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Event-related covariances during a bimanual visuomotor task. II. Preparation and feedback ¹

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Summary Event-related covariance (ERC) patterns were computed from pre-stimulus and feedback intervals of a bimanual, visuomotor judgment task performed by 7 right-handed men. Late contingent negative variation (CNV) ERC patterns that preceded subsequently accurate right- or left-hand responses differed from patterns that preceded subsequently inaccurate responses. Recordings from electrodes placed at left frontal, midline antero-central, and appropriately contralateral central and parietal sites were prominent in ERC patterns of subsequently accurate performances. This suggests that a distributed cortical 'preparatory network,' composed of distinct cognitive, integrative motor, somesthetic, and motor components, is essential for accurate visuomotor performance.

ERC patterns related to feedback about accurate and inaccurate responses were similar to each other in the interval immediately after feedback onset, but began to differ in an interval spanning an early P300 peak. The difference became even greater in an interval spanning a late P300 peak. For both early and late P300 peaks, ERC patterns following feedback about inaccurate performance involved more frontal sites than did those following feedback about accurate performance.

Together with the stimulus- and response-locked results presented in part I, results of this study on the preparatory and feedback periods suggest that ERCs show salient features of the rapidly shifting, functional cortical networks that are responsible for simple cognitive tasks. ERCs thus provide a new perspective on information processing in the human brain in relation to behavior — a perspective that supplements conventional EEG and ERP procedures.

Key words: Event-related covariances; Event-related potentials; Contingent negative variation; P300; Spatiotemporal mapping; Preparatory networks; Feedback networks; Performance accuracy

As a step towards characterizing the distributed functional cortical networks that underly higher cognitive functions, we have been measuring the spatial synchronization of event-related potentials

(ERPs) (Gevins et al. 1981, 1983, 1985, 1987). In this experiment, we measured the spatial synchronization of ERPs related to preparation, stimulus processing, response execution and feedback about response accuracy during a 4 sec long bimanual visuomotor task. The results reported in part I (Gevins et al. 1989) showed that event-related covariance (ERC) patterns of stimulus processing and response execution correspond to existing models of the spatial and temporal organization of cortical function. The results presented in this second report show that the ERCs of pre-stimulus and feedback intervals are related to the accuracy of performance and are also consistent with recognized neurocognitive models. ERCs provide a new

¹ A part of the preparation results reported here have appeared in abbreviated form in Gevins et al. 1987. In addition to a more complete description of cue-locked ERPs, this paper presents the ERPs and ERCs for the feedback-locked event, and a discussion relating the contingent negative variation (CNV)- and P300-interval results to each other and to other psychophysiological research.

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means of characterizing performance-related aspects of neural processing and thereby open new avenues for understanding the CNV and P300 waves.

Methods

Subjects, task and recordings

Detailed methods of this study were presented in part I and will be reviewed briefly here.

EEGs were recorded from 7 right-handed, healthy male adults while they performed a well-practiced visuomotor task. Each trial of the task began with a cue symbol ('V'), which was slanted to the right or left to indicate with which hand the subject should respond. One second after this cue, a visual stimulus (no. 1–9) appeared. In 'response' trials, the stimulus was slanted in the same direction as the cue. The subject had to respond quickly with the index finger of the indicated hand, by producing a pressure from 0.1 to 0.9 kg linearly related to the stimulus number. In a randomly distributed 20% of the trials, the stimulus was slanted in the direction opposite to the cue. In these 'no-response' catch trials, the subject had to withhold the finger response.

Feedback was presented visually 1 sec after the subject's peak response pressure in response trials. Feedback indicated the actual pressure (to a tenth of a stimulus unit) the subject made. If the response was sufficiently close to the required response (according to a continuously updated tolerance of adaptive error), the feedback number was underlined to indicate a 'win.' The purpose of the adaptive error tolerance was to adjust the margin for winning as performance fluctuated. The error tolerance was computed for each hand separately as a function of performance during the previous 5 trials. Subjects earned a bonus of 5 cents for each win and were penalized 10 cents for each response to a 'no-response' catch trial. Summaries of performance and the amount of money earned were presented at the end of each block of 17 trials. Together with frequent rest breaks, these procedures were intended to help subjects remain alert during the 5–7 h recording session.

Using visual editing, we discarded trials that contained physiological or instrumental artifact, slow, hesitant, or delayed responses, or any sign of EMG in the non-responding hand or in the cue-to-stimulus epoch in the responding hand.

Performance accuracy

In order to identify neuroelectric patterns associated with preparation and quality of performance, each subject's trials were sorted according to hand and response accuracy. 'Accurate' and 'inaccurate' data sets contained trials in which the response error (deviation from required finger pressure) was less or greater, respectively, than the mean error calculated over each subject's entire recording session. Accurate and inaccurate trials were distributed uniformly across the session and, therefore, did not differ because of learning or possible systematic shifts in arousal across the session.

Trials were also sorted according to hand and accuracy during feedback-locked intervals. Behavioral variables such as response time, pressure, and duration were carefully balanced to eliminate the possibility that differences in post-response activity, unrelated to our neurophysiological hypotheses, might extend to the onset of feedback.

Laplacian derivation wave forms and event-related covariances

Sixteen laplacian derivation (LD) channels were computed from recordings by a total of 26 scalp electrodes. The 16 were the non-peripheral scalp electrodes with adequate sampling of surrounding potential. Enhanced, averaged, event-related, LD time series were formed from sets of trials that contained detectable event-related signals (Gevins et al. 1986). A positive peak in the LD wave form represented the emerging current at the scalp and is referred to as a 'current source.' (This terminology should not be confused with an actual neural source or 'generator.') Since most LD peaks changed polarity across the scalp, all peaks were labeled according to standard ERP terminology (e.g., CNV, P300).

ERCs for each of the 120 pairwise combinations of the 16 non-peripheral channels were computed from the enhanced, filtered, 7-person aver-

aged LD wave forms (see part I). A delta (0.1–3 Hz) bandpass filter and a covariance interval width of 375 msec were used to emphasize the low-frequency, late post-cue CNV component of the LD wave form. A theta (4–7 Hz) bandpass filter and a 187 msec wide covariance interval were used to analyze the post-feedback LD components. Measuring the covariance between narrow bandpass-filtered wave forms was equivalent, in principle, to computing the magnitude of the cross-spectrum in the frequency domain. However, working in the time domain made it easier to derive the optimal trade-offs between time and frequency resolution in our data. Working in the time domain also made computations efficient, since we could calculate only over the band of interest, and not over the entire spectrum.

All ERCs with significance of $P < 0.05$ were displayed for pre-stimulus CNV intervals. Time delays could not be computed for the CNV, because an interval wide enough to allow an adequate estimate of the delay would have included components related to processing of the cue and would thus have not related solely to the CNV. ERCs within 2 S.D.s of the maximum ERC value were displayed for the feedback intervals, because of the many highly significant ERCs. As described in part I, ERC patterns were compared for differences in magnitude by the Student's t test, and for differences in pattern by the 'bootstrap' correlation method (Efron 1982).

We used pattern classification procedures to determine how well the pre-stimulus ERCs could predict the subsequent performance accuracy, and to assess differences between subjects. A non-linear, 2-layered 'neural network' pattern classification algorithm (Viglione 1970; Gevins 1980) classified each trial for subsequent performance accuracy by forming weighted combinations of the pre-stimulus ERCs. Classification equations that consisted of weighted combinations of the decisions of discriminant functions were computed using a recursive procedure. The discriminant functions themselves consisted of weighted combinations of a subset of the ERCs shown in Fig. 2. We validated this procedure by classifying the trials of each subject by equations developed on the trials of the other 6 subjects. We used a

binomial distribution to determine the significance of the average of the 7 validations. A more detailed discussion of the application of pattern classification procedures to neuroelectric signals can be found in Gevins (1980, 1987) and Gevins and Morgan (1986, 1988).

Results

Behavioral analysis

For accurate trials, the mean deviation of response pressure from the required pressure was 0.035 ± 0.020 kg for the right hand, and 0.039 ± 0.020 kg for the left hand. The comparable values for inaccurate performance were 0.162 ± 0.066 kg for the right hand and 0.166 ± 0.076 kg for the left hand. Mean reaction times for the 4 performance conditions in the final data sets ranged consistently from 610 to 618 msec.

Cue-locked wave forms

Although visual inspection of the pre-stimulus CNV in the 7-person averaged, delta-filtered LD wave forms (Fig. 1) suggested differences in amplitude that were related to condition, such differences were not statistically significant. The mean squared amplitude (over channels) of the CNV wave form, thought to be related to preparatory set (Walter 1967; reviewed in Tecce 1972), was measured for 375 msec wide intervals (corresponding to covariance analysis intervals) under subsequently accurate and inaccurate, right- and left-hand conditions. In the interval centered at 687 msec post cue (covering the late peak of the CNV), the amplitudes of the CNV wave form for subsequently accurate and inaccurate performances did not differ significantly for either hand. The similarity of the late CNV amplitudes was also confirmed by the bootstrap correlation procedure. When we compared the distributions of amplitude of the 687 msec interval of subsequently accurate and inaccurate trials, the correlations were 0.84 ± 0.16 for right-hand trials and 0.83 ± 0.14 for left-hand trials. Thus, the late CNVs under conditions of accurate and inaccurate performance did not differ either in magnitude or in spatial pattern.

CUE TO PREPARE FOR AN INDEX FINGER RESPONSE

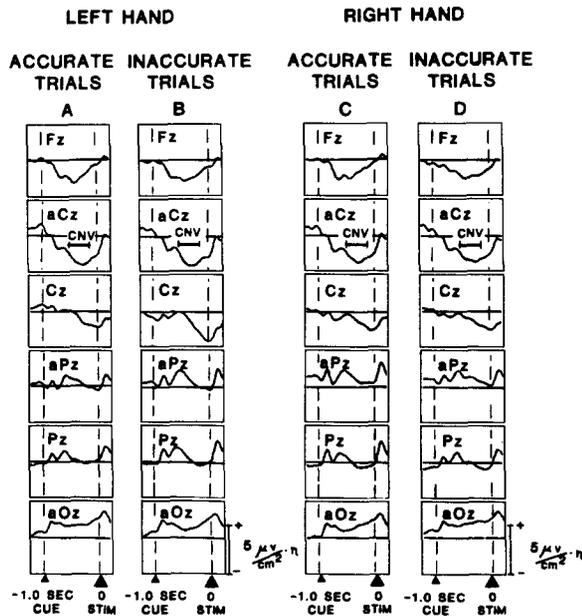


Fig. 1. Laplacian derivation (LD) wave forms from midline electrode sites, showing the contingent negative variation (CNV), and the event-related covariance (ERC) analysis interval centered at 687 msec post-cue in the cue-to-stimulus period. The mean late CNV amplitudes, from low-pass filtered (below 3 Hz) averages of 7 subjects, are not significantly different for the comparison of left-accurate (A) with left-inaccurate (B) conditions, or right-accurate (C) with right-inaccurate (D) conditions.

In contrast to the non-specific CNV amplitude patterns that were seen across all LD channels, there were differences in the CNV amplitude of the left and right antero-central (motor-related)

TABLE I

Mean absolute amplitude of the laplacian derivation wave form from a 375 msec wide interval centered at 750 msec post cue on the late CNV. The left and right antero-central sites (aC3 and aC4) are thought to overly primary motor areas. The antero-central CNV was larger contralateral to the hand indicated by the slant of the cue preceding accurate and inaccurate performance. The asymmetries that preceded inaccurate performance tended to be larger. Values are expressed in units of $\mu\text{V}/\text{cm}^2$.

Electrodes	Accurate		Inaccurate	
	Right cue	Left cue	Right cue	Left cue
aC3	0.63	0.15	0.83	0.14
aC4	0.18	0.36	0.14	0.50

sites. The results summarized in Table I show that the absolute amplitude of the late CNV, for the 375 msec wide interval centered at 750 msec post cue, was appropriately lateralized to the hemisphere contralateral to the corresponding hand for both accurate and inaccurate performance. For the right hand, the left antero-central amplitude was greater than the right by more than 4:1. For the left hand, the right antero-central was greater than the left by 2:1 or more. If CNV amplitude lateralization is taken as a sign of response preparation, it is surprising that the asymmetries preceding inaccurate performance tended to be larger.

Cue-locked ERCs

ERCs were computed from delta band-filtered, averaged LD wave forms in each of several intervals during the 500 msec preceding the stimulus. Visually distinct and statistically reliable performance-related differences were first clearly apparent in the interval centered 687 msec post cue,

Fig. 2. View of the significant ($P < 0.05$) late CNV ERC patterns (colored lines), superimposed on maps of late CNV amplitude. Both ERCs and CNV amplitude measurements are from an interval 500–875 msec after the cue for subsequently accurate and inaccurate right-hand (A,B) and left-hand (C,D) visuomotor task performance by 7 right-handed subjects. The thickness of an ERC line is proportional to its significance (from 0.05 to 0.005). A violet line indicates that the ERC is positive, while a blue line indicates that the ERC is negative. Because of the short ERC analysis interval, time delays could not be computed for the CNV. The color scale at the left of each picture represents wave amplitude and covers the range from the minimal to maximal values of the 2 maps. ERCs involving left frontal and appropriately contralateral central and parietal electrode sites are prominent in patterns for subsequently accurate performance by both hands. The magnitude and number of ERCs that precede subsequently inaccurate left-hand performance are greater and are more widely distributed compared to the accurate pattern. For the right hand, fewer and weaker ERCs characterize subsequently inaccurate performance. The amplitude maps are very similar for the 4 conditions and do not indicate any of the specific differences evident in the ERC patterns.

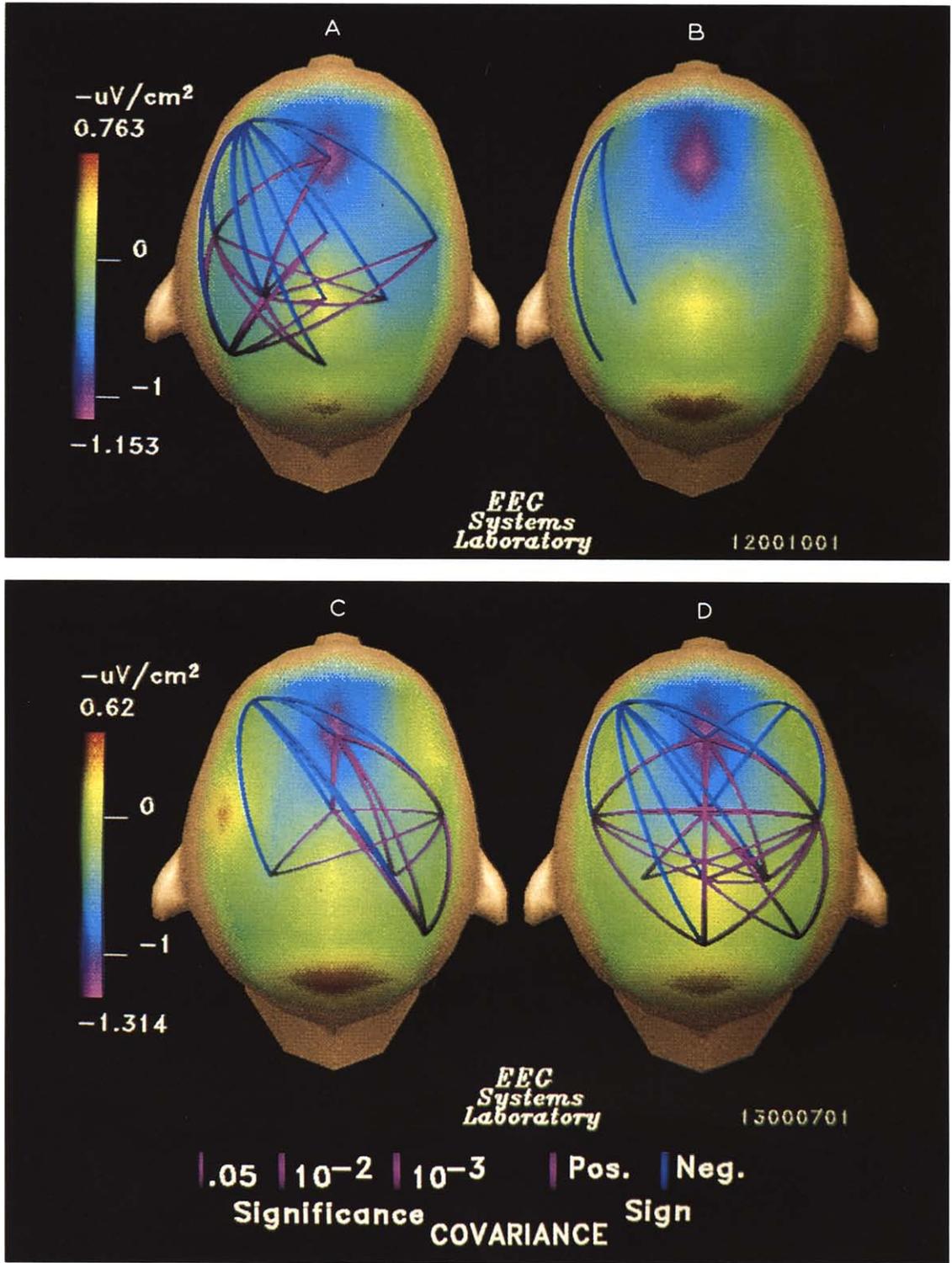


TABLE II

Location of maximum exiting (+) and entering (–) current, and peak latency and amplitude at that site for the 2 P3 waves elicited by feedback in accurate and inaccurate trials. Note that the site of maximum exiting current for accurate performance shifts from midline antero-central (aCz) to midline antero-parietal (aPz) in going from the early peak to the later component. Note also the larger amplitude of the early wave for feedback to accurate performance and the late wave for feedback to inaccurate performance.

Condition	Early P3 ('P3E')			Late P3 ('P3L')		
	Site of maximum	Latency (msec)	Amplitude ($\mu\text{V}/\text{cm}^2$)	Site of maximum	Latency (msec)	Amplitude ($\mu\text{V}/\text{cm}^2$)
<i>Accurate</i>						
Right hand	aCz+	320	4.7	aPz+	461	3.4
	F4–	289	–2.3	F4–	400	–2.0
Left hand	aCz+	328	4.6	aPz+	430	2.9
	F4–	305	–1.9	F4–	500	–1.9
<i>Inaccurate</i>						
Right hand	aCz+	305	3.6	aCz+	460	4.2
	F4–	305	–2.2	F4–	500	–1.4
Left hand	aCz+	328	3.5	aCz+	460	3.8
	F4–	305	–2.2	F4–	500	–2.1

i.e., 313 msec pre stimulus (Fig. 2). These ERC patterns were quite distinct from those related to overt finger response pressures (part I).

During the period between the cue and the stimulus, the averaged event-related muscle potential (right and left EMG) and eye movement (vertical and horizontal EOG) channels were at the noise level and did not differ between conditions. These low levels confirmed that the ERCs were neural in origin and were not associated with overt movements (Fig. 3).

In the 687 msec centered interval, ERCs associated with subsequently accurate right-hand performance involved sites primarily over the left hemisphere (Fig. 2A). All 24 significant ERCs involved left-sided sites and 18 (75%) of these were exclusively left-sided. The most significant ERCs involved left frontal, central, and parietal sites.

The 687 msec centered pattern of subsequently accurate left-hand performance involved a greater proportion of right hemisphere sites than did the accurate right-hand pattern (Fig. 2C). Of 18 significant ERCs, 13 (72%) involved electrode sites over the right hemisphere. There was only 1 left-sided intrahemispheric covariance, between aP1 and F3.

During this same interval, there were only 2 significant ERCs associated with subsequently in-

accurate, right-hand performance, namely left parietal and antero-parietal to left frontal (Fig. 2B). ERCs for subsequently inaccurate left-hand performance (Fig. 2D) were more bilaterally symmetric and complex than those for subsequently accurate left-hand performance.

For right-hand performances, the mean magnitude of event-related covariance in the 687 msec centered interval was significantly larger when performance was subsequently accurate (4.86 ± 0.34) than when it was subsequently inaccurate (3.90 ± 0.41) (Student's $t = 7.7$, $df = 23$, $P < 5 \times 10^{-8}$). By contrast, the mean ERC preceding accurate left-hand performance (4.10 ± 0.68) was smaller than that preceding inaccurate left-hand performance (4.93 ± 0.73) ($t = 5.6$, $df = 38$, $P < 5 \times 10^{-6}$).

We calculated the bootstrap correlation between the distributions of significant ERCs of accurate or inaccurate conditions, to assess the similarity of ERC patterns irrespective of the difference in magnitude. Right-hand, subsequently accurate and inaccurate ERC patterns were correlated at 0.57 ± 0.09 , while the correlation for the left hand was 0.10 ± 0.14 . Thus, accurate and inaccurate preparatory patterns differed in both magnitude and pattern for both hands. The right-hand correlation was quite high (0.57), given that

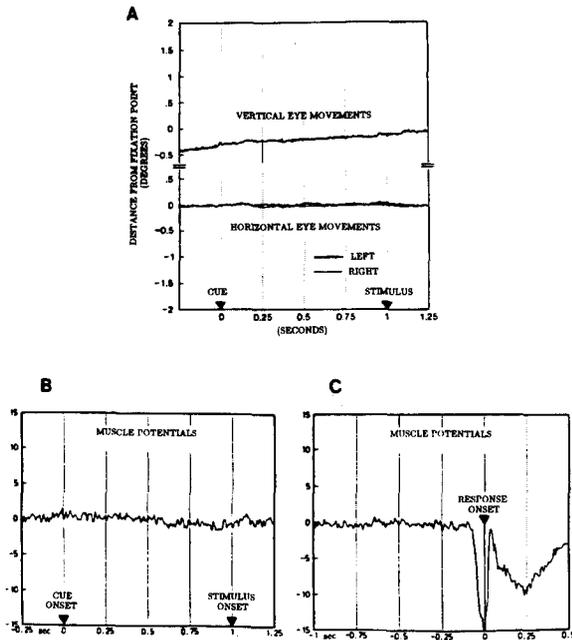


Fig. 3. Averaged vertical and horizontal eye movement signals during the period between the cue and the stimulus for right- and left-hand trials from 7 subjects (A). Averaged muscle potential signals from right flexor digitorum during the cue-to-stimulus epoch (B). Muscle potentials during overt movements were many times larger (C). Averaged muscle potential signals from left flexor digitorum showed the same relation. Since there is no evidence of eye or muscle movements during preparation of either the right- or left-hand, the ERC patterns in Fig. 2 are not the result of overt movements.

there were only 2 significant ERCs in the right inaccurate pattern (Fig. 2B). This indicates that the ordering of the non-significant ERCs in that pattern was roughly similar to that of the accurate pattern, and that the difference in magnitude was the overriding effect.

We used statistical pattern classification of ERCs during the interval between the cue and the stimulus to assess how well the ERCs discriminated subsequent performance on a trial-by-trial basis, and to measure differences between subjects. These results have been described elsewhere (Gevins et al. 1987) and are summarized here.

ERCs from 6 of the subjects were used to discriminate the subsequent accuracy of the remaining subject's performance. This was repeated

7 times. The ERCs shown in Fig. 2 were the variables that we submitted to these discriminations. Using this leave-out-one-person validation, both left- and right-hand overall classifications (57% and 59% respectively) were significant at $P < 0.01$. Six of the 7 subjects had similar patterns for right-hand discriminations, while there were 2 distinct groups for left-hand discriminations. For the subject with the most trials, the single-subject classification was 68% ($P < 0.001$) for subsequent right- and 62% ($P < 0.01$) for subsequent left-hand performance (as determined by 5 leave-out-one-fifth replications). Thus, the subjects' preparatory patterns for both accurate and inaccurate right-hand performances were very similar, while their left-hand patterns distinguished the subjects into 2 groups. More detailed analysis of individual sub-

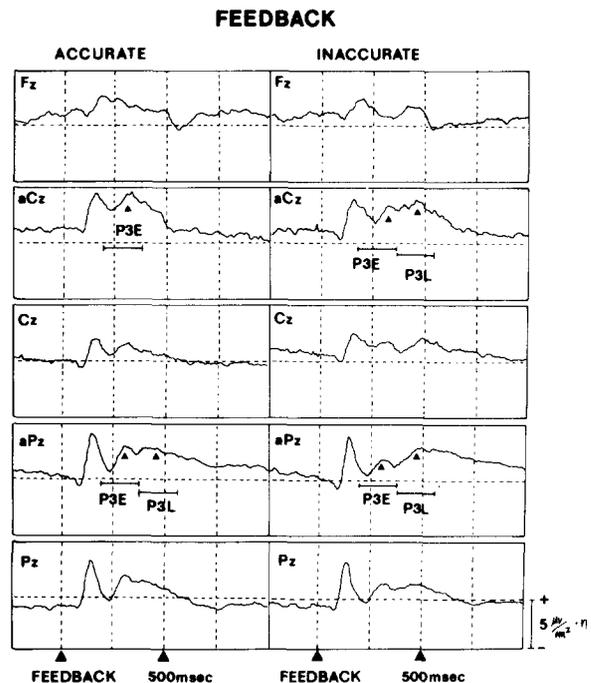
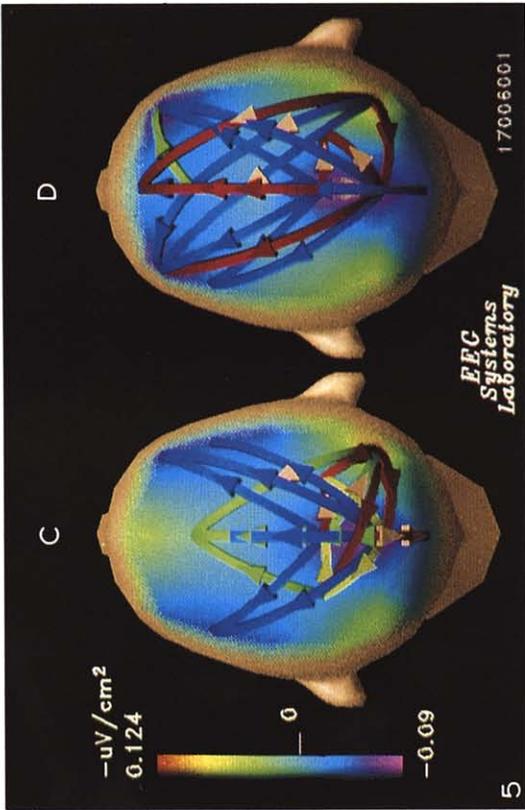
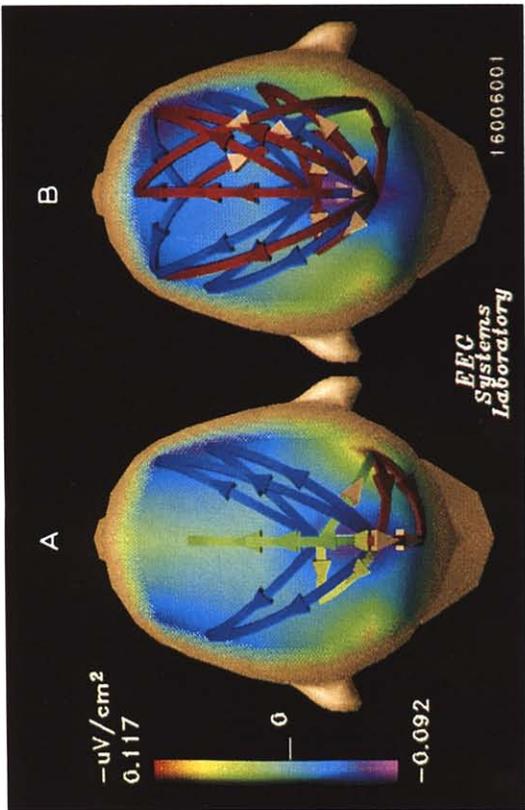
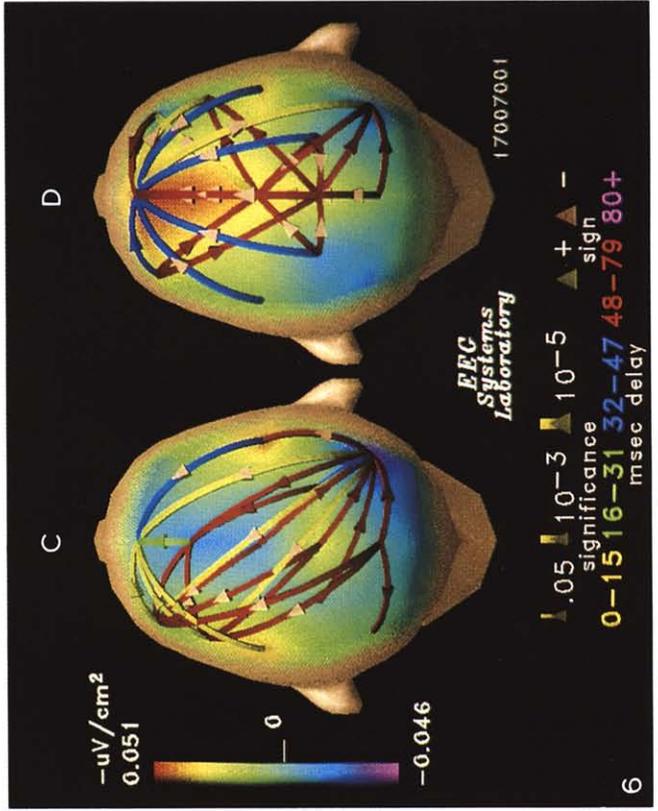
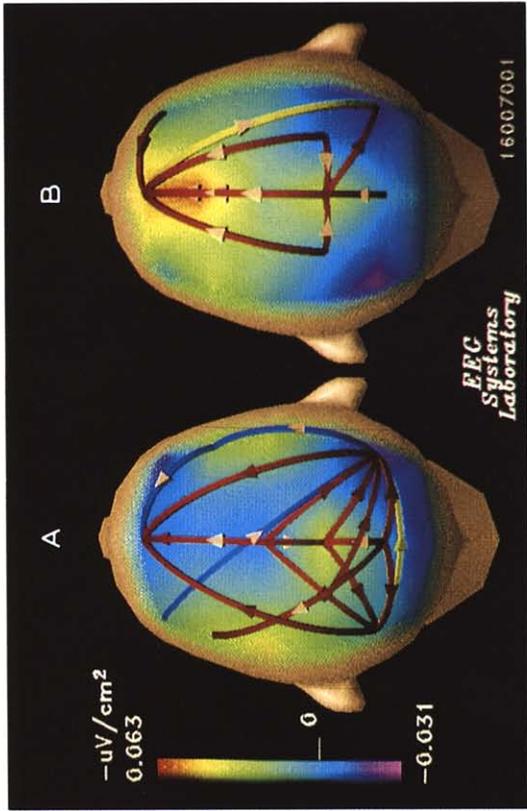


Fig. 4. Feedback-evoked LD wave forms at midline sites for left-hand accurate and inaccurate performance trials, showing early and later, more long-lasting, P3E waves. The early P3 (P3E) is larger for feedback about accurate than for feedback about inaccurate performance, while the later P3 (P3L) is larger for feedback about inaccurate performance. Both components can be seen clearly at some sites, including aPz. This demonstrates that there are in fact 2 separate components and not a single P3 whose latency is shifted at different sites.



ject data will be presented elsewhere (Gevins et al. in prep.).

Feedback-locked wave forms

The 7-person averaged, unfiltered LD wave forms (Fig. 4) contained early peaks before 200 msec after the feedback. They corresponded to N1 and P2 and were similar to those seen in the stimulus event (see part I). A small peak, corresponding to the N2 wave, was distinguishable at about 250 msec, with entering current at the midline antero-occipital site and exiting current at the lateral parietal sites (not shown).

Two closely overlapping late LD peaks, corresponding to positive potentials, had differing topographies in the different experimental conditions. Theta band filtering accentuated the condition-specific differences of these wave forms by removing the delta band portion of the wave form. Table II shows the sites of the maxima for current sources and sinks of the positive peaks during feedback about accurate and inaccurate right- and left-hand performances.

There was a robust early 'P3E' peak at 281–328 msec during feedback about accurate performance, with emerging current at all midline sites and lateral parietal sites (maximal at the midline antero-central site), and entering current at lateral frontal sites (maximal at the right frontal site). The later, wider 'P3L' peak at 430–500 msec had its maximal current source at the midline antero-parietal site, and its maximal sink at the right frontal site. The amplitude of the P3E peak was larger than that of the later P3L.

Feedback about inaccurate performance was also characterized by 2 peaks that occurred between 300 and 600 msec. The P3E peak, at 305–328 msec, was similar in topography to that of the accurate performance, but had a lower overall amplitude. The later P3L, at 460–600 msec, was larger than that of the accurate performance. The site of maximal exiting current for the P3L was more anterior, at the midline antero-central site, and its amplitude was larger than the amplitude of the P3E.

For both accurate and inaccurate performance, peak amplitudes at 500 msec during feedback about right-hand performance were larger at the left central and left antero-central sites than at corresponding sites of the right hemisphere. Similarly, amplitudes at 500 msec for feedback about left-hand performance were larger at the right antero-central site for accurate performance, and larger at the right central site for inaccurate performance.

Feedback-locked ERCs

In the interval spanning the early 'exogenous' N1 and P2 feedback peaks, ERCs from theta band-filtered, averaged LD wave forms did not differ according to accuracy of each hand and resembled the early stimulus-locked patterns shown in part I.

Differences between accurate and inaccurate conditions began to emerge in the interval centered at 281 msec that spanned the early P3 peak (P3E). When the ERC patterns for feedback to accurate and inaccurate performance were compared, the

Fig. 5. Most significant (top 2 S.D.s; within 2 S.D.s of largest value) early P3 (P3E) feedback ERC patterns for feedback about accurate and inaccurate performance by the right hand (A and B) and left hand (C and D). ERC patterns are superimposed on color maps of wave amplitude. The thickness of an ERC line is proportional to the negative log of its significance (from 0.05 to 0.00005). The color scale at the left of each picture represents wave amplitude and covers the range from the minimal to maximal values of the 2 maps. Both the ERCs and amplitude maps are derived from a 187 msec wide interval, centered at 281 msec after the onset of feedback, on theta band-filtered wave forms averaged over all 7 subjects. A major difference between accurate and inaccurate patterns is that the left and midline frontal sites are only involved in the inaccurate patterns. The involvement of these sites may reflect the fact that greater processing is required after inaccurate performance, in order to improve subsequent performance.

Fig. 6. Most significant (top 2 S.D.s) late P3 ERC patterns for feedback to accurate and inaccurate performance by the right hand (A and B) and left hand (C and D). Both the ERCs and amplitude maps are derived from a 187 msec wide interval, centered at 468 msec after feedback onset, on theta band-filtered 7-subject averaged wave forms. Involvement of the left parietal site, greater involvement of the right parietal site, and absence of the right frontal site distinguished the accurate patterns from the inaccurate.

bootstrap correlation was 0.36 ± 0.35 for right- and 0.73 ± 0.05 for left-hand performance. The ERC patterns for feedback about accurate performance by the two hands (Fig. 5A and C) were highly similar (bootstrap correlation = 0.91 ± 0.01), and involved midline antero-central, central, antero-parietal, parietal and antero-occipital sites, left antero-parietal and antero-central sites, and right parietal, antero-parietal, antero-central, and frontal sites. These accurate patterns involved many long-delay (32–79 msec) ERCs. The wave forms of the frontal and antero-central sites consistently lagged those of more posterior sites.

The ERC patterns during feedback about inaccurate performance by the left and right hands (Fig. 5B and D) were also very similar (bootstrap correlation = 0.90 ± 0.02). They involved most of the same sites as the accurate patterns, with the striking exception of the left and midline frontal sites. Again, frontal wave forms lagged those of the more posterior sites with which they covaried. There were even more long-delay ERCs than in the accurate patterns.

In the interval centered at 468 msec, spanning the late P3 peak (P3L), the patterns for accurate and inaccurate performance were still very different (bootstrap correlation = -0.38 ± 0.27 for right- and 0.13 ± 0.08 for left-hand performance). The patterns during feedback about right- and left-hand accurate performance had many sites in common (e.g., midline parietal, antero-parietal, central, antero-central, and frontal sites, bilateral parietal sites, and left antero-central and frontal sites), although they were less similar than in the early P3 interval (bootstrap correlation = 0.58 ± 0.06) (Fig. 6A and C). The absence of the right frontal site from these patterns was conspicuous, considering its prominence in the accurate patterns from the early P3 interval. The inaccurate patterns were also less similar than in the early P3 interval (bootstrap correlation = 0.77 ± 0.04). They differed from the accurate ones, particularly in that the right frontal site was involved, the left parietal site was absent, and the right parietal site was less involved (Fig. 6B and D).

Feedback patterns about left-hand accurate and inaccurate performance had more ERCs than did patterns during feedback about right-hand perfor-

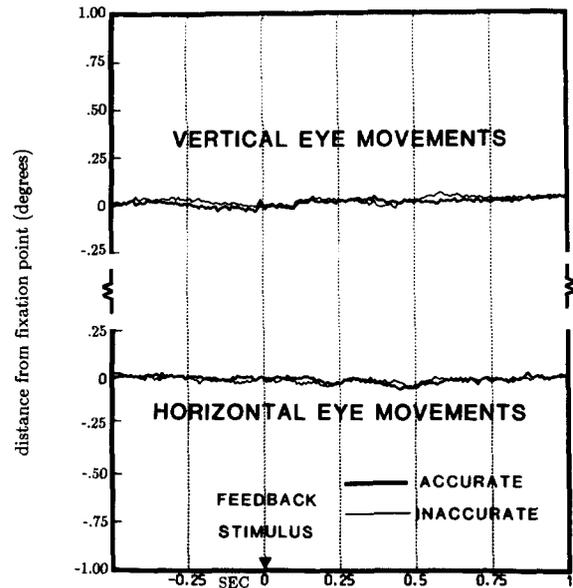


Fig. 7. Averaged vertical and horizontal eye movement signals from 7 subjects during feedback about accurate and inaccurate left-hand performance.

mance. As was the case during the P3E interval, the similarity of P3L ERC patterns between the 2 hands, regardless of performance accuracy, was greater than between accurate and inaccurate patterns for either hand. This implies that the feedback ERC patterns in both intervals were related more to performance accuracy than to the hand used.

Vertical and horizontal EOG channels were at the noise level for all conditions of accuracy and handedness (Fig. 7).

Discussion

Although the event-related preparatory and feedback covariance patterns reported here appear to represent signs of 'functional coordination' between nodes within a cooperative cortical network, we must again caution that such an interpretation is speculative until the generators of these patterns are determined. With this in mind, we offer the following comments on the results of this study.

Preparation

The prominence of the left frontal site in our preparatory patterns prior to actual response ex-

ecution by either hand is consistent with clinical evidence that prefrontal cortical areas are involved in the synthesis of preparatory sets (Luria 1966), and that the left dorsolateral prefrontal cortex is specifically involved in cued delayed response tasks (Jacobsen 1935; Pribram et al. 1977; Shallice 1982; Fuster 1984). Similarly, the prominence of the midline central and antero-central sites suggests the presence of an integrative motor component. The involvement of these sites in the preparatory patterns is consistent with clinical evidence for involvement of the premotor and supplementary motor regions when existing motor schemes are initiated, or when new ones are established (Penfield and Jasper 1959; Goldman-Rakic 1984; Milner and Petrides 1984; Goldberg 1985; Stuss and Benson 1986). The integrative motor component, strong in the pattern preceding accurate left-hand performance and weaker in the pattern preceding accurate right-hand performance, may indicate that a greater degree of motor control is necessary when strongly right-handed subjects execute a fine motor response with their left hands. The existences of appropriately lateralized somesthetic and motor preparatory components are supported by experimental evidence for distinct firing patterns of neurons in the motor and premotor cortices preceding motor responses in non-human primates (Evarts et al. 1984). The difference between ERC patterns corresponding to preparation and to actual response execution (see part I) suggests that they reflect different organizations of neural activity.

The detailed spatial organization and interelectrode covariance of the late CNV clearly reveal several anatomically and functionally distinct processes. Although traditional CNV studies have tended to view the CNV as a unitary brain process that reflects anticipation of a response based on the contingency between 2 stimuli (S1 and S2) (Walter 1967; reviewed in Tecce 1972), there has been growing evidence that the CNV is a multi-component process (Ruchkin et al. 1986; Loveless et al. 1987). There has also been some debate as to whether the CNV reflects only motor preparation, or whether there is also a cognitive component related to the expected stimulus (S2) (Gaillard 1977 (reviewed in Gevins and Cutillo 1986);

Rohrbaugh et al. 1980; Ruchkin et al. 1986). As discussed above, the present results support the idea that preparation is a multi-component process that includes not only motor-somesthetic preparation but also cognitive and high-level integrative motor components. Finally, inconsistent results of previous studies that related the CNV to the quality of subsequent performance could be attributed, at least in part, to insufficient spatial sampling and analysis (for recent examples, see Macar and Vitton 1982; Macar and Besson 1986).

Our preparatory findings are consistent with 'continuous flow' models of the temporal organization of human cognition (Erikson and Schultz 1979; Coles et al. 1985). The temporal evolution of the ERC patterns that follow the cue indicates that response preparation begins with evaluation of the cue, well before stimulus presentation. Like previous workers (Rohrbaugh et al. 1976; Coles and Gratton 1986), we found a slightly larger CNV amplitude over motor areas contralateral to the subsequently responding hand. The paper by Coles and Gratton demonstrated that the response is more likely to be made with the correct hand when the CNV is lateralized contralaterally, rather than ipsilaterally, to the hand indicated by the stimulus. The ERC patterns appear to be more sensitive to preparatory set than do amplitude patterns; they clearly distinguished subsequent near-target (accurate) from far-from-target (inaccurate) index finger pressures, both of which were performed with the correct hand.

Feedback

The ERC patterns of both the early and late P3 peaks in the feedback interval appeared to reflect a difference between 'confirming' (following accurate performance) and 'disconfirming' (following inaccurate performance) feedback, with a greater difference for the later peak. In the early interval, the main difference between the confirming and disconfirming patterns was that all frontal sites were involved in disconfirming feedback, whereas the left and midline frontal sites were absent for confirming feedback. For the late peak, the left and midline frontal sites, as well as the left parietal site, became involved in the pattern for confirming feedback, and the right frontal site was no longer

involved. The patterns from the late interval for disconfirming feedback were quite different from those of the early interval, although the changes were different for the 2 hands.

ERC patterns for P3 peaks that followed disconfirming feedback involved more frontal sites than did patterns that followed confirming feedback. We would expect a greater resetting of performance-related neural systems following disconfirming feedback, as well as a strong frontal involvement, given the importance of the frontal lobes for the integration of sensory and motor activities (Fuster 1984; Stuss and Benson 1986). The difference between right- and left-hand patterns was greater for the late than for the early peak, with both left-hand patterns having a greater number of ERCs than the right-hand patterns. This suggests that in the right-handed subjects of this study, resetting these systems after left-hand performance required more processing during the late peak.

Prior experiments dealing with feedback-evoked potentials have shown differences in P3 latency between confirming and disconfirming feedback to auditory stimuli, with confirming feedback eliciting a short-latency P3, and disconfirming feedback eliciting a long-latency P3 (Squires et al. 1973). The latency of our early P3, however, did not vary with feedback conditions as it did in previous studies, and our late P3 for disconfirming feedback was delayed only about 30 msec. Rather, the late P3 LD peak at the site of maximum exiting current was larger than the early P3 peak during feedback about inaccurate responses, but was smaller during feedback about accurate responses (Fig. 4). The major difference between confirming and disconfirming feedback wave forms in our study, therefore, was related to the relative amplitudes of the early and late P3 peaks, rather than to their latency.

The P3 peaks in our data relate to late positive waves reported in other studies on feedback about accuracy. From studies of time estimation, Johnson and Donchin (1978, 1985) concluded that the early P3 is associated with the identification and classification of the feedback, while the later P3 is associated with the utilization of feedback information in the reinforcement or revision of the

response (time estimate). In other studies, particularly those in which monetary bonuses served as an incentive for good performance (e.g., Poon et al. 1974; Steinhauer 1981), the second positive wave was attributed in part to additional processing (such as assessing current assets), once the nature of the feedback has been determined. Likewise, Stuss and Picton (1978) suggested that serial processing, i.e., recognizing the meaning of a feedback stimulus, followed by using that information, is reflected in a P3 component followed by a long-latency, broad duration, later component (which they termed 'P4'). The increasing divergence over time of confirming and disconfirming feedback ERC patterns is consistent with the general conclusion of these researchers that the second late positive wave is related to utilization of information extracted from the feedback stimulus.

Conclusion

Using modern recording and signal processing technologies, we have attempted to improve the spatial, temporal, and neurocognitive specificity of earlier studies. In the spatial domain, we increased the number of channels recorded simultaneously and reduced volume conduction blurring. Even with these advancements, the specificity of the results suggests that a further increase in spatial sampling will be beneficial. In the temporal domain, we measured shifts on the order of tens of milliseconds between event-related peaks of different channels. Since the analysis was restricted to specific frequency bands, there is a wealth of data in other frequency regions and their accompanying time intervals, that has yet to be explored.

We have isolated specific cognitive processes related to different events in the 4 sec trial, using highly controlled tasks. The time evolution of ERC patterns over the course of the whole 4 sec trial should provide deeper insight into the neurocognitive processing involved. In light of the striking findings reported here and in part I, determining the generators of scalp-recorded event-related covariance patterns is the next essential step in characterizing the dynamic functional cortical networks that underly cognition and behavior.

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