Spatio-Temporal Cortical Patterns Evoked in Monkeys by a Discrimination Task

Don Krieger and Robert J. Sclabassi
University of Pittsburgh

Richard Coppola and Richard Nakamura
National Institute of Mental Health

Abstract

■ The primary experimental objective of this work was to demonstrate localization and temporal sequencing of the functional steps carried out by nonhuman primate subjects during performance of a sensory discrimination task, i.e., to identify the locale and sequence of activation of regions that participate in sensory discrimination, stimulus classification, and response preparation. Multivariate statistical procedures were applied to evoked transcortical recordings to identify the location and order of occurrence of signals that are effective in discriminating task conditions and parameters. (1) Sensory discrimination, (2) stimulus classification, and (3) response preparation occurred in the expected sequence. Information that enabled discrimination using these procedures was distributed widely across the cortex; however, the maximum information content was localized to striate and prestriate cortex, anterior inferior parietal cortex, and temporal and premotor cortex, respectively. This work provides a perspective on brain mechanisms responsible for cognition and demonstrates a set of powerful multivariate analytic tools for functional mapping, i.e., identifying the location and sequencing of cognitive functions. ■

INTRODUCTION

Psychologists have depended on reaction time experiments with complex task manipulations and timing analysis to examine the sequence of functional steps that were used by human subjects. Beginning with the work of Donders at the end of the last century, a wide range of performance and discrimination tasks have been studied with methods designed to test hypotheses about such sequences. In most such studies, the predictor variable on which inferences are drawn has been reaction time (Posner, 1978; Woestenburg, Verbaten, Van Hees, & Slangen, 1983a). However in the last two decades neuroscientists have added neurophysiological measurements to reaction time in an effort to bring biological insight to bear on questions involving the nature of brain function and the details of its role in mediating behavior (Donchin, 1979; Gevins, 1986; Hillyard & Picton, 1987; John, 1980; Squires & Donchin, 1976).

The overall goal of the work reported here is to elucidate the information processing activities in which the brain is engaged during cognitive task performance. The technical approach is one in which a visual discrimination task is presented with simultaneous bipolar recording of electrophysiological signals from widely spaced cortical locations. Features are extracted from the raw data to produce a multivariate characterization for each trial. Stepwise linear discriminant analysis is applied to these characterizations to identify those variables that are relevant to the steps of information processing; those variables may be directly interpreted in terms of cortical localization. Strict separation of training and test data sets produces very strong statistical findings with consequent confidence in inferences drawn on the results.

Two types of questions regarding cortical mediation of the steps of information processing are addressed by the results:

1. **Temporal Sequencing.** At what time following stimulus presentation do stimulus discrimination, stimulus classification, and response preparation occur?
2. **Localization.** At what cortical locations is the information that is useful in carrying out these steps identifiable in the activity of the tissue?

This work represents a fusion of approaches. It uses the power of the task manipulations used in reaction time paradigms along with the power of detailed single

trial neurophysiological analysis. An automatic algorithm is used to make single trial measurements rather than manual scoring (Kutas, McCarthy, & Donchin, 1977; Ritter, Simson, & Vaughan, 1972) and the algorithms are applied in the time rather than in the frequency domain (Basar, 1980; Woestenburg, Verbaten, & Slangen, 1983b). The techniques are applied to multiple sites recorded simultaneously rather than to a single channel (Krieger & Dillbeck, 1987; Optican & Richmond, 1987; Richmond & Optican, 1987; Skarda & Freeman, 1987), thereby enabling localization.

Recordings were obtained from 16 bipolar placements at a time from the striate, prestriate, parietal, temporal, motor, premotor, and frontal cortical convexity of chronically implanted rhesus monkeys. For each electrode pair, one wire rested on the cortical surface; the other penetrated 2.5 mm below. The electrode montages are shown in Figure 5. The use of bipolar recordings from pairs of wires 2 mm apart (each wire has a 0.5-mm tip exposure) produces highly localized recordings and virtually eliminates contamination by muscle activity (Nakamura, Coppola, & Mirsky, 1984; Nakamura, Juhannesen, & Mirsky, 1985).

Animals were trained prior to electrode placement to perform a visual GO/NOGO discrimination task with reversals. The stimulus set consisted of four stimuli of four dots each (Fig. 5). As shown in the figure, two of the patterns form diagonal lines; the other two form diagonal diamonds. The monkey's task was to release a lever in response to two of the stimulus types (e.g., GO to the diagonals) and not to the other two (e.g., NOGO to the diamonds). All stimulus types were presented with equal probability. The monkey was water deprived to motivate good performance; with a correct response on each GO trial, he received a squirt of water. Amplifier bandpass was set at 1.0 and 100.0 Hz and the recordings were digitized at 200 Hz/channel. Task timing is illustrated in Figure 1 and is detailed in the Experimental Protocol section.

RESULTS

Single Trial Feature Measurement

Averaged evoked potentials (AEPs) are shown in Figure 2. Each trace is the average across all the trials from a session ($N \simeq 1000$). The AEPs are consistent across sessions with the most notable exception being for LU, trace G. The AEP for the NOGO trials (not shown) shows no such inconsistency. Both the AEP and single trial GO waveforms (not shown) show a high amplitude signal beginning coincident or immediately preceding the response, suggesting a movement-induced electrode artifact. Note that this apparent "electrode pop" does not overlap the time segments used for feature measurement.

Time segments for which features were measured are indicated in Figures 2, 4, and 5 with horizontal bars. Although these segments were selected based on visual inspection of one set of AEPs, they overlap distinctive waveforms in many channels for all three animals. The indicated segments were chosen for this reason and because they occur between stimulus and response; they are 50 msec long and begin 205 and 255 msec following the initiation of data acquisition. Stimulus presentation occurred approximately 120 msec following initiation of data acquisition; the response typically occurred 350–430 msec following initiation of data acquisition. For each trial the data from each channel were demeaned. The amplitude across each 50-msec segment was then averaged to produce a single number, i.e., each number was the average of the 11 observations included in a 50-msec data segment. The 32 averaged amplitudes of the single trial waveform, 2 segments from each of 16 channels, constituted the feature for a single trial.

For each trial, a template matching step was carried out prior to feature measurement. The purpose of this step was to identify shifts in waveform latencies on each trial and thereby obtain more comparable features between trials. The AEP from the data from two sessions in which response contingencies were reversed was computed. The 200-msec segment of this AEP that brackets the 50-msec segments is used as the template, i.e., the template begins at 150 msec after initiation of data acquisition and ends at 350 msec. This AEP segment was then used as the template for all single trials from those two sessions. The multivariate cross-correlation between the template and the single trial was computed for 20 lags. The lag for which the cross-correlation was maximum was taken as the temporal shift in the single trial data compared with the template. The single trial amplitudes in the shifted time segments were then recorded as the feature.

Histograms of the time segment shifts are shown in Figure 3. These are consistent both across sessions and across animals. For readily identifiable single trial peaks, such a histogram would be expected to be peaked about lag zero; for data with low signal/noise, the histogram would be expected to show no peak. The histograms are highly peaked at lag zero, consistent with the high amplitude signals evident in the averaged responses shown in Figure 2. This suggests that there was high measurement accuracy for single trial features by the template matching used here.

Spatial Pattern Identification

Spatial pattern identification was carried out by statistically testing for the ability of single trial features to discriminate between stimulus type (four patterns as shown in Fig. 5), stimulus orientation (leaning left/leaning right), stimulus class (diagonal/diamond), and response type (GO/NOGO). Within a single session the imperative (GO) and nonimperative (NOGO) stimuli are always the

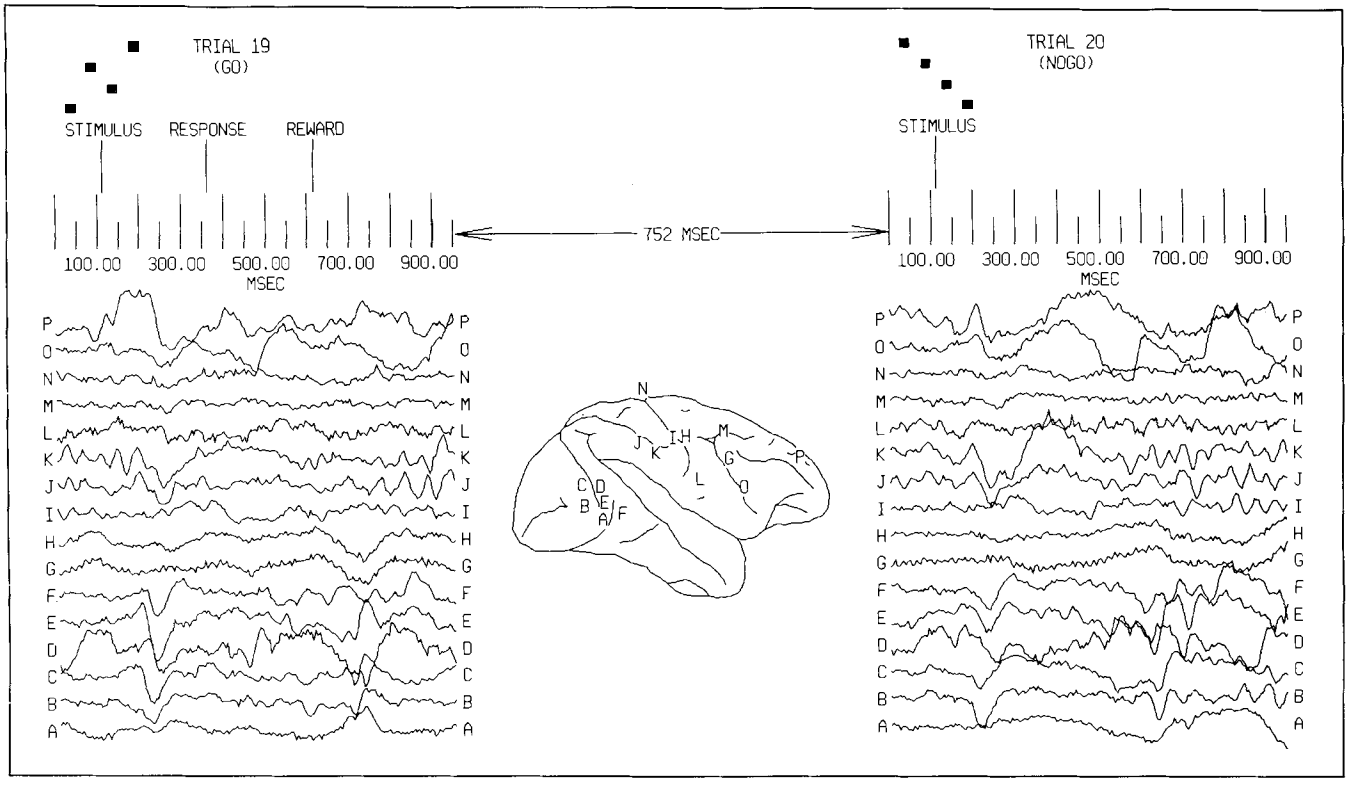

Figure 1. Trial presentation temporal sequence. This figure shows a sequence of two trials with time scales, the raw data that were collected, the stimuli that were presented, and markers indicating the temporal occurrence of the task relevant events. Each trial consists of a 950-msec period during which data are acquired at 200 Hz on each of 16 recording channels. The stimulus is presented approximately 120 msec after the beginning of data acquisition. For GO trials on which the correct response occurs within 500 msec following stimulus presentation, the reward is presented exactly 500 msec poststimulus. Intertrial intervals vary randomly between 0.5 and 1.25 sec.

same. The data were pooled from two sessions in which the response contingency was reversed, i.e., in one session a diagonal signaled a GO trial, and in the other session a diamond signaled a GO trial. This combined data set construction enables analysis of stimulus class while controlling for response type and vice versa. Note that experimental design does not permit separation of GO/NOGO and REWARD/NOREWARD effects, since a reward was presented only on GO trials. Each combination data set consisted of features from each of approximately 1980 single trials. Two such data sets were analyzed from one animal, GE, and one each from each of two others, TI and LU.

Each single trial feature constitutes a spatiotemporal pattern of intensity. Using a pseudorandom number generator, the pattern from each trial was assigned to either the training or test subset. The training subset was used to develop linear discriminant functions (BMDP7M, 1985) which were optimal in performing the classification. BMDP7M uses a stepwise algorithm that includes only those variables with F-to-include greater than a set threshold; in this case the default 4.0 was used. Thus all channels with F less than this threshold were discarded. These discriminant functions were used to classify patterns from the subset, i.e., patterns that were developed from one subset were tested on a different subset. Using the χ^2 statistic, the number of patterns classified correctly from the test subset was compared with the number that would be expected to be classified correctly by chance. For results which were significant ($p < 10^{-4}$), a second χ^2 test was performed to determine if equal accuracy was achieved across classification groups. Results were rejected which were significant on this test ($p < .05$), i.e., unequal classification accuracy. This combination of steps, reiterated in the list below, was taken to produce highly conservative statistical results and thereby provide maximum confidence in inferences drawn on the results.

1. Single trial measurements were randomly assigned to training and test subsets rather than using the less rigorous "jackknife" technique.
2. A non-parametric and consequently "weak" statistic was used, i.e., χ^2.
3. To test for the significance of classification accuracy, a conservative cutoff p value was chosen: 10^{-4}.
4. A second test was introduced to test for equal classification accuracy, providing an additional criterion for obtaining an acceptable result. Here also a conservative cutoff p value was chosen: .05. Note that the requirement to pass this test was $p > .05$.

The classification accuracy for stimulus type was significant for all animals and ran as high as 74% (p =

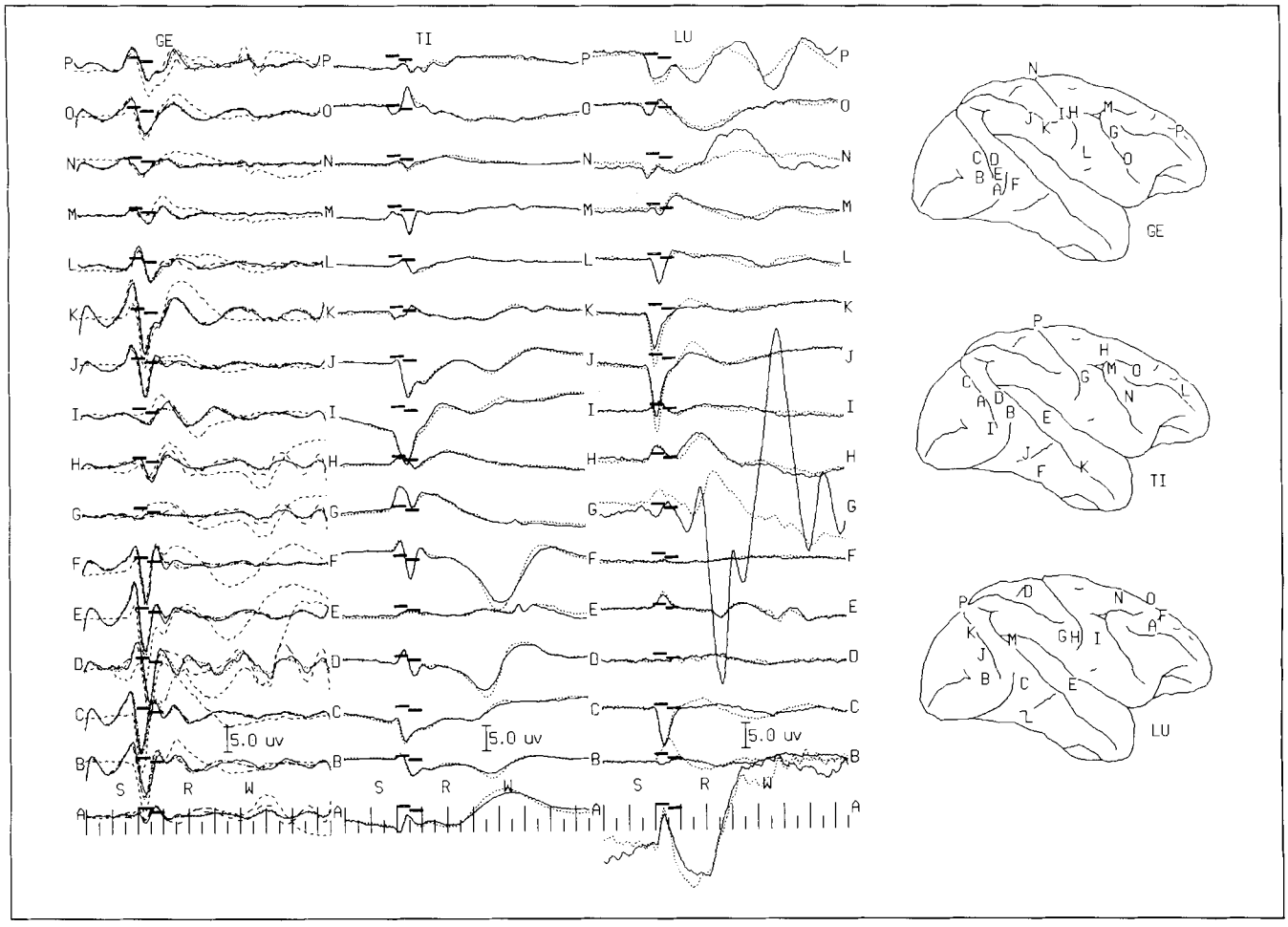

Figure 2. Averaged evoked potentials. Evoked potentials were averaged for each placement over all trials from each of four sessions for GE (column 1), and for each of two sessions for TI (column 2) and LU (column 3). Electrode placements are indicated in the schematic cortical representations with letters corresponding to the rows of traces. At the bottom of each column are timing hash marks (50 msec apart) with letters indicating the stimulus (S), response (R), and reward (W). The horizontal hash marks represent the trace segments used for single trial feature measurement.

10^{-231}). However, the test for unequal classification was failed for all but one data set, probably due to inadequate or at least unequal sampling of primary visual cortex by the electrode montages. We therefore report only the results for stimulus orientation, stimulus class, and response type. These are summarized in Figure 5 for all three animals.

The classification accuracy results are indicated in the figure with percentages. The exact probabilities for getting at least 90, 80, 70, and 60% accuracy in classifying 1000 trials are 6.7×10^{-160}, 8.2×10^{-84}, 8.8×10^{-36}, and 1.4×10^{-9}, respectively. The astronomical p values obtained in this study imply that there is virtually no chance that these results were due to random occurrences. This is likely due to the high signal/noise in the data, the presence of real information relevant to the task present at the cortical placements used, and the large number of single trials included in the analysis.

The bars superimposed on the montages represent the F-to-remove that electrode's contribution to the discrimination result, i.e., the size of the bar is a measure of the importance of the information from that electrode in making the discrimination. In cases where the bar is very large for one electrode compared with all others, e.g., the inferior prestriate lead for TI in the descrimination between stimulus orientations, that electrode is described as "predominant," consistent with the fact that it is information from that placement that is of primary value in making the discrimination.

The horizontal/vertical bars indicate the statistics for the early/late peak height measurements. There are several points worthy of note from this figure.

1. Results from both data sets from GE are similar, indicating that the measures are replicable across many days.

2. The electrode placements that contribute to the discrimination results are consistent with those that would be expected based on current information: stimulus orientation (leaning right/left)—striate and pres-

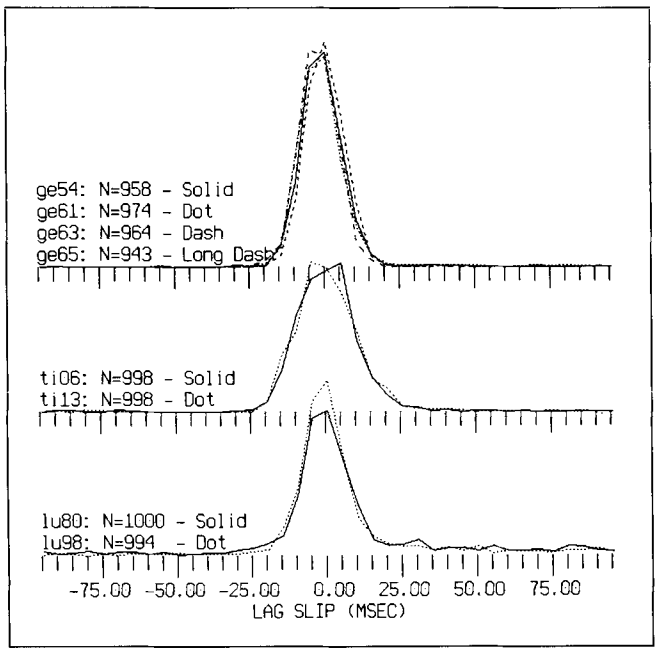

Figure 3. "Fit-slip" histograms from multivariate template matching. The multivariate cross-correlation between the averaged EP was used to measure the "lag slip" for single trial EPs. Lag slip histograms are shown for GE (top), TI (middle), and LU (bottom). All histograms are normalized to the same area.

triate, stimulus class (diagonal/diamond)—anterior inferior parietal and temporal, and response type (GO/NOGO)—premotor, motor, and temporoparietal.

3. Although results for discrimination between classes are significant for all three animals, those for TI (no parietal leads) are weaker than for the others and show no predominant electrode. This contrasts sharply with the results from GE and LU. LU in particular has leads in both temporal and parietal locations, yet it is a parietal location that predominates. To check that this result was not due to the artifact present in this placement (LU's electrode G in Fig. 2), the analysis was repeated with electrode G excluded. Results were very similar but with the predominant electrode now being the neighboring anterior parietal lead (H in Fig. 2).

The results above demonstrate which electrode placements are useful in obtaining the specified classifications. To determine which electrode placements might be critical to each result rather than simply useful, discriminant analyses were run with electrode subgroups suppressed. Subgroups were defined by location as shown along with the results in Figure 6: posterior (striate and prestriate), temporal, parietal, and frontal. When electrodes were suppressed which were primary contributors to discrimination as shown in Figure 5, results were reduced but still significant in almost all cases. This suggests that although it is localized to a certain extent, information sufficient to make the discriminations is distributed widely across the cortex.

For stimulus orientation, the posterior and, to a lesser extent, the parietal subgroups contribute to discrimination. LU's results are less significant than the others, likely because his montage includes no prestriate placements, these being the ones that contributed most for GE and TI as shown in Figure 5. For stimulus class, the parietal subgroup is the primary contributor to discrimination. TI's results are less significant than the others, likely because his montage includes no parietal placements. For response type, the frontal and temporal subgroups are important but not predominant for discrimination.

Temporal Sequencing

To look more closely at the time sequence of discrimination, discriminant analysis was used as the basis for constructing the traces shown in Figure 5. An important result of this manipulation is the collapse of a 32-dimensional characterization into a single variable for temporal sequencing. The steps for obtaining these constructions are detailed as follows and in Figure 4.

Discriminant analysis is applicable to multivariate data for which one wishes to identify linear combinations of the original data (canonical variables) that are effective in classifying cases into groups. In general for N groups $N-1$ canonical variables are required, e.g., one canonical variable is required for classification into two groups. Column 1 of Figure 4 shows sample AEPs from all 16 placements for the two stimulus classes (solid lines—diagonal; dotted lines—diamond). The column of numbers shows the weights generated by the discriminant analysis and used to compute the linear combination (weighted sum) of the AEPs, which is most effective in classifying single trials into groups according to stimulus class. The second column shows these weights applied to the AEPs, i.e., these are the linear combinations. The third column waveform is the algebraic difference of the two waveforms from the second column. The point in time at which this departs from zero (arrow) is the point when discrimination might begin. Note the differences in the solid and dotted waveforms in columns one and two; the AEPs show few differences whereas the weighted sums clearly diverge.

The traces shown in column 2 of Figure 5 are the differences between AEPs projected onto the discriminant functions for all three discrimination results. Note that the discrimination between stimulus orientation (row 1) occurs earliest followed by discrimination between stimulus class (row 2) and finally response type (row 3). This sequence is repeated for all three animals and is consistent with a simple model for visual task performance, viz. stimulus discrimination by visual cortex followed by classification into diagonal/diamond grouping by association cortex followed by motor preparation mediated by temporal and frontal cortex.

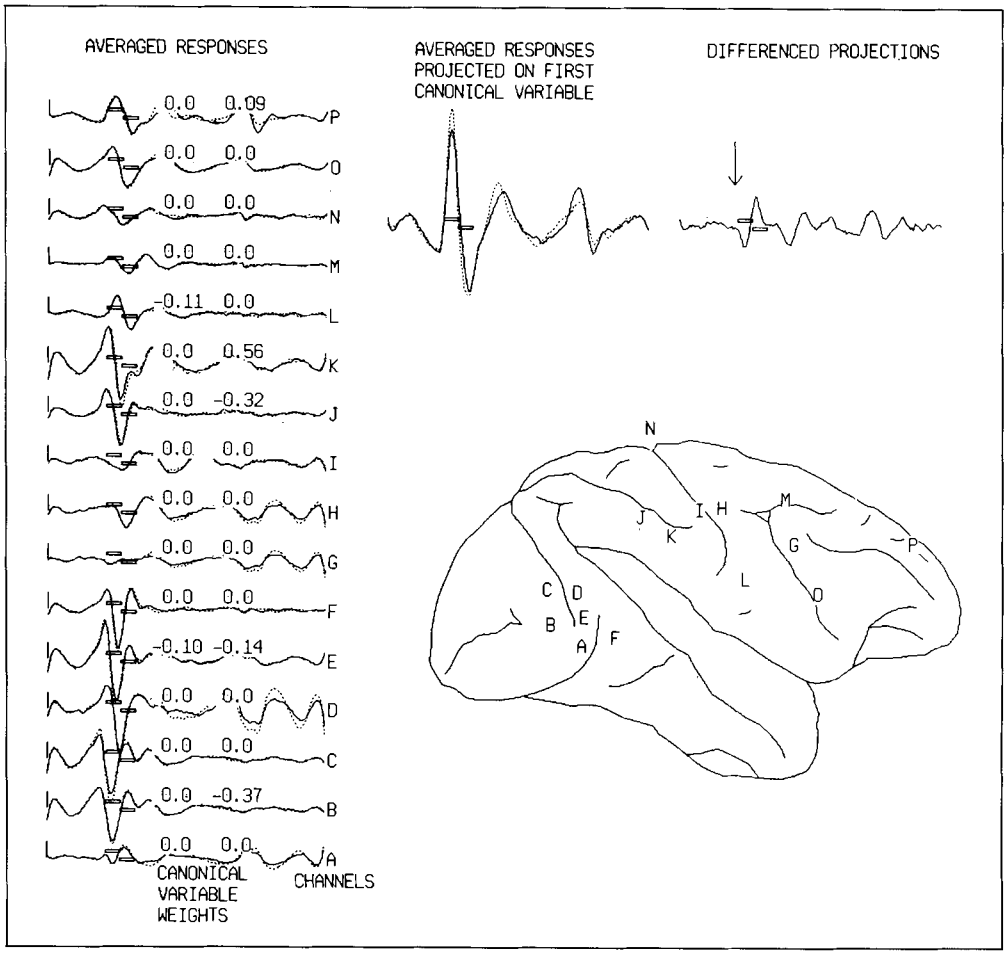

Figure 4. Temporal sequencing procedure. AEPs averaged across two sessions with reversals are shown in column 1. The solid/dotted traces in the first 2 columns represent averages for trials on which diagonals/diamonds were presented. The montage is shown in the cortical schematic. The numbers shown for each channel are weights for the canonical variable, which was identified for classifying trials according to stimulus class. The second column represents the weighted AEPs, i.e., the projections of the AEPs onto the canonical variable. The third column is the algebraic difference between the traces shown in column 2. The arrow indicates the time point at which the discrimination might begin.

DISCUSSION

Temporal Sequencing

Shown below is a simple and plausible sequence of information processing steps required to execute the task studied here:

1. stimulus discrimination (represented by discrimination between stimulus orientations),
2. stimulus classification (represented by discrimination between diagonal and diamond stimuli), and
3. response preparation (represented by discrimination between GO and NOGO trials).

This model is supported by the results shown in Figure 5. The traces there are weighted sums of AEPs; the weights are those identified in the discriminant analyses to be most useful in discriminating between orientations, classes, and responses respectively. The point in time at which a trace diverges from zero is interpreted as the onset of discrimination. It is noteworthy that although the same signal segments were used for all discriminations, nonsynchronous results were obtained by this technique.

For GE, stimulus classification onset follows stimulus discrimination onset by 30–50 msec, which is in turn followed by response preparation onset by about 25 msec (arrows in Fig. 5). For TI, stimulus classification onset follows stimulus discrimination onset by about 30 msec, which is in turn followed by response preparation onset by about 40 msec. For LU, stimulus classification onset follows stimulus discrimination onset by about 50 msec, which is in turn followed by response preparation onset by about 25 msec. Thus not only is the sequence preserved across data sets and animals, but also the interclassification latencies are similar.

This result is an appealing one in that it is consistent with the simple model stated above. The consistency of the sequence across all data sets provides some confidence in its verity. Although trace divergence from zero is fairly sharp and consistent, return to flat, i.e., discrimination offset, is not. One likely cause for this is that it is from the early part of the signal that the discriminant functions were computed; it is therefore the early part of these traces that would be expected to most accurately reflect discrimination. For GO/NOGO discrimination the nonzero trace consistently persists past reward presentation. This is not unexpected since accurate GO trials are always accompanied by a reward whereas accurate NOGO trials are not.

The model that is proposed above and that is sup-

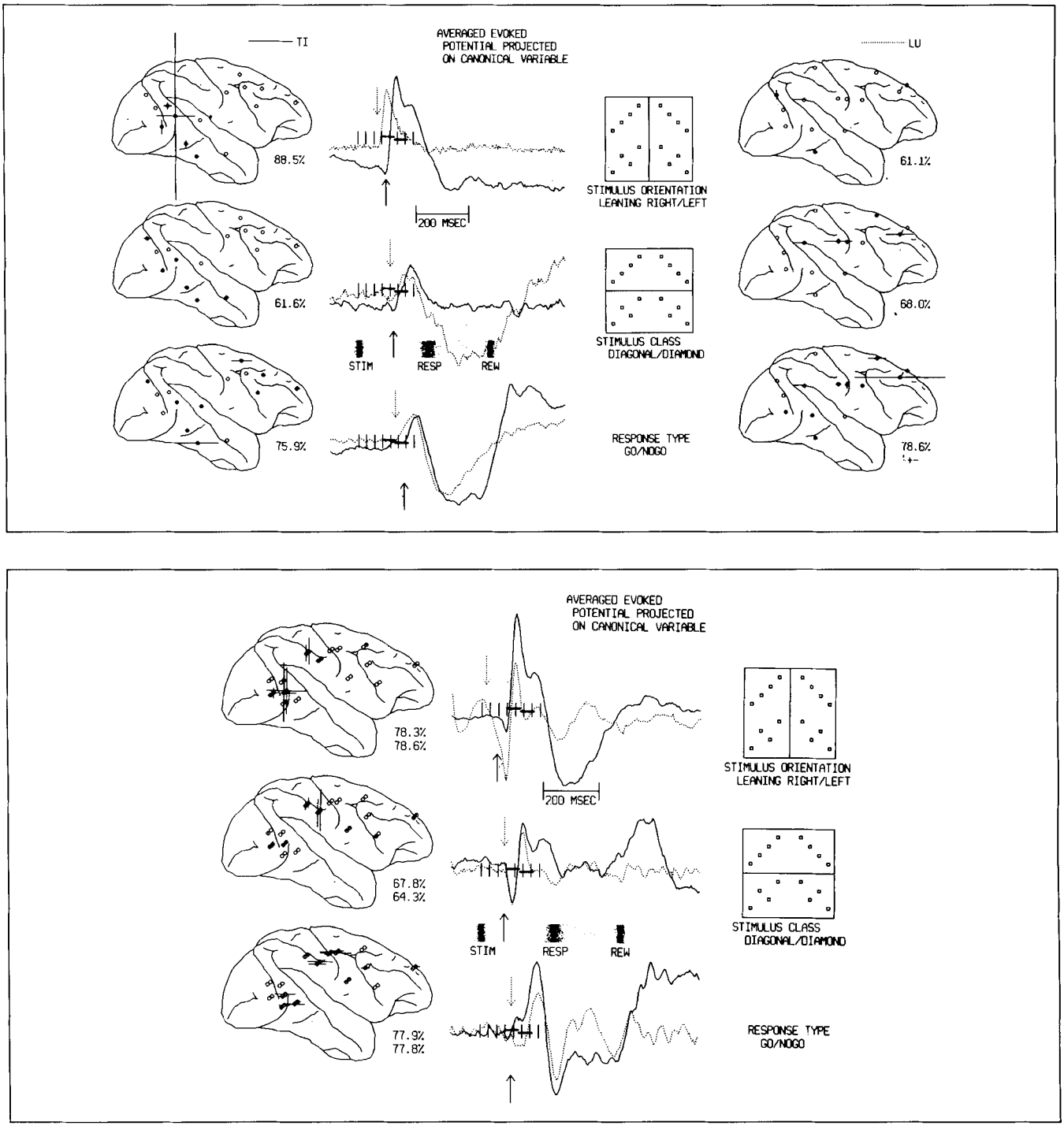

Figure 5. Localization and temporal sequencing. The pattern of peak height across the entire montage was tested for its ability to classify each trial according to stimulus orientation (row 1), stimulus class (row 2), and response type (row 3). The horizontal hash marks represent the trace segments used for peak height measurement. One-half of the trials, the training set, was used to construct discriminant functions. These functions were then applied to the other half of the trials, the test set, to determine classification accuracy (shown as percentages next to each montage). Classification accuracy and consistency were tested with the χ^2 statistic. Patterns are shown only for classifications that were significant ($p < 10^{-4}$) and for which classification accuracy was equivalent across classification groups ($p > .05$). Each horizontal/vertical bar represents the magnitude of the F to include the corresponding early/late peak measurement in the discriminant analysis divided by the number of degrees of freedom used to compute the discriminant functions. This represents the magnitude of the contribution of the corresponding electrode placement independent of the number of trials. The electrode montages are shown in the cortical schematics at the extreme left and right sides of the figure. For each of the three discrimination results, AEPs were projected onto the canonical variable as detailed in Figure 4. The traces in rows 1, 2, and 3 represent the results for discrimination between stimulus orientations, stimulus classification, and response classification, respectively. The arrows indicate the times at which the difference traces begin to diverge from zero and represent the time points at which the discrimination might begin. The lower panel shows the results from four sessions (two combination data sets) for GE. The upper panel shows the results from two sessions (one combination data set) for TI (left column and solid traces) and LU (right column and dotted traces).

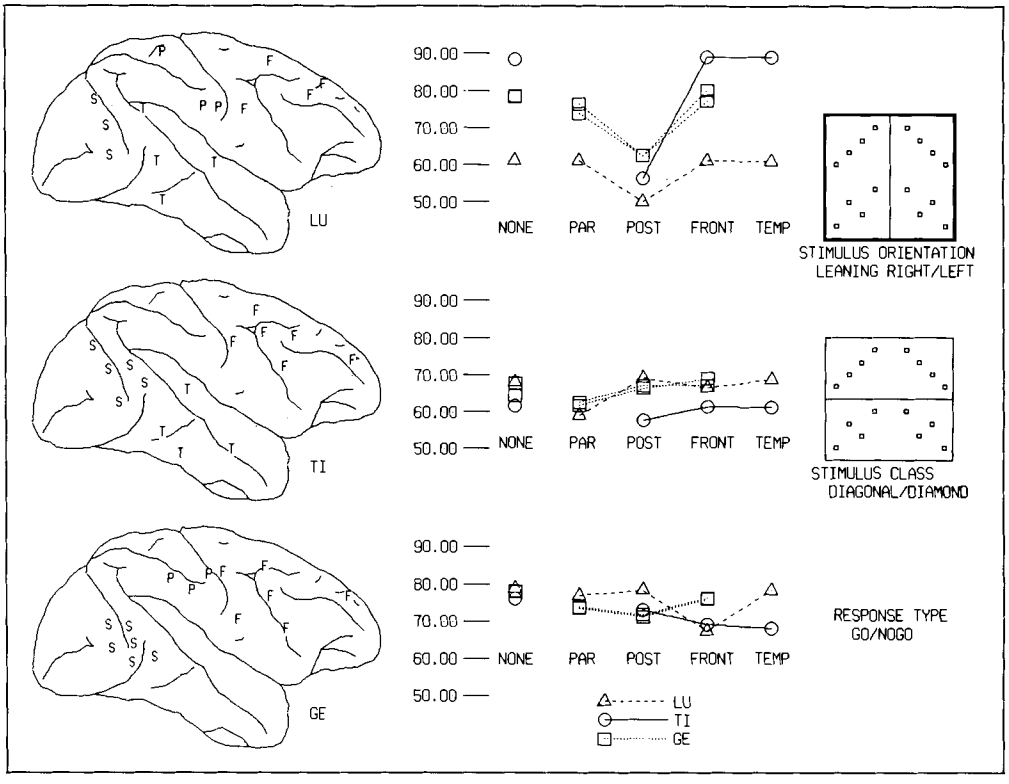

Figure 6. Localization with electrode subgroups excluded. Discriminant analyses as described in Figure 5 were run with electrode subgroups excluded. Subgroups were defined anatomically as shown in the montages in the leftmost column: (S) posterior subgroup—striate and prestriate electrodes, (P) parietal subgroup, (T) temporal subgroup, and (F) frontal subgroup. Classification accuracy is shown in percentile for three types of discrimination as indicated in the rightmost column: stimulus orientation, stimulus class, and response type. Results are shown with all electrodes included and then with each subgroup excluded individually.

ported by these results is a serial one. However the relatively short interclassification latencies and overlapping waveforms suggest that these activities occur in parallel. The data are a set of overlapping waveforms from which separate traces corresponding to distinct functions have been extracted. The sequencing techniques applied in this work thus provide results that are consistent with a relatively complete model of task performance.

Localization

The initial formal question encountered in analyzing neurophysiological recordings acquired in a behavioral task is: Is there task-related information in the recordings? A common approach is to divide the data into two subsets along some behavioral dimension, e.g., stimulus class—diagonal/diamond, compute AEPs for each class, and then superimpose resultant traces as in Figure 4, column 1. Visual examination may then be used to identify in which traces and at which points in time the responses differ.

The approach here uses averaging too, but does so in a way that takes advantage of more information, i.e., to produce a covariance matrix, and thus produces strong statistical inferences. The key to this approach is the ability to extract usable information from single trial data. This in turn depends on the quality of the data, which is high with these direct recordings, and is verified both by the histograms shown in Figure 3 and by the highly significant p values obtained on classification accuracy with linear discriminant analysis.

It is the posterior electrode subgroup, composed of striate and prestriate leads, which is the optimal contributor to discrimination between stimulus orientations; suppression of this subgroup produces a 10% dropoff in classification accuracy in all cases. Furthermore, there is a single prestriate lead that is the predominant contributor. Discrimination accuracy does, however, remain significant with suppression of the posterior subgroup except for LU.

It is the parietal subgroup that is the optimal contributor to discrimination between classes, but suppression of this subgroup produces only a 5% dropoff in classification accuracy. It is noteworthy that an overall dropoff in classification accuracy is present for TI compared with the other animals and that the suppression of the temporal leads has virtually no effect on classification accuracy for either TI or LU. The suggestion that it is anterior inferior parietal cortex that is responsible for stimulus classification rather than temporal lobe cortex is surprising in that removal of the inferior temporal lobe causes severe impairment in visual discrimination ability whereas posterior parietal lesions do not (Mishkin, Ungerleider, & Macko, 1983). This discrepancy may be due to the fact that the "discrimination" required to classify an object into one of two groups is a higher level task than that used by Mishkin. The recordings at the parietal leads may reflect projected activity from the temporal lobe (Goldman-Rakic, 1988), or the inferior temporal lobe may simply be inadequately sampled in this study.

The information used by the discriminant analysis to classify GO vs. NOGO trials is distributed to virtually every subgroup and is not consistently reduced by suppression of any particular subgroup. Furthermore, the motor cortex leads do not make a major contribution in any case, suggesting that the time segment selected for feature measurement is prior to the time at which motor cortex activation occurs. This is supported by analysis of resonant oscillations occurring in the interval between response execution and reward presentation (Krieger, Nakamura, Coppola, & Sclabassi, 1990). In that work motor and frontal pole electrodes were found to be the primary contributors to GO/NOGO discrimination.

These results coupled with those for temporal sequencing demonstrate a technique that produces a functional map of the cortex. Only those functions that are actually utilized in performance of the task and that may be isolated by comparing task subsets can be mapped. Single trial information must be extractable, not only to obtain formal statistics on classification accuracy, but also to collapse the data into a single variable for temporal sequencing.

EXPERIMENTAL METHODS

The preparation and execution of these experiments was carried out at the Laboratory for Neuropsychology, the National Institute of Mental Health (NIMH). The data were transferred to the Center for Clinical Neurophysiology (CCN) at the University of Pittsburgh for much of the analysis. This facility provides ready access to 80 Model DN3000 workstations (HP-Apollo; Chelmsford, MA), each of which can execute 10^5 floating point operations per second. The nature of the calculations allows for the use of distributed simultaneous processing by multiple machines with no loss in efficiency. This coarse grained parallelism facilitated the execution of this computationally intensive work.

Recording Preparation

Electrode implantation was carried out in two operations separated by 1 month. All transcortical electrodes were placed on the right side of the brain, i.e., contralateral to the hand used during the experiment (left). Adult rhesus monkeys were premedicated with ketamine and then anesthetized with nembutol. The calvarium was removed and burr hole positions selected using sulcal markings on the inner surface of the cranium. Burr holes were made for all electrodes and stainless steel screws were placed in each. The calvarium was then replaced and the monkey was allowed to recover for a month. After refusion of the cranium the second operation was carried out to place the recording electrodes. Under the same anesthetic technique, the placement of each transcortical recording electrode pair was carried out:

1. The screw that had been placed at the first operation was removed.
2. A tiny opening was made in the exposed dura with a sharp needle.
3. Each electrode consisted of a teflon coated platinum pair of wires, each with a 0.5 mm exposed surface. The electrode was advanced through the dura until one wire was resting against the dural surface with the other wire in the cortex 2.5 mm below.
4. The electrode pair was fixed to the skull with dental cement and the wires were fixed to a nearby skull screw.

An additional monopolar screw electrode was placed for isolation grounding. The monkeys were allowed to recover for at least 2 weeks before proceeding with the experiment. The data reported here were collected several months following surgery. The electrode montages are shown in Figure 5. Results from eight recording sessions from three different animals are reported here.

Experimental Protocol

Animals were trained prior to electrode placement to readily accept chair restraint for the 1 hr sessions and to perform a visual GO/NOGO discrimination task with reversals. A stimulus set was used which consists of four stimuli of four dots each. As shown in Figure 5, two of the patterns form diagonal lines; the other two form diagonal diamonds.

The animal's head was fixed to a head holder 57 cm from the display screen; at this distance, 1 cm on the screen subtends a visual angle of 1°. The stimulus patterns are formed by subsets of eight square dots situated at the corners of two concentric squares. Each dot is 9 mm on a side; the inner square is 2 cm on a side; the outer square is 6 cm on a side. No single dot can be used to distinguish between the stimulus classes (diagonal/diamond); the animals must base their responses on the spatial relationship of the dots.

The stimuli were presented for 100 msec on a shutter controlled screen. The monkey's task was to release a lever in response to one stimulus class (e.g., GO to the diagonals), and not to the other (e.g., NOGO to the diamonds). For these data all stimulus types were presented with equal probability. Although the monkey was water deprived, his water consumption and behavior were carefully monitored to ensure adequate hydration over the course of the experiment.

To initiate trial presentation, the monkey held down a press bar with his left hand. Interstimulus intervals varied randomly between 0.5 and 1.25 sec. Data were recorded for 950 msec/trial at 200 Hz on each of 16 channels. Approximately 120 msec following the initiation of data acquisition, the stimulus was presented. This latency was varied randomly over a 25 msec range in order to avoid synchronization of stimulus presentation with 60 Hz line noise. For correct responses on GO trials, viz. releasing

the lever, the reward was presented 500 msec following stimulus onset. On releasing the lever, the monkey was again required to hold down the press bar to maintain continued trial presentation. The temporal sequences that constitute GO and NOGO trials are shown in Figure 1.

If the monkey responded incorrectly, i.e., released the lever on a NOGO trial or failed to release it on a GO trial, the same stimulus type was repeated until he responded correctly. Only data from the first in a sequence of incorrect trials were recorded. One thousand trials were presented at a time; each session was completed in approximately 35 min. The data used for this study came from sessions in which overall performance exceeded 95% correct. Trials were excluded from analysis on which errors occurred or during which an electrical artifact was present as determined by a threshold algorithm.

Data Acquisition

Bipolar cortical neuroelectric activity was differentially amplified using Model 7P511J (Grass Inc.; Quincy, MA) amplifiers. Low and high pass filters were set at 1 and 100 Hz (3 dB point with 6 dB/octave roll-off). Gain settings were individually adjusted for each channel to maximize signal amplitude and to avoid exceeding input maxima (clipping). Amplified signals were digitized at 200 Hz/channel using a Model 3362 analogue/digital converter (Data Translation; Marlboro, MA) attached to a PDP11 computer (Digital Equipment Corp.; Maynard, MA). This machine controlled stimulus and reward presentation as well as data acquisition.

Acknowledgments

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Reprint requests should be sent to Dr. Don Krieger, Department of Neurological Surgery, 3470 Children's Hospital, 3705 Fifth Avenue, Pittsburgh, PA 15213

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