

Reflection of working memory: ERP mnemonic effects

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Abstract

The study of working memory often utilizes a delayed matching to sample paradigm (DMS). Typically in the matching condition, the test and sample stimuli are identical, raising the possible confound of retinotopic projections for the matching stimuli in contrast to the non-matching stimuli. In the present study, 65 healthy subjects performed a modified delayed matching to sample task while monitoring their ERP waveforms. The stimuli consisted of 60 different sample stimuli (S1) and 60 different test stimuli (S2). Half of the S2s were complementary to the sample stimuli (Fit), the other half of the S2s were not complementary (Nonfit). After S2, the subjects pressed one of the buttons to indicate whether the test stimulus fits the sample stimulus. Our statistical results indicated that the ERPs to sample stimuli differed from the ERPs to test stimuli from 200 ms poststimulus to the end of the recording epoch. The ERPs to fitting stimuli were significantly different from those to non-fitting stimuli from 200 to 400 ms poststimulus. The ERP patterns in the present study may reflect ERP mnemonic effect for working memory. Our results ruled out the retinotopic confound as a potential mediator variable, and are in agreement with other animal or human neurophysiological studies on memory. © 1997 Elsevier Science Ireland Ltd.

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1. Introduction

The term working memory typically refers to a system for temporary maintenance and manipulation of information in the brain, a function critical for a wide range of cognitive operations (Goldman-Rakic, 1994). It has been proposed that working memory consists of two parts, a set of buffers that temporarily store information in either a phonological (phonological loop) or visuospatial (visuospatial sketchpad) form, and a central executive system (CES) that determines which information is made available for conscious processing (Baddeley, 1992, 1986). However, a complete specification of these various systems has been difficult to obtain from behavioral data because these data reflect the combination of three aspects of working memory: storage, maintenance, and retrieval operations. A popular approach for disentangling these three operations is the use of the delayed

matching to sample task (DMS), with electrophysiological recording to specify their respective spatiotemporal patterns. The DMS paradigm contains the basic processes of working memory such as information encoding, maintaining, retrieving, and comparing; the electrophysiological recording techniques, among which the event related potential (ERP) technique is most applicable for studies in human cognition, provide a method for making references about the timing and general scalp localization of working memory processes.

The inferior temporal (IT) cortex has long been thought to be essential for object vision and visual memory (for review see Tanaka, 1996). It is not only assumed to code visual images of objects, but also to remember the coded images for a short time (working memory). It has been found that IT cells maintain firing during the delay period while a monkey performs a DMS task (Fuster and Jervey, 1981, 1982; Miyashita, 1988; Miyashita and Chang, 1988). These discharges are assumed to be a neural correlate of working memory inasmuch as the discharges of some of the cells are selective for the sample stimulus, and the monkey has to remember the sample stimulus during the delay period. Another pos-

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sible neural correlate of working memory is that responses of some IT neurons are suppressed to matching stimuli, compared with the neuronal responses to non-matching stimuli (Mishkin, 1982; Baylis and Rolls, 1987; Fuster, 1989; Miller et al., 1991; Riches et al., 1991; Goldman-Rakic, 1994; Miller and Desimone, 1994). It is thus suggested that the decrease in the neural response is the representation of the stimulus presented as a sample.

The tight relationship between the prefrontal cortices and working memory has been supported by recent human and animal studies (for review, see Funahashi and Kubota, 1994). The frontal lobes coordinate and fuse incoming and outgoing products of several sensory and motor areas of the cortex. Prefrontal lesions result in a loss of 'immediate' memory (Goldman-Rakic, 1987). There are neurons in the prefrontal region with the same firing pattern to image stimuli as the neurons in IT cortex (Chelazzi et al., 1993; Goldman-Rakic, 1994); it has been demonstrated that principal sulcal neurons increase their rate of firing during the delay only when information must be remembered over the delay period (Goldman-Rakic, 1987). The ventral portion of the prefrontal region is anatomically connected with IT cortex (Fuster, 1989). Therefore, electrophysiological phenomena observed in monkey studies, can at least partly describe the processes of working memory.

However, the DMS paradigm may be questionable for the possible confound of retinotopic projections for the matching stimuli in contrast to the non-matching stimuli, though the studies in monkeys have indicated inferior temporal mechanisms for invariant object recognition (Ito et al., 1995; Lueschow et al., 1994). It has been shown that the interaction of the current stimulus with the memory trace is invariant over size and retinal translation, but the retinal location and size of an image are treated like other object features by IT neurons (Lueschow et al., 1994). As a matter of fact, the adjustment of an object's size and position on the retina for subsequent recognition may occur even at primary visual cortex. Recent studies of cortical representational remodeling following restricted retinal lesions (Chino et al., 1992; Gilbert and Wiesel, 1992) documented a probable capacity for at least limited learning-inducible plasticity in area 17. Since IT mechanisms for invariant object recognition exist, the identical contents between sample and test stimuli may produce an identical neural representation. Thus, mnemonic effects might be due to a literal, or 'pixel-by-pixel,' comparison of the current stimulus to previously seen stimuli. The only way to eliminate this possible confound is to make all matching stimuli also differ from sample stimuli; consequently, the judgment on matches or mismatches between test and sample stimuli can only be gained after further deductive reasoning. Moreover, the encoded information can either be held in working memory to prevent forgetting during the process of maintenance (maintenance rehearsal) or be further processed and lead to an increase in the depth at which an item is encoded (elaborative rehearsal) (Baddeley, 1990). One of the most

powerful features of human complex cognitive activities is the ability to reason or recognize objects that have been transformed in some way from the time of their first appearances. Therefore, a DMS paradigm with such a task requirement can strongly activate both the visuospatial sketchpad and the central executive of working memory, providing a best way to describe the mechanism of working memory. Apparently, a DMS task with such a demanding requirement is too difficult to be performed by monkeys, but can be easily carried out by humans (Aggleton et al., 1988; Bardenhagen and Bowden, 1995).

Incorporating the DMS paradigm with ERP technique, We (Begleiter et al., 1993, 1995; Hertz et al., 1994; Zhang et al., 1995) have identified a visual memory potential (VMP) which indexes visual short-term memory. The ERP component to matching stimuli is around 240 ms post-stimulus, and is much smaller than that to non-matching stimuli. This ERP component, which is generally located in the occipitotemporal regions, is in keeping with the temporal and spatial characteristics of the electrical activities recorded in single cell studies in monkeys (Baylis and Rolls, 1987; Chelazzi et al., 1993; Eskandar et al., 1992; Fahy et al., 1993; Miller and Desimone, 1994; Miller et al., 1991, 1993). In order to more closely describe the processes of working memory with ERP technique, we further modified our DMS paradigm to minimize the possible retinotopic confound for the matching stimuli compared to the non-matching stimuli. Moreover, we assume that the paradigm used in the current study can not only tap the visuospatial sketchpad, but also simultaneously tap what is probably the most crucial component of working memory, the central executive. Thus, we explored the reflections of visual working memory on ERPs in this experiment. We also used 61 electrodes and scalp current density to assess topographically the ERP mnemonic effects of working memory.

2. Methods and materials

2.1. Subjects

The study included 65 subjects ranging from 19 to 36 in age. These subjects were recruited from the students and staff of the SUNY Health Science Center via ads posted on the campus. The screening procedure for the subjects required that each potential subject fill out a questionnaire regarding alcohol and drug use, as well as medical and psychiatric histories of himself/herself as well as family members. All the subjects were right-handed and reported no history of treatments for alcohol, drug abuse, neurological, and psychiatric disease. All subjects had normal vision or corrected normal vision and were paid for the participation in the study. Of the 65 subjects, there were 40 males (mean age 23.38 ± 3.38) and 25 females (mean age 22.72 ± 3.59). There was no statistical difference in age between the male and female subjects ($F = 1.00$,

$P = 0.319$). Informed consent was obtained from each subject.

2.2. Stimuli and stimulus presentation

The stimuli consisted of 60 different sample stimuli (S1) and 60 different test stimuli (S2). Each individual stimulus was different from the other and hard to verbalize. A matching set of stimuli (S1 and S2) consisted of two complementary geometric figures which did fit together to form a final uniform shape or form. Half of the test stimuli were complementary to the sample stimuli (FIT), the other half of S2 were not complementary (NONFIT). Fig. 1 illustrates two pairs of stimuli in the Fit and Nonfit trials, respectively. All trials were presented consecutively and randomly on a computer display. Each image was shown inside a 10×10 cm dim frame, thus subtending a visual angle of $5-6^\circ$. The dim frame was sustained in the center of the CRT for an entire trial while the duration of presentation for each geometric figure was 300 ms. The inter-stimulus interval (S1–S2) was fixed to 1324 ms, and the inter-trial interval (S1 + S2) was 2134 ms.

2.3. Subjects' task

The subjects' task was to judge whether the two stimuli within a trial were complementary to each other. The subjects were instructed to press a mouse key in one hand after a trial when they saw the second stimulus (test) and the first (sample) fitted together to form a regular form (a square or a circle, e.g.), or to press a mouse key in the other hand if the pair of stimuli was not complementary. The designation of

the hand indicating 'Fit' or 'Nonfit' was alternated across subjects. Response accuracy and speed were equally stressed.

2.4. Electrophysiological recording

The subject was seated in a reclining chair located in a sound-attenuated RF shielded room and fixated a point in the center of CRT located 1 m away from his or her eyes. Each subject was fitted with a 61-lead electrode cap (ECI, Electrocap International). We used the entire 10/20 international montage along with an additional 42 sites as follows: Fpz, Afz, Af1, Af2, Af7, Af8, F1, F2, F5, F6, Fcz, Fc1, Fc2, Fc3, Fc4, Fc5, Fc6, FT7, FT8, C1, C2, C5, C6, Cpz, Cp1, Cp2, Cp3, Cp4, Cp5, Cp6, Tp7, Tp8, P1, P2, P5, P6, Poz, Po1, Po2, Po7, Po8 and Oz (Standard Electrode Position Nomenclature, American Electroencephalographic Association, 1990). All scalp electrodes were referred to Cz. Subjects were grounded with a nose electrode and the electrode impedance was always below 5 k Ω . Two additional bipolar derivations were used to record the vertical and horizontal EOG. The signals were amplified with a gain of 10 000 by an EPA-2 amplifier (Sensorium) with a band-pass between 0.02 and 50 Hz, and recorded on a Concurrent 55/50 computer. The amplified signals were sampled at a rate of 256 Hz during an epoch of 190 ms of prestimulus baseline and 800 ms following each stimulus presentation. Trials with excessive eye movements ($>73.3 \mu\text{V}$) were rejected on-line.

2.5. Data analysis

ERPs were derived by averaging the artifact-free EEG epochs with correct responses, yielding three categories of ERPs according to different stimulus conditions: ERPs to S1 (Sample), ERPs to S2-fit (Test Fit), and ERPs to S2-non-fit (Test Nonfit). As illustrated in Fig. 2, these ERP waveforms consisted of 3 components (c) which were most clearly discernible at the more posterior electrodes: c1 ranging between 100 and 140 ms, c2 ranging between 140 and 210 ms, and c3 ranging between 210 and 350 ms. In addition, a slow late ERP component (LC) occurred after c3 and lasted to the end of the recording epoch. However, measurements of these peaks' and troughs' amplitudes and latencies across all 61 electrode sites proved to be problematic because there is no convincing way to identify a component recorded from two distant electrodes, and having different latencies, as the same component. Meanwhile, it was also difficult to determine the latency of the LC. We used varimax rotated principal components to describe our ERP data set because they distribute the variance accounted for by successive factors sequentially across the ERP latency epoch. The voltage baseline of each ERP was defined as the mean of the 50 points before stimulus was presented, and was subtracted out. Principal component analysis (PCA) was done using the covariance matrix by SAS factor

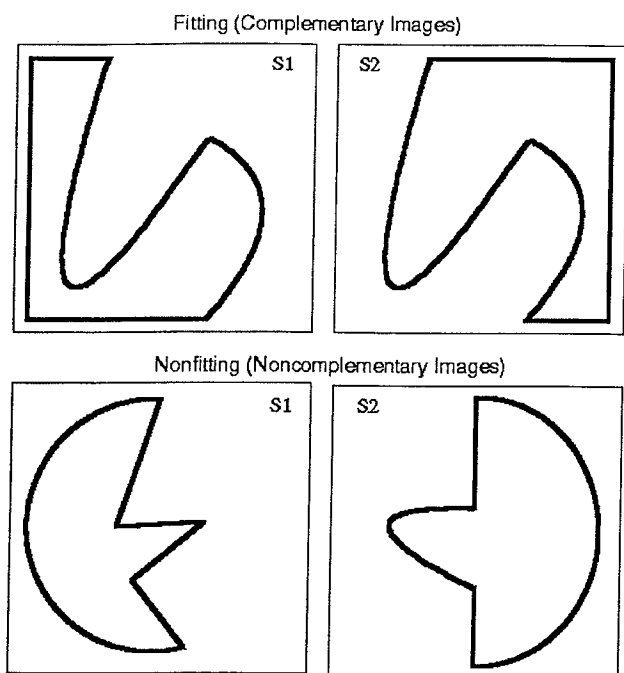


Fig. 1. This illustrates the complementary and non-complementary stimuli used in the study.

procedure (SAS v6.11). The observations were the concatenated 200 point ERPs from each electrode, and the number of observations was 11 700 (65 subjects \times 60 electrodes \times 3 stimulus conditions). By the eigenvalue-one criterion, we derived 4 principal components (PC) which accounted for 87.12% of variance for the entire data set. Fig. 3 illustrates the factor loadings of the 4 PCs. The loading patterns of the 4 factors fit the description of ERP waveforms shown in Fig. 2. Factor 1 is a rather broad component peaking at 640 ms poststimulus and mainly representing the ERPLC; Factor 2, mainly ranging from 200 to 450 ms and peaking at 280 ms, covers c3 which shows maximal difference in amplitude between the FIT and NONFIT stimulus conditions as suggested by the ERP waveform in Fig. 2. Factor 3, peaking around 110 ms, seems to be the best representative of c1, and Factor 4, peaking around 170 ms, represents c2. Table 1 explicitly illustrates the relationship between the factors of PC and ERP components.

The PC scores of each electrode were organized into groups by region. The frontal region consisted of Fp1, Fp2, Fpz, Af7, Af8, Af1, Af2, Afz, F7, F8, F5, F6, F3, F4, F1, F2, Fz; the central region consisted of Fc1, Fc2, Fc3, Fc4, Fc5, Fc6, Fcz, C1, C2, C3, C4, C5, C6; the parietal region consisted of Cp1, Cp2, Cp3, Cp4, Pz, P1, P2, P3, P4; the occipital region consisted of Po1, Po2, Poz, O1, O2, Oz. The left temporal region consisted of T7, Tp7, Cp5, P5, P7, Po7; and the right temporal region consisted of T8,

Tp8, Cp6, P6, P8, Po8. A number of MANOVAs were carried out separately for each PC score at each regional electrode array as a dependent vector for comparisons among different stimulus conditions.

Because the scalp potentials may reflect the average activity of multiple neural sources recorded at a distance, they are neither reference-free, nor independent of the volume conductor effects. These limitations mean that ERP components will be altered if the placement of the reference is changed or if it is not a 'quiet' reference (Nunez et al., 1991) and there may be spatial smearing of the potential record as a consequence of volume conductor effects. For further visual descriptive display of our electrophysiological data, we made topographic maps of SCD (Source Current Density). The SCD represents both scalp sources and sinks of current, reflecting mainly cortical activities; a scalp region having a positive current density corresponds to a source region where a local radial current is flowing through the skull into the scalp.

3. Results

3.1. Behavioral data analyses

The subjects performed with a very high percentage of correct response, namely, more than 99% for Nonfit and

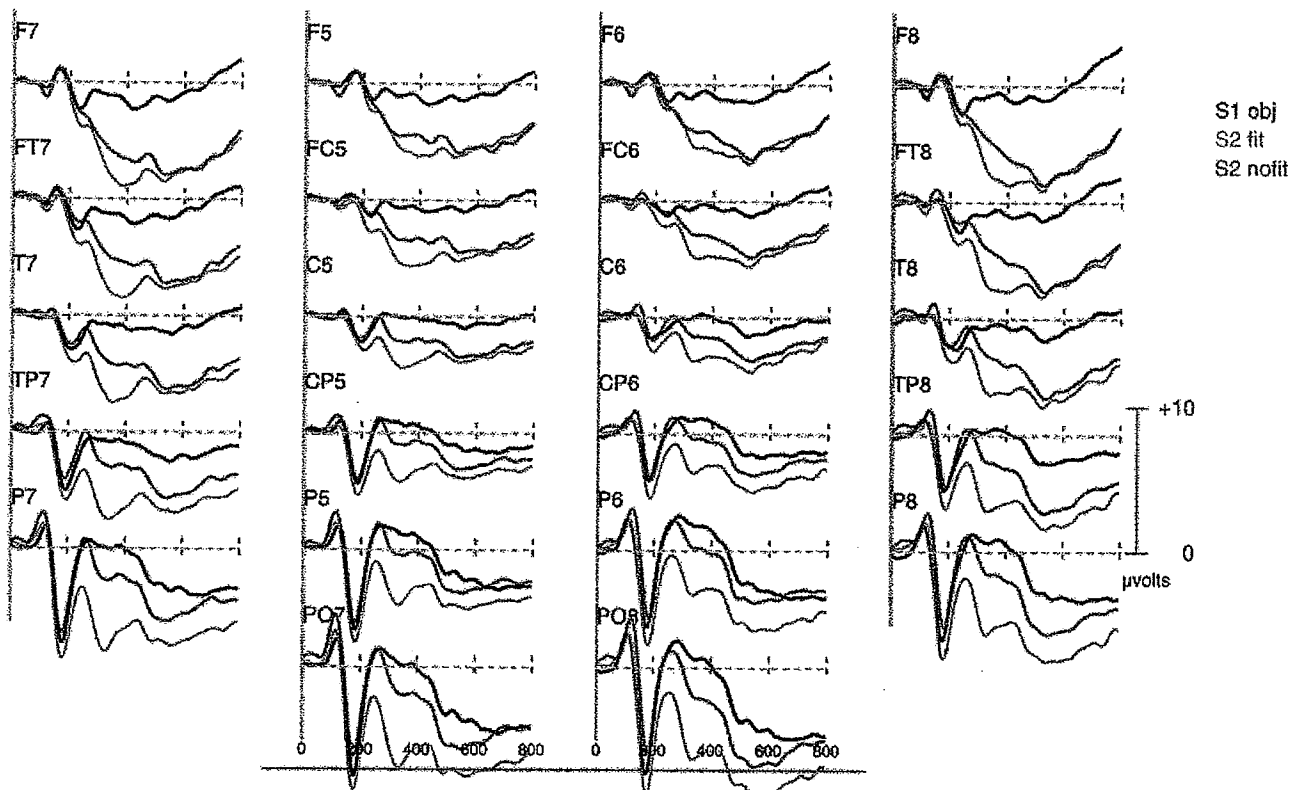


Fig. 2. Grand mean wave forms of ERPs. An upcoming wave form represents relative positivity at the recording electrode compared to the reference at Cz, but there was no determination of absolute polarity.

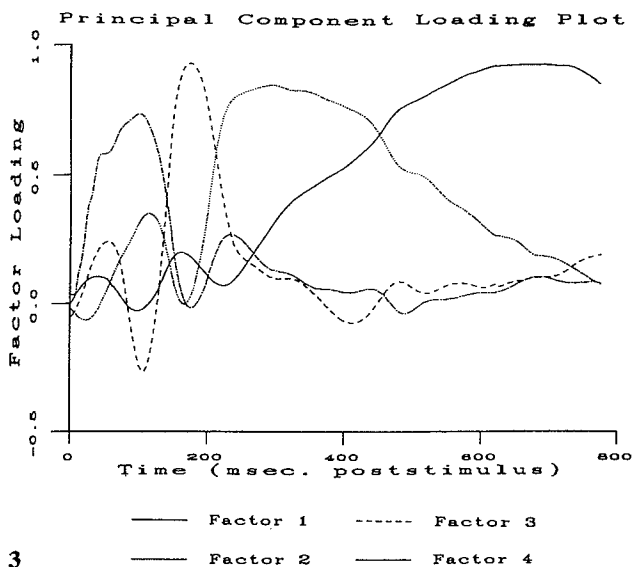


Fig. 3. Principal component results using all ERPs.

98% for Fit stimuli. The response time to Nonfit stimuli (831 ± 179 ms) was shorter than that to Fit stimuli (891 ± 199 ms). however, the difference only approached significance ($T = 1.819$, $P = 0.0711$).

3.2. Erp data analyses

A number of MANOVAs was performed to make comparisons between corresponding scores in different stimulus conditions. MANOVAs on the scores of the first factor revealed significant effects of stimulus condition at several brain regions: left ($F(14,372) = 6.03$, $P < 0.001$) and right ($F(14,372) = 8.52$, $P < 0.001$) frontal region, parietal region ($F(20,366) = 2.75$, $P < 0.001$), and left ($F(14,372) = 9.13$, $P < 0.001$) and right ($F(14,372) = 10.34$, $P < 0.001$) temporal regions. Further analyses indicated that these significant differences on the scores of the first factor were attributable to the difference between sample and test stimulus conditions, i.e. sample vs. FIT and the sample vs. NONFIT stimulus conditions. No significant effects on the scores of the first factor could be demonstrated by MANOVAs within the test stimulus conditions at any brain regions. The stimulus conditions reflected strong effects on the scores of the second factor at the fol-

lowing brain regions: left ($F(14,372) = 4.42$, $P < 0.001$) and right ($F(14,372) = 3.92$, $P < 0.001$) frontal regions, left ($F(14,372) = 5.68$, $P < 0.001$) and right ($F(14,372) = 3.90$, $P < 0.001$) temporal regions, occipital ($F(12,374) = 3.56$, $P < 0.001$) region, and parietal ($F(20,366) = 2.30$, $P < 0.005$) region. In addition to the significant differences between the scores in sample and in test stimulus conditions, the two kinds of test stimuli also significantly affected the second factor scores at the right frontal ($F(7,122) = 3.03$, $P < 0.01$), the right temporal ($F(7,122) = 3.38$, $P < 0.005$), and the left temporal ($F(7,122) = 3.59$, $P < 0.005$) regions. No significant effects of stimulus condition on the scores of the third and fourth factor were demonstrated by MANOVAs.

3.3. Scd topographic maps

As c3 has the mostly distinctive difference in amplitude across the 3 stimulus conditions, we selected it to assess its topographic current source distributions. As Fig. 4 illustrates, there are conspicuous current fields at the occipito-temporal regions in both the FIT and NONFIT stimulus conditions. However, the differences between the two stimulus conditions in SCD maps are readily apparent. Compared with the locations of the SCDs at the occipitotemporal regions in the NONFIT condition, the SCDs elicited by the FIT stimuli are more localized. Stronger current sources over the frontal regions in FIT condition than in NONFIT condition may also suggest the two kinds of stimuli required different neural processes.

4. Discussion

The present results not only describe the operations of working memory, but also imply that several scalp regions, where cortical regions are known to be involved in working memory are strongly activated in our paradigm. Meanwhile, some characteristics of the experimental paradigm were reflected by the behavioral data.

In the experiment, the response times to the Fit stimuli were longer than those to Nonfit stimuli. This response pattern is contrary to most studies on RTs in which the RTs to repeated or matching stimuli are generally shorter than those to unrepeated or non-matching stimuli (Kroll and Potter, 1984; Bentin and Moscovitch, 1988; Schacter et al., 1991; Cave and Squire, 1992; Begleiter et al., 1993, 1995; Hertz et al., 1994; Zhang et al., 1995). However, the reversed RT pattern in the present experiment, in turn, indicates the unique mode of our stimuli. By avoiding the identity of the sample and test stimuli in the matching trials (Fit trials) in the modified DMS paradigm, we confidently removed the physical repetition priming effect to which implicit memory contributes substantially. In this experiment, we increased memory loading on the 'match' and 'non-match' trials more equally than other previous studies

Table 1

Relationship between factors of PC and ERP components.

ERP component	Time range (ms)	Factor of principal component
C1	100–140	Factor 3
C2	140–210	Factor 4
C3	210–350	Factor 2
LC	>350	Factor 1

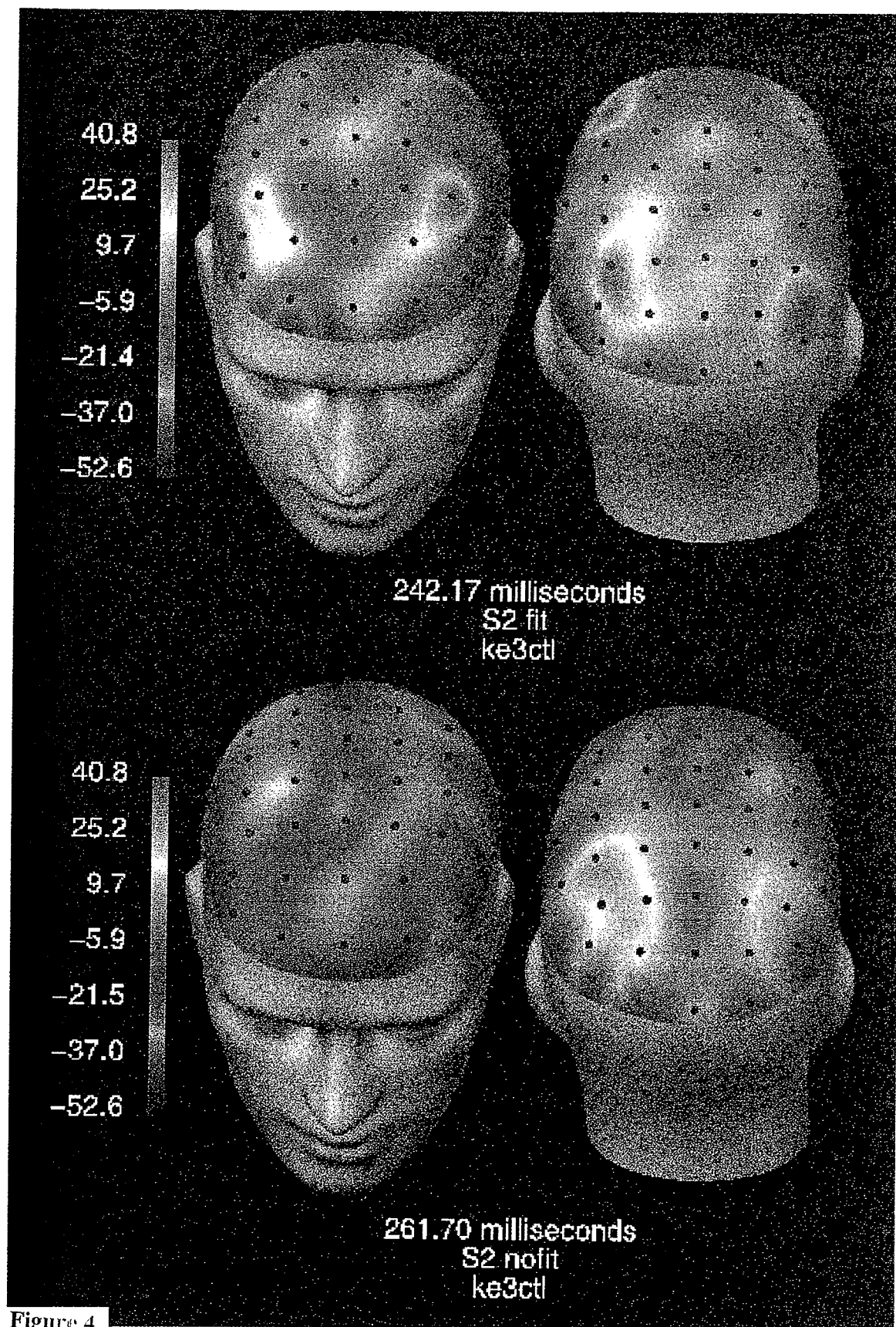


Figure 4

Fig. 4. These are the current density maps obtained to the S2 fit VMP and the S2 non-fit VMP.

to ensure the activation of subjects' working memory. However, the longer RTs in the Fit trials than in the Nonfit trials, though not statistically significant, might suggest that the memory loading is greater in the processing of the Fit stimuli than the Nonfit stimuli. Thus, it takes a comparatively longer time for the subjects to respond in the Fit trials than in the Nonfit trials.

One of the prominent phenomena of the ERP pattern is that, approximately 200 ms poststimulus, the ERPs to sample stimuli significantly differ from those to test stimuli. The unique neural process for the sample trials is information retention-rehearsal. Timing of the phase when ERPs to sample stimuli differs from those to test stimuli may index aspects of the retention-rehearsal activity and reflect the temporary storage mechanism. As suggested by Fig. 2 and confirmed by MANOVAs, this difference is widespread across scalp and most remarkable at the frontal regions. The sustained activation during the delay has been observed in prefrontal neurons during the performance of behavioral tasks which require the subject to actively retain information (Kojima and Goldman-Rakic, 1982; Fuster et al., 1982; Watanabe, 1986). Since working memory is considered to be an active short-term storage mechanism for information, the fact that the activation is sustained throughout the entire delay period suggests that activation during the delay period could be a neural correlate of mechanisms associated with working memory. Moreover, in human ERP studies using variations on the delayed matching to sample paradigm, it has been demonstrated the ERP slow wave amplitudes and topographies have varied as a function of the type of material and information load (Barrett and Rugg, 1990; Lang et al., 1992; Rugg and Doyle, 1994). The sensitivity of the slow negativities responsive to manipulation of memory load and the timing of these load-related negative shifts link them to storage and retention of information in working memory (Ruchkin et al., 1995). We propose that our results, especially those on late components at frontal region, may reflect the activation of central executive system of working memory, because one of the most important functions of frontal lobes is to maintain a proper level of attention and vigilance during various cognitive operation; and the central nerve system (CES) controls attention and information flow to and from verbal and spatial memory buffers (Baddeley, 1992). This proposal is in accordance with the recent neuroimaging studies that have related frontal regions with the central executive system of working memory (D'Esposito et al., 1995). Studies on single cell recordings in awake monkeys performing DMS tasks also indicated that the frontal lobe involvement may possibly be associated with the executive control of visual memory (Quintana et al., 1988; Goldman-Rakic 1988, 1994). Moreover, this ERP result is also consistent with the PET observations that dorsolateral prefrontal cortical areas appear to contribute to the maintenance of both verbal and non-verbal information (Fiez et al., 1996).

However, we have to point out that the neural processes

for the central executive system are unclear; and apparently, frontal lobes are not the only regions involved in the central executive system. The differences between ERPs to sample and to test stimuli in the present study can also be demonstrated in other brain regions. Of interest are temporal and parietal regions in the present study. These results may suggest that the two areas are also involved in the active rehearsal-retention processes in working memory. Both areas are closely related to the visuospatial sketchpad which is involved in setting up and manipulating visuospatial imagery. The existence of an extensive interconnection between temporal cortex and parietal cortex has also been put forward (Harries and Perrett, 1991). This pathway (processed by cells responsive to faces) may possibly provide information as to where in the environment other individuals are directing their attention. It has been suggested that a passive, visuospatial slave system is able to be responsible for temporary maintenance of a visuospatial stimulus (Logie et al., 1990; Parr, 1992). Experiments in monkeys also indicated that the maintained discharges of some cells in inferior temporal regions are selective for the sample stimulus; and these discharges are assumed to be a neural correlate of working memory (Fuster and Jervey, 1981; Miyashita and Chang, 1988; Tanaka, 1992). Thus, the current results of the involvement of these areas in active rehearsal-retention processes in working memory may be an extension of the central executive system or a manifestation of active mechanism of visuospatial sketchpad or, most possibly, the reflection of both systems.

Our data also show that the sample stimuli significantly influence the ERP patterns to the test stimulus, depending on whether or not it is complementary to an immediately preceding sample stimulus. Within a time window approximately between 200 and 400 ms poststimulus, the amplitudes of the ERPs to fitting stimuli are significantly decreased compared to those to nonfit stimulus. This phenomenon could be typically demonstrated at the right temporal, left temporal, and right frontal regions. The response reduction in amplitude of ERP suggests that memory of a sample image influence the neurophysiological response to subsequent test stimuli. It may well be the similarity between the inner representation from the present stimulus and the memory trace for that stimulus which results in a significant reduction of the ERP. However, the degree of reduction cannot be taken to reflect solely the process of retrieval, but instead, involves a number of different processes including encoding of the original stimulus, active maintenance of the memory trace, and retrieval and comparison stimuli. The current results are in agreement with both our previous studies on humans (Begleiter et al., 1993, 1995; Hertz et al., 1994; Zhang et al., 1995) and experimental results in monkeys performing DMS tasks (Baylis and Rolls, 1987; Riches et al., 1991; Lueschow et al., 1994; Miller and Desimone, 1994; Tanaka, 1996). However, the current experiment has some novel implications. Although

it has been shown that neuronal responses in monkey inferior temporal cortex do not vary with the size and position of stimulus images on the retinas (Lueschow et al., 1994), the memory of a sample stimulus did not prime the incoming test stimulus by its initial content in the present experiment. In order to make a judgment as accurately and quickly as possible, the subject may actively process the encoded information from sample stimulus and/or reason out a possible fitting representation (elaborative rehearsal) while maintaining the information in memory. Thus, the memorization of a stimulus within the working memory system could derive from, but not necessarily duplicate the original form of the stimulus in details. The ERP component between 200 and 400 ms poststimulus in the present study, which was indicated as a memory potential (VMP) by a series of our previous studies (Begleiter et al., 1993; Begleiter et al., 1995; Hertz et al., 1994; Zhang et al., 1995), is again shown to be a reflection of ERP mnemonic effects in human beings.

The SCD topographic maps in the present study again indicate the involvements of the occipito-temporal regions in processing the visual stimuli. These involvements are in agreement with the former demonstration that the inferior temporal region is implicated in highest levels of visual object representation (Plaut and Farah, 1990). However, the SCD topographic maps in the FIT and NONFIT stimulus conditions also show the differences in terms of the current source distribution pattern. The main locations of current sources over occipitotemporal regions in NONFIT stimulus condition suggest that the occipitotemporal regions are strongly involved in setting up and manipulating the new imagery in working memory; however, the comparatively confined current sources over the occipitotemporal regions and active current sources and sinks over the frontal regions in the FIT stimulus condition may suggest that an inner representation from preceding stimulus is activated by 'comparing and matching' with the new representation being encoded from test stimulus. Studies on humans with fMRI also indicate that the frontal cortex also engages in the processes within the working memory (Andreasen et al., 1995). Thus, the SCD maps for the FIT and NONFIT stimulus conditions may reflect different neural processes within working memory.

In conclusion, the present data suggested that discrete processes within working memory are overlapping temporally and functional anatomically. The present study also indicated that an ERP component, occurring approximately at 250 ms poststimulus, may be a reflection of ERP mnemonic effect for working memory. Our results rule out the retinotopic confound as a potential mediator variable in DMS paradigms, and are in agreement with other neurophysiological studies on memory. The current results also imply that visual information can be actively processed and the inner representations in working memory is not necessary to be identical to the original visual forms of the visual stimuli.

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