

High-resolution EEG Mapping of Cortical Activation Related to Working Memory: Effects of Task Difficulty, Type of Processing, and Practice

Alan Gevins, Michael E. Smith, Linda McEvoy and Daphne Yu

EEG Systems Laboratory & SAM Technology, 101 Spear Street, #204, San Francisco, CA 94105, USA

Changes in cortical activity during working memory tasks were examined with electroencephalograms (EEGs) sampled from 115 channels and spatially sharpened with magnetic resonance imaging (MRI)-based finite element deblurring. Eight subjects performed tasks requiring comparison of each stimulus to a preceding one on verbal or spatial attributes. A frontal midline theta rhythm *increased* in magnitude with increased memory load. Dipole models localized this signal to the region of the anterior cingulate cortex. A slow (low-frequency), parietocentral, alpha signal *decreased* with increased working memory load. These signals were insensitive to the type of stimulus attribute being processed. A faster (higher-frequency), occipitoparietal, alpha signal was relatively attenuated in the spatial version of the task, especially over the posterior right hemisphere. Theta and alpha signals increased, and overt performance improved, after practice on the tasks. Increases in theta with both increased task difficulty and with practice suggests that focusing attention required more effort after an extended test session. Decreased alpha in the difficult tasks indicates that this signal is inversely related to the amount of cortical resources allocated to task performance. Practice-related increases in alpha suggest that fewer cortical resources are required after skill development. These results serve: (i) to dissociate the effects of task difficulty and practice; (ii) to differentiate the involvement of posterior cortex in spatial versus verbal tasks; (iii) to localize frontal midline theta to the anteromedial cortex; and (iv) to demonstrate the feasibility of using anatomical MRIs to remove the blurring effect of the skull and scalp from the ongoing EEG. The results are discussed with respect to those obtained in a prior study of transient evoked potentials during working memory.

Introduction

The sensitivity of the human electroencephalogram (EEG) to changes in mental effort has been known since Hans Berger (1929) reported a decrease in the amplitude of the dominant (alpha) rhythm of the EEG during mental arithmetic. In this paper, carefully controlled 'working memory' tasks (i.e. tasks demanding the effortful attention required to hold information in mind for several seconds in the context of cognitive activity) were combined with recording and analysis methods designed to improve the anatomic specificity of EEG measures. The results complement a recent report on high-resolution evoked potentials (EPs) recorded in the same tasks (Gevins *et al.*, 1996), and highlight similarities and differences in the topography and task-sensitivity observed with the two approaches.

Substantial progress has been made towards characterizing the neural basis of human working memory. The anatomical substrate of working memory does not appear to depend on the corticolimbic circuitry that is necessary for retrieval of information when a delay of more than a few seconds is interposed between study and test trials of a memory task (e.g. Wickelgren, 1968; Cave and Squire, 1992). Rather, lesion studies have indicated that the frontal lobes often play a critical role in

this function (e.g. Petrides and Milner, 1982; Frisk and Milner, 1990; Owen *et al.*, 1990). Similarly, recent neuroimaging studies have found metabolic increases in regions of the frontal lobes as well as in other areas of association cortex during working memory tasks (e.g. Jonides *et al.*, 1993; Paulesu *et al.*, 1993; McCarthy *et al.*, 1994; Smith and Jonides, 1995; Courtney *et al.*, 1996; Owen *et al.*, 1996; Smith *et al.*, 1996).

Electrophysiological methods have also been utilized to measure activity related to working memory. Recordings of neuronal activity in primates have indicated that the neural representation of information over short delays is associated with transient activation of widespread populations of association cortex neurons (e.g. Fuster and Jervey, 1981, 1982; Miyashita and Chang, 1988; Funahashi *et al.*, 1989; Koch and Fuster, 1989; Chelazzi *et al.*, 1993; Wilson *et al.*, 1993; Miller and Desimone, 1994). In humans, electrophysiological studies have focused on EP measures in an effort to track the subsecond time course and distribution of working memory processes (e.g. Starr and Barrett, 1987; Ruchkin *et al.*, 1990, 1992, 1995; Lang *et al.*, 1992; Gevins and Cutillo, 1993; Raney, 1993; King and Kutas, 1995; Gevins *et al.*, 1996). In a companion paper to the present study, Gevins and colleagues (1996) identified phasic, subsecond changes in brain electrical signals over frontal and parietal cortex, that, in agreement with the studies of neuronal activity in primates, provided a dynamic picture of momentary changes in the spatial distribution of working memory effects over the course of individual trials, as well as evidence for differences in the activity elicited between trials that have different decision requirements.

Averaged EPs index specific operations being performed on internal representations. In contrast, task-related modulation of the ongoing EEG reflects changes in the state of the functional networks underlying task performance (cf. Lopes da Silva, 1991), providing a complementary view of brain electrical activity during working memory. Two prominent EEG features are highly sensitive to variations in mental effort. The alpha rhythm tends to *decrease* in strength as tasks become more difficult (e.g. Gevins *et al.*, 1979a,b,c; Gundel and Wilson, 1992; Serman *et al.*, 1994). This inverse relationship of alpha amplitude to task difficulty has sometimes been interpreted as indicating that the alpha rhythm represents a form of cortical idling (e.g. Steriade, 1981; Van Winsum *et al.*, 1984). In contrast, the frontal theta rhythm has been noted to *increase* in strength as tasks require more focused attention (e.g. Ishihari and Yoshii, 1972; Gevins *et al.*, 1979a,b,c; Miyata *et al.*, 1990; Yamamoto and Matsuoka, 1990; Gundel and Wilson, 1992). Although many studies have described task-related changes in these features, none have systematically examined their relationship to working memory.

In the present study, working memory tasks were devised which permitted manipulation of task difficulty, task content,

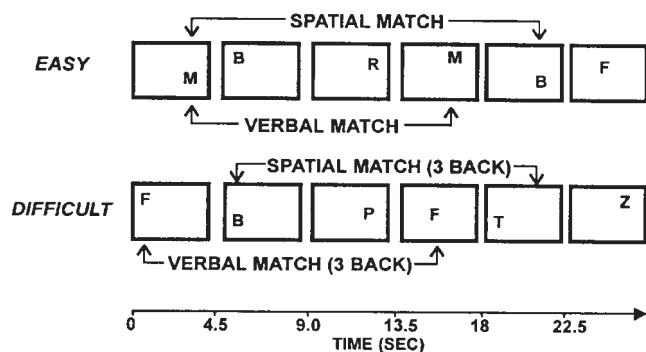


Figure 1. Diagram of the matching tasks. Equivalent stimuli were presented and equivalent behavioral responses were required in each condition, while processing strategy and working memory load were varied. The difficult tasks (bottom) required a decision as to whether the letter stimulus on each trial matched either the spatial location or the verbal identity of the stimulus occurring three trials previously. The easy tasks (top) simply required that the subject recognize a particular letter or spatial position, held constant over the course of a block of 53 trials. This figure illustrates a typical series of trials, and indicates the match trials that would occur in the different task conditions.

and amount of practice, while isolating perceptual and motoric confounds. These tasks were used to characterize the task correlates of working memory-related modulation of the frontal theta and alpha rhythms of the ongoing EEG. The regionalization of that task-related modulation was characterized by improving the spatial detail of scalp recordings and integrating physiological and anatomical images. This was accomplished by recording from 115 scalp electrodes and utilizing a recently devised spatial deblurring method that makes it possible to combine scalp-recorded EEG with realistic, subject-specific head models to estimate the topography of potential fields as they would appear just above the exposed superficial cortical surface (Gevins *et al.*, 1991, 1994; Le and Gevins, 1993). The 'finite element deblurring' method is an inverse solution of Poisson's equation using finite element models of volume conduction through the skull and scalp that are constructed from anatomical information derived from each subject's magnetic resonance image (MRI). The anatomical and electrical modeling is combined with high-density electrode arrays in order to prevent aliasing of high spatial frequencies.

Materials and Methods

Subjects

Eight (four female) fully informed, healthy, right-handed (one ambidextrous) volunteers (mean age 27 years) participated in the study.

Cognitive Tasks

Participants were seated facing a videomonitor at a distance of ~60 cm. They performed four versions of a continuous matching task (Figure 1). Matches occurred on 30% of the trials. Equivalent stimuli were presented and equivalent behavioral responses were required in each condition, with type of processing and working memory load varying across conditions. Each stimulus item was drawn from a set of 12 capital letters. The letter on a given trial appeared at one of 12 positions, each of which was on one of six equidistant radii of an imaginary circular array 1 or 3.5 cm from the screen's center (the inner and outer circles of this array respectively subtended ~1.5° and ~4.5° of visual angle). Letter name and position were counterbalanced across conditions so that each letter and position occurred with equal probability. Critical stimuli were presented for 250 ms once every 4.5 s. A fixation point appeared at the center of the screen 1.5 s before the stimulus.

In two difficult task conditions that imposed a heavy load on working

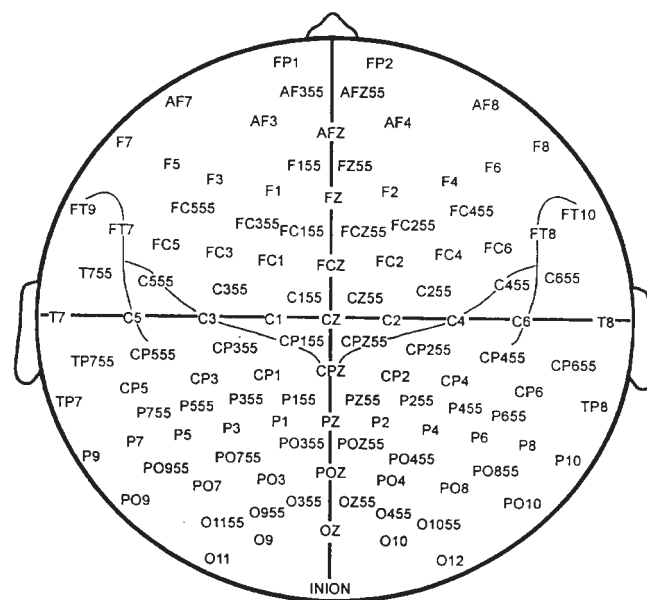


Figure 2. Two-dimensional projection of the approximate relative locations of the 115 scalp electrodes. The nose is at the top.

memory, the participants judged whether the stimulus on a trial matched the stimulus presented three trials previously. In different blocks either the name or the spatial location of the stimulus was matched to prior stimuli. These difficult task conditions thus required concurrent maintenance of a sequence of three letter names or three spatial locations. Since each trial lasted 4.5 s, accurate performance in these conditions required that stimuli be retained for ~13.5 s. Subjects had to update the sequence on each trial by retaining the most recent stimulus and could drop the stimulus from four trials back. Simply detecting that the current stimulus was a repetition of some previous event was not sufficient to ensure accurate performance; both the precise sequence and the name or location of a letter had to be remembered. In the two easy working memory tasks, only the verbal name or spatial location of the first stimulus of each block had to be remembered and compared to each subsequent stimulus. Subjects were informed of the task type and difficulty level at the initiation of each block of trials. In all four conditions subjects were required to respond by pushing a microswitch with the right-hand index finger for non-matching stimuli (those that did not match the name or spatial location of the comparison stimulus) and a second microswitch with the right-hand middle finger for matching stimuli. Subjects were requested to respond as quickly and accurately as possible. Stimuli in each of the four conditions were presented in blocks of 53 trials. Since for difficult task conditions no matches could appear in the first three trials of a block, data from those trials were excluded from analyses in all conditions. On the day before the experimental session, subjects performed ~200 training trials for each condition. On the day of the recording they performed seven blocks of each task condition (i.e. 350 trials in each of four conditions). Block order was randomized for each subject. Blocks were self-paced and several breaks were taken over the course of the session.

Recordings

EEGs were recorded from a 115 channel array (Figure 2) of electrodes placed in an extended 10–20 system montage amplified 9.24K, band-pass filtered at 0.05–100 Hz, and sampled at 256 Hz. This montage was referenced to mastoid electrodes that were linked after placing a resistor in series with each lead to compensate for any imbalance in impedance between the two mastoids (cf. Pivik *et al.*, 1993). Further, all statistical analyses were computed across a group of subjects, and it can reasonably be assumed that the direction of any impedance imbalances would be randomly distributed over the subjects. As a result, there is no reason to expect any systematic bias in voltage topography associated with this

choice of reference. Reference impedances were reduced to <3 k Ω , and impedances on other channels were reduced to <10 k Ω , prior to recordings. Vertical and horizontal eye movements were also recorded.

The recording array provided average interelectrode distances of ~2.25 cm. The three-dimensional positions of each scalp electrode and fiducial anatomical reference points (including the nasion, the tragus of each ear, the outer canthus of each eye and the tip of the nose) were magnetically digitized for registration of the recording array with subject-specific MRI-derived anatomical models. MRIs were recorded with a Siemens Magnetron scanner in three-dimensional acquisition mode to obtain T₁-weighted images of contiguous 1.5 × 1.0 × 1.0 mm voxels.

Analysis

All EEG and MRI processing was performed with the MANSCAN® software system. Trials with instrumental artefacts, amplifier saturation, visually detectable vertical and horizontal eye movement potentials, and muscle activity over ~80 μ V peak-to-peak were eliminated prior to further analyses. Approximately 30% of the trials were rejected because of artefactual contaminants.

To create high-resolution EEG images, EEG spatial topography was enhanced utilizing the ‘finite element deblurring’ method. This method provides an estimate of the electrical fields that would be recorded near the cortical surface. It uses MRI-derived, anatomically realistic, subject-specific models of volume conduction to downwardly project scalp-recorded signals (for details, see Le and Gevins, 1993; for a general overview of finite element techniques applied to electrical field problems, see Chari and Silvester, 1980; for comparison of results to those provided by the Laplacian derivation, see Gevins *et al.*, 1994). The models are in the form of many small tetrahedral elements representing the tissues of scalp, skull and brain. By assigning each tissue a conductivity value, it is possible to calculate the potential at all finite element vertices using Poisson’s equation. The finite element modeling of tissue below the scalp surface was limited to structures above a horizontal plane that bisected the head of each subject just above the sinus cavity.

Given that the actual conductivity value of each finite element is unknown, a constant value was used for the ratio of scalp to skull conductivity (80:1); the conductivity of each finite element is set by multiplying this constant by the local tissue thickness as determined from the MRI. Even though true local conductivity is unknown, the procedure is well-behaved with respect to this source of uncertainty, because it successfully accounts for relative conductivity variation due to regional differences in scalp and skull thicknesses. Simulation studies have shown that relative spatial topography and field maxima are not appreciably affected by changes in this parameter (Le and Gevins, 1993). Further, since the same conductivity ratio is used in all conditions, relative differences in potential amplitude between task conditions are not influenced by this parameter. After the deblurring procedure, a spatial low-pass Gaussian filter was applied to the data in order to eliminate spatial frequencies higher than those which can be resolved with the spatial sampling set by the interelectrode spacing on the scalp (cf. Gevins *et al.*, 1994; Le and Gevins, 1993).

Results

Behavior

Reaction times (RTs) to correctly classified stimuli were longer in the difficult conditions than in the easy conditions (770 versus 570 ms; $F(1,7) = 54.90$, $P < 0.001$). No significant difference in RT was observed between matching and non-matching stimuli, or between the spatial and verbal tasks, and there was no interaction between difficulty and task-type ($F_s < 1$). Accuracy was lower in the difficult tasks than in the easy tasks [$d' = 2.45$ versus $d' = 4.40$; $F(1,7) = 134.03$, $P < 0.0001$], but there was no significant effect of task-type [$F(1,7) = 1.8$, $P < 0.221$], and no significant interaction [$F(1,7) = 3.1$, $P < 0.122$]. Lack of any overall difference in the speed or accuracy of performance between the spatial and verbal versions of the tasks indicates that the task-types were of equal difficulty. When comparing performance between the first and last blocks of 50 trials in each

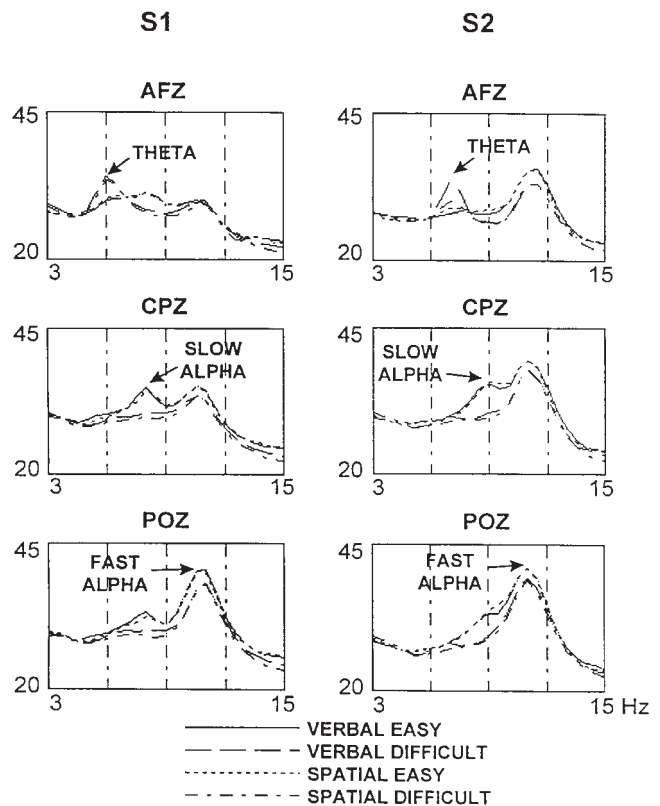


Figure 3. Average EEG spectra over the 3–15 Hz interval for each task condition at anterior frontal midline (AFZ), parietocentral midline (CPZ) and occipitoparietal midline (POZ) locations for two subjects. Vertical scale is in decibels power. Three distinct spectral peaks can be identified in this interval in these subjects.

task version, match detection accuracy was slightly higher, and RTs faster [$F(1,7) = 7.51$, $P < 0.03$]. This improvement in performance suggests that subjects remained attentive during the session, and that over time they developed more efficient strategies.

Electrophysiology

Fast Fourier transforms computed over 50% overlapped, 512 sample (i.e. 2 s) Hanning windows were calculated for all contaminant-free EEG segments for correctly performed trials. Average power spectra were then computed across segments for each task condition in each subject. Preliminary inspection of these spectra indicated that no reliable differences occurred between match and non-match trials so data were collapsed across this dimension.

Although individual subjects often displayed idiosyncratic task-related modulation at both lower and higher frequencies, the most pronounced and reliable task-related modulation of spectral power occurred in the theta (4–7.5 Hz) and alpha (7.5–14 Hz) bands. Most subjects showed a clear spectral peak at midline frontal electrodes in the theta band (average 6 Hz, range 5–7 Hz). This response displayed highest energy in the difficult task conditions. In the ongoing EEG of subjects in which frontal theta activity was most pronounced, this phenomenon appeared as tight envelopes or bursts of high amplitude activity at frontal sites, with a typical duration of 0.5–2 s. These bursts did not in general appear to be time locked to any particular task event. As suggested by the power spectra measures, the highest amplitude individual bursts were observed in the most difficult task conditions.

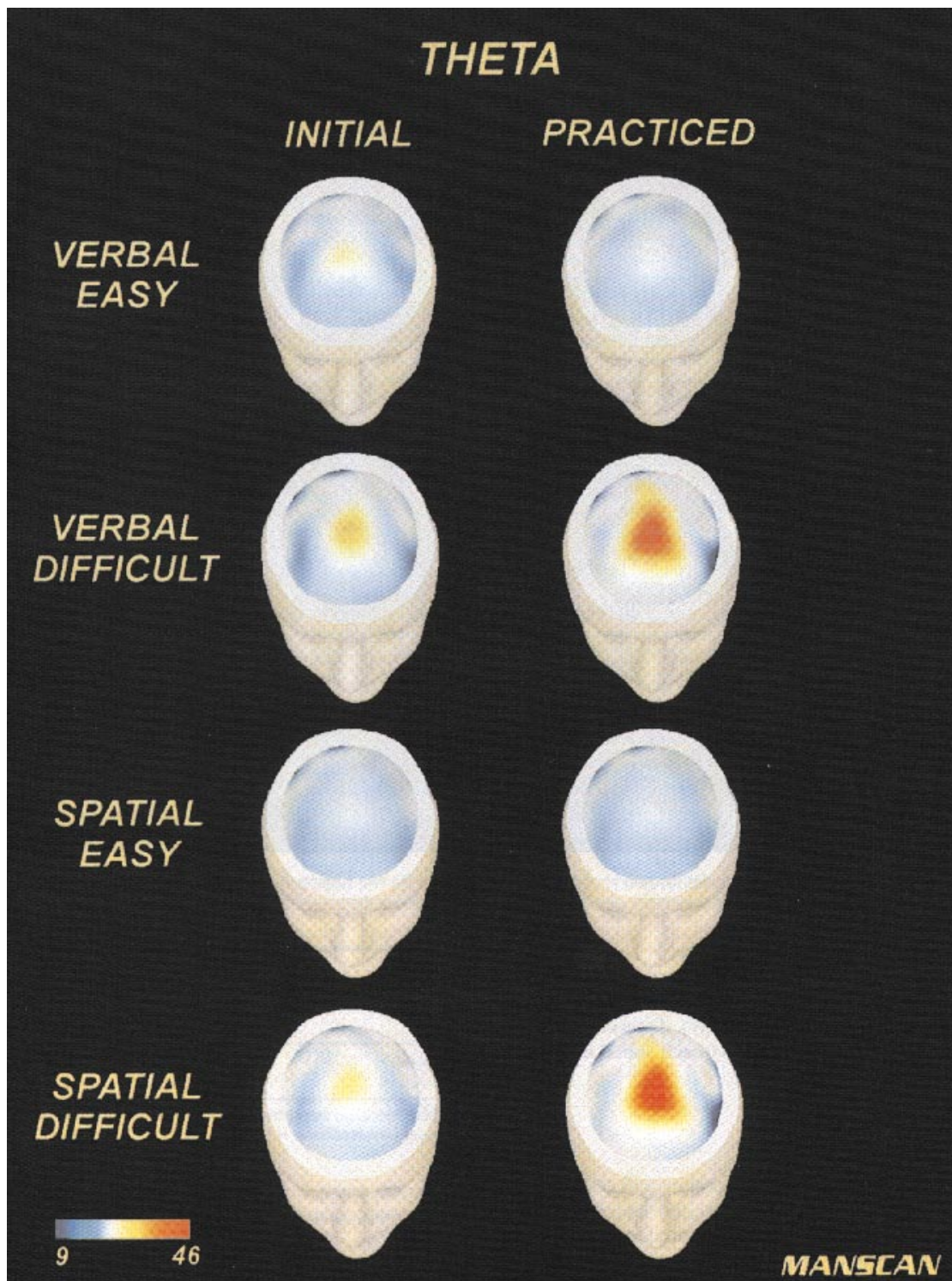


Figure 4. High-resolution EEG topographic maps showing the deburred topography of the frontal midline theta rhythm in subject S1 from Figure 3, during performance of easy and difficult versions of the spatial and verbal matching tasks in the first (initial) and last (practiced) test blocks. On average across the eight subjects, this theta signal is higher in amplitude in the more difficult task conditions than in the easy task conditions, and is higher after practice. Data displayed are power at peak frequency, scale is in arbitrary units.

Many subjects also displayed a spectral peak in the lower frequency portion of the alpha band that reached maximum energy at parietocentral sites, and those in which a clear 'slow' alpha peak was not apparent nevertheless did display large differences in the lower frequency portion of the alpha band that maximally discriminated between test conditions at central

locations (average 9 Hz, range 8–10.5 Hz). Finally, all subjects had a distinct, relatively higher frequency 'fast' alpha peak that reached maximum signal intensity over midline occipitoparietal sites (average 11 Hz, range 10–13.5 Hz). Both the 'slow' parietocentral and 'fast' occipitoparietal alpha signals were larger in the easy task conditions than in the difficult task



Figure 5. Anatomical registration of equivalent dipoles (arrows) computed for theta bursts for the two subjects whose spectra are illustrated in Figure 3. The base of each arrow represents the location of the dipole in the region of the anterior cingulate cortex, and the direction of the arrow indicates its orientation.

conditions. Figure 3 displays spectra in the 3–15 Hz interval for two subjects in which these different spectral peaks can be easily discerned. Statistical analysis of each of these (frequency-domain and topographically) distinct phenomena appears below, and the topography of each signal is illustrated with high-resolution EEG images.

Frontal Midline Theta

Figure 4 portrays the deblurred topography and task correlates of the theta rhythm in one subject, illustrating its highly localized distribution in the midline frontal region, its larger amplitude in the difficult tasks, and its increase in amplitude with practice. The localized midline topographical distribution suggests that the frontal theta rhythm most likely arises from a compact, relatively superficial, medial source. Single-dipole source models were thus fit to individual theta bursts to identify the center of mass of the area responsible for generating the theta rhythm. In order to minimize localization error introduced by spatial noise, the three subjects who displayed the largest magnitude theta peak power in their average spectral measures, and in whom distinct, high-amplitude theta bursts could be discerned in the ongoing EEG, were selected for dipole modeling. Results from two of these subjects are illustrated in Figure 5. Similar results were obtained for the other subject. Equivalent spatial dipolar sources for large-amplitude theta

Table 1
Effect of task difficulty on EEG frontal theta power

	Difficult task	Easy task
Spatial	0.84 (0.51)	–1.01 (0.33)
Verbal	0.98 (0.38)	–0.81 (0.49)

Note: Normalized mean (standard deviation) spectral peak power at anterofrontal midline site AFZ in each task condition ($n = 8$).

bursts were calculated using an iterative three-dimensional search algorithm and a three-shell spherical model to represent the scalp, skull and brain. This spherical model was fit to the actual measured locations of the scalp electrode array, and resulting equivalent dipoles were registered with anatomical images derived from each subject's MRI. Average dipoles were computed over 10 theta bursts at the time point of maximum amplitude for each burst. These equivalent dipole models on average accounted for >99% of the variance in the distribution of theta bursts at the scalp, and were found to cluster around medial regions of the prefrontal cortex (Figure 5) in the area of the anterior cingulate cortex (ACC).

To test whether frontal theta activity was affected by the task-difficulty and task-type manipulations, repeated-measures ANOVA was applied to normalized (z -scores computed across task conditions within each subject) measurements of signal

Table 2

Effect of practice on EEG frontal theta power

	Spatial		Verbal	
	Difficult task	Easy task	Difficult task	Easy task
Initial	-0.44 (0.67)	-1.16 (0.39)	-0.08 (0.41)	-0.95 (0.37)
Practiced	1.30 (0.41)	0.01 (0.27)	1.32 (0.64)	0.01 (0.92)

Note: Normalized mean (standard deviation) spectral peak power at anterofrontal midline electrode site AFZ in each task condition at beginning (initial) and ending (practiced) blocks of the session ($n = 8$).

Table 3

Effect of task difficulty on EEG 'slow' parietocentral alpha power

	Spatial		Verbal	
	Difficult task	Easy task	Difficult task	Easy task
Left hemisphere	-1.03 (0.48)	0.60 (0.45)	-1.08 (0.52)	0.70 (0.37)
Right hemisphere	-0.29 (1.15)	0.96 (0.39)	-0.79 (0.51)	0.92 (0.45)

Note: Normalized mean (standard deviation) spectral peak power at left and right lateral parietocentral sites (CP3, CP4) in each task condition ($n = 8$).

power at theta peak frequency at anterofrontal midline electrode AFZ (halfway between sites FZ and FPZ of the international 10–20 System) (Table 1). This analysis indicated that the difficult tasks elicited a larger theta signal than did the easier tasks [$F(1,7) = 492.59, P < 0.0001$]. No difference in power at this frequency was observed between the verbal and spatial task conditions [$F(1,7) = 0.65, NS$]. There was no interaction between difficulty and task-type.

To examine whether the frontal theta rhythm significantly changed with practice, measures of peak theta power were compared between the first and last blocks of trials in each task condition. As in the prior analysis, repeated-measures ANOVA applied to normalized theta peak power at electrode site AFZ (Table 2) indicated that throughout the session the difficult tasks elicited a larger theta signal than did the easier tasks [$F(1,7) = 23.00, P < 0.002$]; again there was no difference in theta peak power between the verbal and spatial tasks ($F = 1.13, NS$). Power increased between the first and last blocks of the session [$F(1,7) = 137.33, P < 0.001$]. There was also a significant interaction between the task-difficulty and task-practice factors [$F(1,7) = 9.89, P < 0.02$], with theta increasing relatively more in the difficult tasks than in the easy tasks.

'Slow' Parietocentral Alpha

Figure 6 portrays the deblurred topography and task correlates of the 'slow' alpha signal, illustrating its distribution over the parietal region and its sensitivity to the experimental manipulations. To examine effects of the task-difficulty and task-type manipulations, repeated-measures ANOVA was applied to measurements of signal power at peak frequency (or in the case of subjects without a distinct peak, at the frequency of maximum discrimination between tasks at parietocentral sites), at left and right lateral parietocentral sites CP4 and CP3 (Table 3). The difficult tasks elicited a smaller signal than did the easy tasks [$F(1,7) = 159.43, P < 0.001$]. No difference in spectral energy at this frequency was observed between the verbal tasks and the spatial tasks, there was no significant difference between hemispheres, and no interactions. Repeated-measures ANOVA applied to normalized power at parietocentral midline site CPZ (Table 4) indicated that power increased slightly between the first and last blocks of the session [$F(1,7) = 7.28, P < 0.05$].

Table 4

Effect of practice on EEG 'slow' parietocentral alpha power

	Spatial		Verbal	
	Difficult task	Easy task	Difficult task	Easy task
Initial	-0.63 (1.00)	0.28 (0.77)	-0.77 (0.93)	0.14 (0.79)
Practiced	-0.42 (0.94)	0.98 (0.64)	-0.53 (0.42)	0.95 (0.85)

Note: Normalized mean (standard deviation) spectral peak power at parietocentral midline site (CPZ) in each task condition at beginning (initial) and ending (practiced) blocks of the session ($n = 8$).

Table 5

Effect of task difficulty on EEG 'fast' occipitoparietal alpha power

	Spatial		Verbal	
	Difficult task	Easy task	Difficult task	Easy task
Left hemisphere	-1.31 (0.45)	-0.05 (1.00)	-1.08 (0.67)	0.17 (0.84)
Right hemisphere	-0.59 (0.76)	1.24 (0.52)	0.13 (0.85)	1.49 (0.46)

Note: Normalized mean (standard deviation) spectral peak power at left and right lateral occipitoparietal sites (PO7, PO8) in each task condition ($n = 8$).

Table 6

Effect of practice on EEG 'fast' occipitoparietal alpha power

	Spatial		Verbal	
	Difficult task	Easy task	Difficult task	Easy task
Initial	-1.00 (1.00)	0.02 (0.82)	-0.69 (0.83)	0.48 (0.81)
Practiced	-0.65 (0.42)	1.05 (0.25)	-0.25 (0.91)	1.04 (0.31)

Note: Normalized mean (standard deviation) spectral peak power at an occipitoparietal midline site (POZ) in each task condition at beginning (initial) and ending (practiced) blocks of the session.

'Fast' Occipitoparietal Alpha

Figure 7 portrays the deblurred topography and task correlates of the 'fast' alpha signal, illustrating its relatively posterior distribution with maximum signal strength over occipital and occipitoparietal regions. This posterior topography is consistent with distributed generators in secondary visual cortex in both hemispheres. To examine its sensitivity to the task-difficulty and task-type manipulations, repeated-measures ANOVA was applied to measurements of signal power at 'fast' posterior alpha peak frequency at left and right lateral occipitoparietal electrodes PO7 and PO8 (Table 5). As with the slow parietocentral alpha signal, the difficult tasks attenuated the signal relative to the easy tasks [$F(1,7) = 29.38, P < 0.001$]. In contrast to the slow alpha signal, a significant difference in spectral energy was obtained between the verbal and the spatial tasks [$F(1,7) = 6.11, P < 0.05$], with less attenuation in the verbal tasks than in the spatial tasks. There also was a significant difference between hemispheres, with higher signal amplitude over the right occipitoparietal area [$F(1,7) = 9.02, P < 0.03$], and a significant three-way interaction between the difficulty level, task-type and hemispheric factors [$F(1,7) = 7.30, P < 0.05$]. *Post-hoc*, paired *t*-tests comparing the two task types at each difficulty level at each hemisphere revealed that over the right occipitoparietal region, alpha for the difficult spatial task was significantly attenuated relative to the difficult verbal task [$t(7) = 4.33, two-tailed P < 0.005$]. No other *post-hoc* comparisons were significant. Repeated-measures ANOVA applied to normalized posterior alpha power at occipitoparietal midline site POZ (Table 6) produced only a marginal increase in this signal between the first and last blocks of the session [$F(1,7) = 5.45, P < 0.06$].

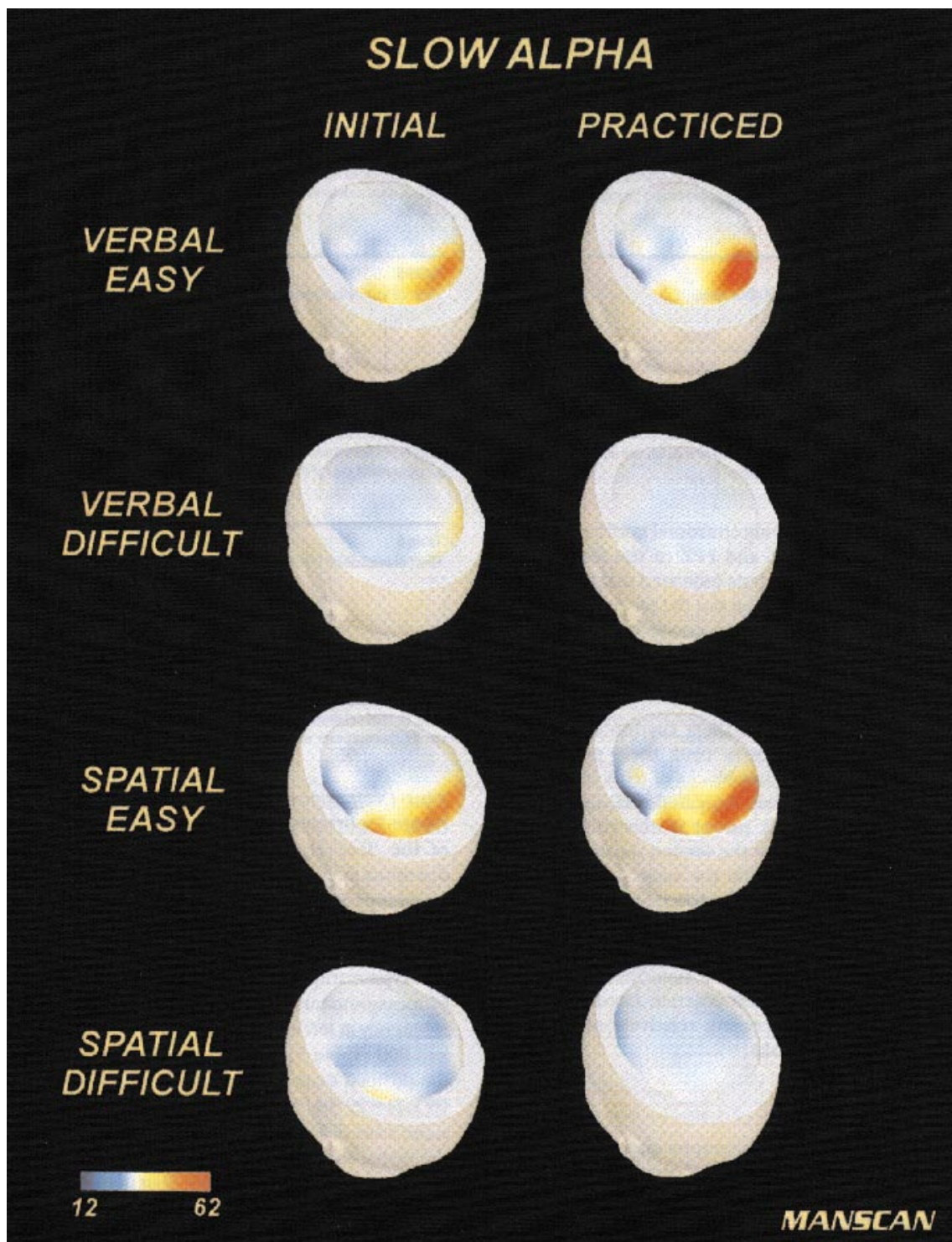


Figure 6. High-resolution EEG topographic maps showing the deblurred topography of the 'slow' parietocentral alpha signal (displayed at peak frequency) in subject S2 from Figure 3, during performance of easy and difficult versions of continuous spatial and verbal matching tasks in the first (initial) and last (practiced) test blocks. On average across the eight subjects, this alpha signal is higher in amplitude in the easy task conditions than in the difficult task conditions, and is higher after practice. Data displayed are power at peak frequency, scale is in arbitrary units.

Discussion

This study attempted to identify how spectral features of the ongoing EEG are modulated during performance of continuous working memory tasks requiring focused attention and sustained mental effort, and to better characterize the topography of those features by improving the spatial resolution

of the EEG and by integrating physiological and anatomical images. At least three signals in the 3–15 Hz frequency band could be reliably distinguished by their characteristic frequency, topography and task correlates. A frontal midline theta rhythm increased in strength with increased task difficulty, whereas a parietocentral, relatively slow (low-frequency), alpha signal

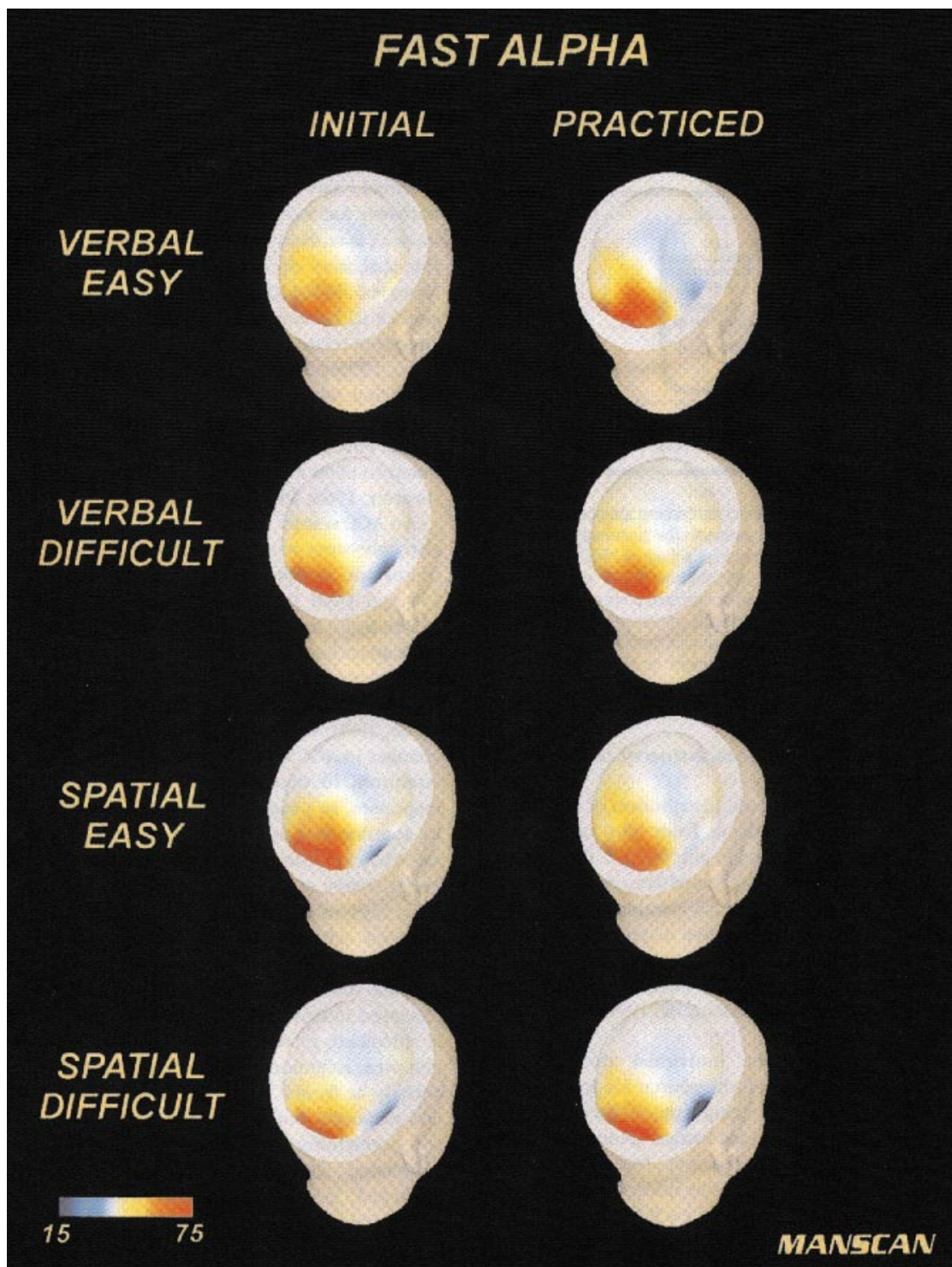


Figure 7. High-resolution EEG topographic maps showing the deblurred topography of the 'fast' occipitoparietal alpha signal (displayed at peak frequency), during performance of easy and difficult versions of continuous spatial and verbal matching tasks in the first (initial) and last (practiced) test blocks from the testing session. On average across the eight subjects, this alpha signal is higher in amplitude in the easy task conditions than in the difficult task conditions, in the verbal task conditions than in the spatial task conditions, and after practice. Data displayed are power at peak frequency, scale is in arbitrary units.

decreased in magnitude with increased task difficulty. Both the frontal theta rhythm and the slow alpha signal were largely insensitive to the type of information being attended to and remembered. With increased practice on the task, both the theta rhythm and the slow alpha signal increased in amplitude. In

contrast, an occipitoparietal, faster alpha signal, which was also attenuated in difficult tasks, showed less change in amplitude with practice, and was suppressed more when attending to spatial than verbal information. These results and their significance are discussed below.

TIMING OF ATTENTIONAL PROCESSES

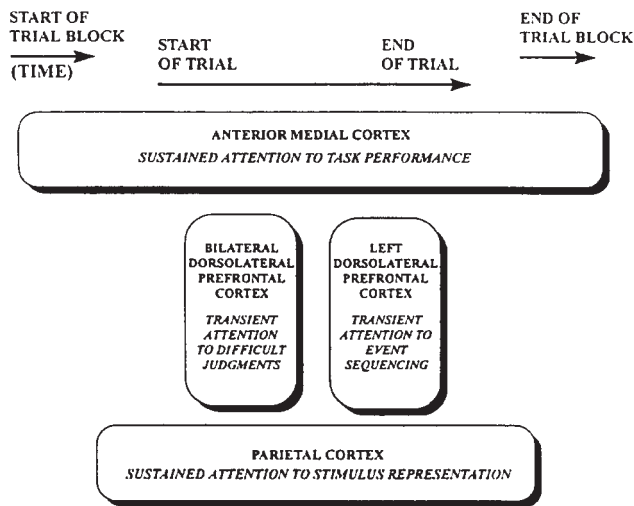


Figure 8. Speculative diagram of subsecond and multisecond attentional processes during the working memory tasks of this experiment. The sustained mental effort required to keep attention focused over the course of a block of trials is reflected in tonic enhancement of the frontal midline theta rhythm. Phasic engagement of dorsolateral frontal cortex during the comparison and decision processes immediately following stimulus presentation might be reflected in the enhancement of the P305 and P450 evoked potential components. In contrast, retaining a stimulus representation in working memory during the interstimulus interval might be reflected both in the posterior slow wave enhancement revealed by the EP analysis, and the tonic reduction in alpha power in the difficult task conditions.

Neurogenesis and Functional Modulation of the Frontal Midline Theta Rhythm

The task correlates and the restricted distribution of the frontal midline theta rhythm distinguish it from the more topographically widespread slow rhythmic activity (cf. Davis *et al.*, 1937) that has been associated with states of decreased alertness. Attentive states that occur during both complex task performance and meditative concentration have often been reported to be associated with high-amplitude theta rhythms over the frontal lobes (Ishihari and Yoshii, 1972; Gevins *et al.*, 1979a,c; Miyata *et al.*, 1990; Yamamoto and Matsuoka, 1990; Gundel and Wilson, 1992; Inouye *et al.*, 1994).

Equivalent dipole models for individual theta bursts, registered with MR images, isolated the source for frontal theta activity to the region of the anterior cingulate cortex (Brodmann areas 24 and 32). Presumably, the anatomical generator of this phenomenon entails a bihemispheric source, but given that the left and right anterior cingulate cortices lie immediately adjacent to one another on the medial surface of each hemisphere, it is reasonable to approximate them with a single dipole source model. In any case, these results must be viewed as preliminary given that the inverse problem presented by source modeling has no unique solution; other source configurations could be created that might produce equivalent results. For example, reports from other source modeling efforts have suggested that this signal could arise either from a midline anterior source as proposed here (Iramina *et al.*, 1996), or from bilateral sources in dorsolateral frontal cortex (e.g. Sasaki *et al.*, 1994; Iramina *et al.*, 1996). Definitive localization of this phenomenon would require detailed invasive studies in neurosurgical patients. However, several convergent sources of evidence are consistent with the hypothesis that frontal midline theta arises from an ACC source.

In this and in other topographic studies (e.g. Inouye *et al.*,

1994; Iramina *et al.*, 1996), frontal attention-related theta had a very restricted anterior midline distribution. Since brain potentials arising in lateral cortical regions have consistently resulted in lateralized potential fields in prior high-resolution studies (e.g. Gevins *et al.*, 1994, 1995, 1996), the focal midline distribution appears unlikely to result from a signal that arises in lateral cortical regions. Similarly, inasmuch as a source distant from the recording electrodes would be expected to produce a broad, low-amplitude, voltage topography, the observed narrowly focused potential field with relatively high amplitude at its peak is unlikely to reflect activity in deeper structures such as the thalamus or medial temporal region. Furthermore, the observed localization of frontal theta is consistent with invasive studies in humans that have found the ACC to be a source of cognition-related evoked potentials (Smith *et al.*, 1990; Baudena *et al.*, 1995), and with reports that in both humans and monkeys the firing rates of individual ACC neurons are associated with performance of difficult tasks (Heit *et al.*, 1990; Shima *et al.*, 1991). Finally, electrical stimulation of the human ACC has been noted to elicit a 3–8 Hz EEG rhythm in frontomedial recordings (Brazier, 1968; Talairach *et al.*, 1973).

An ACC source for the frontal, attention-related theta signal is also consistent with the notion that this anatomical region is an important component of the human attentional system (cf. LaBerge, 1990; Posner and Peterson, 1990; Posner and Rothbart, 1992). Brain lesions that encompass the ACC in humans can produce attentional deficits, increased interference from competing responses, and disorders of voluntary action and of higher cognitive functions (Eslinger and Damasio, 1985; Janer and Pardo, 1990; Vogt *et al.*, 1992). Neuroimaging studies have noted changes in ACC activation when subjects are required to sustain attention, to detect targets and choose between competing responses, to process representations in working memory, and to acquire and act on new information rather than existing associations (Pardo *et al.*, 1990; Frith *et al.*, 1991; Paus *et al.*, 1993; Nenov *et al.*, 1994; Smith *et al.*, 1995). These functional correlates of the ACC suggest that this area of the brain is engaged when tasks require concentration and significant mental effort; from this perspective they are broadly consistent with the functional correlates of the frontal midline theta rhythm observed in this and other studies. That is, frontal midline theta is enhanced, relative to resting states, when subjects engage in complex, attention-demanding tasks. In the current study, theta activity at frontal sites significantly increased with increasing task difficulty, but was insensitive to the type of task the subject was performing. This insensitivity suggests that the mental effort associated with task performance was responsible for the observed modulation, rather than the specific processing activity the subject was engaged in.

Neurogenesis and Functional Modulation of the 'Slow' Parietocentral and 'Fast' Occipitoparietal Alpha Signals

The alpha rhythm is thought to be generated at widespread areas of cortex through thalamocortical interactions (Andersen, 1968; Lopes da Silva, 1991). It appears to reflect a form of cortical idling (Gevins and Schaffer, 1980; Pfurtscheller, 1992), with its amplitude inversely related to the proportion of cortical resources required by task performance (Elul, 1969; Steriade, 1981). In the current study, alpha was most prominent over posterior regions, and it was highly sensitive to task difficulty. This reduction in amplitude during tasks requiring higher mental effort was seen for both the central and posterior alpha

signals, and is consistent with the notion that alpha activity is inversely related to attentional demands (cf. Ray and Cole, 1985).

Previous studies of alpha recorded during task performance have also dissociated 'slow' and 'fast' alpha signals, and have found them to have slightly different task correlates. For example, Klimesch and colleagues (Klimesch *et al.*, 1993, 1994) have argued that the slow alpha signal is most closely related with the attention allocated to task performance, whereas the fast signal is more sensitive to variations in the cognitive content of the tasks being performed. In the current study, the slow parietocentral alpha signal was not sensitive to the type of task being performed, while the fast occipitoparietal signal was significantly smaller for the spatial tasks than the verbal tasks. These results are thus consistent with prior observations (Klimesch *et al.*, 1993, 1994; Pfurtscheller *et al.*, 1988). Further, in addition to this overall reduction in the posterior alpha signal in the spatial tasks versus the verbal tasks, an important hemispheric asymmetry was also observed. Alpha was more attenuated in the difficult spatial task than in the difficult verbal task over the right occipitoparietal region, while no significant difference was observed between the difficult tasks over the left occipitoparietal region or between the easy verbal and spatial tasks at either location. This asymmetry was observed in the absence of differences in stimulus properties, motor requirements, or the apparent difficulty of the two tasks. This observed asymmetry thus suggests that working memory for verbal information results in less functional activation of right posterior cortex than that induced by working memory for spatial information.

Practice-related Modulation of Alpha and Theta

The observed practice-related EEG changes are consistent with commonly held notions regarding practice and cognitive skill development. For example, behavioral evidence indicates that rote tasks, such as classifying recurring patterns of information or responding appropriately to stimuli of a particular class, become automatic with extended practice (e.g. Schneider and Fisk, 1982; Fisk and Schneider, 1984). Automaticity might reflect relegation of some aspects of task performance to subcortical control. In the current context, practice-related alpha enhancement, in conjunction with improvements in task performance measures, suggests that performance required less cortical resources after the subjects became skilled. These results are consistent with reports of decreased cortical blood flow (implying less cortical activation) after practice on complex tasks (Haier *et al.*, 1992; Raichle *et al.*, 1994).

In contrast to the progressive automatization of routine task components, non-routine aspects of complex task performance continue to require sustained and focused attention (cf. Endsley, 1995). Indeed, the effort required to sustain attention to even superficially simple tasks tends to increase after extended periods of performance (Warm *et al.*, 1996). This heightened effort might be responsible for the observed practice-related enhancement of frontal theta. That is, in addition to its increase in amplitude in the more difficult task conditions, frontal theta was also observed to increase with practice on the task, in parallel with performance gains. This increase suggests that as subjects practiced the tasks over an extended period, they had to make an increased effort to maintain a task-related attentional set.

Relationship of Tonic EEG Modulation to Phasic Responses

The task-related changes in the background EEG reported here

reflect modulation of brain electrical activity over a multisecond time course. In a separate paper (Gevins *et al.*, 1996), subsecond, phasic, stimulus-locked EP responses for this data set were described. Briefly, among other effects, frequent, non-matching stimuli elicited a positive, dorsolateral frontal peak at 305 ms (P305), with a duration of ~50 ms, that was larger in the difficult spatial task relative to the other tasks. Irrespective of whether subjects attended to verbal or spatial stimulus attributes, non-matching stimuli in the difficult tasks also elicited an enhanced P450 potential over left dorsolateral frontal cortex with a duration of ~200 ms. The P450 was followed by a sustained low-frequency positivity over superior parietal cortex. These results indicate that the specific processing operations required to perform these tasks engage a distributed system with both task-specific and task-independent components, and that the focus of cortical activity changes over subsecond intervals during the course of stimulus and response processing.

The tonic EEG modulation described in the current paper provides a different, complementary view of brain electrical activity during working memory. Specifically, the changes in EEG spectra are probably more closely related to changes in the state of the functional networks underlying task performance (cf. Lopes da Silva, 1991), while the subsecond EP responses probably more closely index different operations being performed on internal representations (cf. Ritter *et al.*, 1982). For example, the stimulus-following positive polarity EP responses observed over dorsolateral frontal cortex likely reflect cognitive activity that is related to specific, time-limited, transformation and comparison processes. In contrast the tonic, non-specific enhancement of the frontal midline theta rhythm probably indexes the overall mental effort required to concentrate on coordinating all of the varied distributed processes required for task performance. This coordination might be accomplished via the reciprocal connections known to exist between the ACC and widespread regions of frontal and parietal association cortices (Goldman-Rakic, 1987). Similarly, the widespread tonic reduction in alpha in the difficult task conditions is likely to be closely related to the ongoing cortico-cortical feedback presumably required for the recruitment of neuronal subpopulations into a coherent distributed functional network, rather than to some phasic shift of attention to a particular stage of stimulus processing.

Figure 8 summarizes the relative timing and apparent task correlates of the subsecond and multisecond attentional processes identified by analysis of both EPs and EEG during these tasks. Sustained attention to all the component mental operations required to perform the continuous tasks is reflected in tonic enhancement of the frontal midline theta rhythm. Phasic engagement of dorsolateral frontal cortex during the scanning and updating of representations in working memory might be reflected in the enhancement of the P305 and P450 EP components. Although it has been argued (e.g. Klimesch *et al.*, 1994) that there is a close relationship between enhancement of the theta rhythm and late positive components of the EP, these topographical differences between the theta band response and the transient EPs suggest that they are distinct phenomena. In contrast, sustained attention to the stimulus objects being retained in working memory appears to be reflected both in the posterior slow wave enhancement revealed by the EP analysis, and the tonic, largely posterior, reduction in alpha power in the difficult task conditions that are revealed by the EEG analysis. Together these results provide evidence that attention is

associated with a variety of processes that have distinct time courses in distinct neuronal populations.

Notes

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Address correspondence to Alan Gevins, EEG Systems Laboratory and SAM Technology, 101 Spear Street, #204, San Francisco, CA 94105, USA.

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