, a function that activates an occipital-parietal network [22].

4.5. *basal ganglia, dorsal cerebellum and left premotor cortex*

It is obvious that retrieving middle items was more difficult than retrieving terminal ones, but where does the difficulty come from? The different storage dependence discussed above may account for parts of it but different amount of temporal interference between these conditions also contribute to their different difficulties. In primacy condition, subjects only need to distinguish the first item from the following one, and in recency condition, the preceding one. However, in middle condition, subjects must distinguish the target item from both the preceding and the following items. Here we discuss the role of basal ganglia, dorsal cerebellum and left BA6 in this type of temporal processing.

Basal ganglia and cerebellum are brain structures important for timing (see Ref. [9] for a review). Recent studies by Rao et al. [24] and Menon et al. [18] have described more detailed functional properties of these two structures. Besides formulating representation of time or acts as a timekeeper tightly coupled with attention system, basal ganglia also plays a role in maintaining representations in working memory in a manner that contributes to planning and temporal organization of motor sequencing. Cerebellum is important in time perception [15]. In agreement with these findings, during the middle item retrieval, which had more involved temporal order processing, larger activated area of basal ganglia and dorsal cerebellum was observed in the current study.

While basal ganglia and cerebellum provided temporal information, according to Sakurai et al. the stored items were then decoded on demand probably through the arcuate fasciculus to the anterior motor and premotor area [25]. The observation that the response of the middle condition peaked later and took longer time from onset to peak compared to the terminal conditions in present study could thus reflect the longer decoding process of middle items. Although it is not exactly clear what happens in this decoding process, Henson has suggested that premotor area's role in it was rehearsal of phonological traces, particularly their temporal order [12]. Premotor region, of course, is also important for the planning and execution of motor response. The slower response in middle item retrieval was also consistent with the delayed peak of middle response in the premotor area.

Different from the typical free recall method to exam the serial position effect, the present study adopted cued recall, a design more suitable for event-related fMRI research. One of the main differences between the free and cued recall is that the temporal relationship of serial positions is often not specifically retrieved in the former (unless explicitly instructed) but is needed in the latter. In order to retrieve a cued middle digit, subjects may need to review all the digits before it. In addition, counting was probably involved too. The left BA9, visual cortex, basal ganglia and dorsal cerebellum are all probably related to this serial search mechanism, of executive control, visual imagination, and temporal tracking. In this case functional MRI with cued recall provided us with information that would not be available to traditional behavioral experiments using free recall.

It should be noted here that although we tried to distinguish the activation associated with memory storage and that with dynamic searching, this distinction is tentative and is made based on both the current result and the existing knowledge in the literature. For example, the left parietal cortex could serve as a STM store, its larger activation in the M condition could be the result of reviewing preceding items before reporting a middle item, or it could be due to more direct involvement in the memory scanning process.

5. Conclusion

With event-related fMRI, we studied auditory serial short-term memory in healthy human subjects. In addition to the bilateral auditory cortex, left parietal cortex, and left frontal cortex, which are consistently activated in human auditory short-term memory tasks, activation was also seen in basal ganglia, dorsal cerebellum, and visual cortex in the present study. Retrieving items from different serial positions activated these areas to different extent, and with different activation time courses consistent with the prediction based on the serial position effect observed in the behavioral experiment. These data suggest that the retrieval of primacy and recency items is facilitated by their strong traces in the primary auditory input buffer, but retrieval of middle items depends more on STM storage. The slower retrieval of the middle items may be a result of more complex processes of memory scanning, decoding, and attention shifting. Results reported here give additional support to the conjecture that auditory cortex may play a role in retention of information in short-term memory, a view based mainly on animal lesion [7] and human ERP study [1] in the past.

Acknowledgements

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