

PREPARATION TO RESPOND AS MANIFESTED BY MOVEMENT-RELATED BRAIN POTENTIALS

MARTA KUTAS* and EMANUEL DONCHIN

Cognitive Psychophysiology Laboratory, Department of Psychology, University of Illinois, Champaign, Ill. 61820 (U.S.A.)

(Accepted May 29th, 1980)

Key words: brain potentials — readiness potentials — preparation to respond

SUMMARY

Ten subjects were instructed to squeeze a dynamometer in a prescribed manner in order to assess the effects of motor preparation on event-preceding brain potentials. Right and left hand responses were required in 5 different experimental conditions allowing different degrees of advance preparation. Six channels of EEG (F3, F4, C3', C4', P3, P4) and two channels of EMG were digitized over a 3000 msec epoch, and response-locked averages were computed. Event-preceding negative potentials were evident well in advance of movement if the subject was informed of the timing of the response. These premovement potentials were asymmetrical on the scalp (contralaterally dominant at the central sites) if the subject knew which hand would be required to respond. Thus, we conclude that the appearance and asymmetry of these potentials reflect preparation to execute specific motor acts.

INTRODUCTION

Kornhuber and his associates³² were the first to report that a negative-going slow potential appears over the human scalp several hundred milliseconds before a self-paced finger movement. They called this component of movement-related activity the *Bereitschafts-* or *Readiness Potential (RP)*. Vaughan and his coworkers²¹ independently confirmed this report.

It has been suggested that the RP, like other event-preceding negative shifts (EPNs), reflects cortical processes associated with preparatory mechanisms^{2,8,26,27,38}.

* Present address: Department of Neurosciences, University of California, San Diego, La Jolla, Calif. 92093 (U.S.A.)

^{46,62}. Interpretation of the RP, however, has presented some difficulties because it is not clear if it represents activities related to the execution of a specific motor act rather than a generalized, diffuse, preparatory state. Investigators attempting to resolve this issue have typically required subjects to perform different motor acts and assessed the extent to which features of the RP vary with the parameters of the act. For example, Vaughan and his associates⁶¹ reported that the region of the scalp at which the RP is maximal, for different movements, reflects the well known somatotopic representation of the motor system along the central sulcus. Gerbrandt, however, has argued that Vaughan's data are also consistent with the view that at least a portion of the RP represents proprioceptive feedback^{19,20}. The RP, according to Gerbrandt, 'shows too much overlap across the pre- and post-rolandic line to justify identifying it as either a 'somatosensory' or a 'motor' potential'²⁰.

In previous studies^{33,34}, we investigated RPs preceding squeezes of a dynamometer and found that (in right-handed subjects) the RP was largest over the central regions of the hemisphere contralateral to the responding hand. Furthermore, this contralateral 'dominance' was evident as early as one second prior to the movement. Similar findings have been reported by Grunewald-Zuberbier et al.²³ for different types of movements. To provide further support for the conclusion that the RP reflects the preparation to execute a specific motor act, we now report a study in which we manipulated the extent to which subjects could marshal preparatory processes.

Our subjects were required to squeeze a dynamometer under conditions which allowed different forms and degrees of preparation. They were asked to squeeze at their own pace, or as quickly as possible either in response to stimuli preceded by warning signals or in response to unheralded stimuli. In this fashion we were able to assess the extent to which temporal uncertainty and selection of the responding hand influence the waveshape and scalp topography of the RP.

METHODS

Subjects

Ten male students (8 right-handed and 2 left-handed) at the University of Illinois were paid for participating in the experiment.

Stimuli

Tone bursts (98 dB SPL) were delivered binaurally through Grason Stadler TDH 39 headphones. Two tone frequencies, 1000 Hz and 1500 Hz, were used. Each tone lasted 60 msec (including 17 msec rise and fall times). The tones were presented in a mixed order at randomly varying intervals against a continuous background of wideband noise (75 dB SPL).

The output of the force transducer was displayed on an oscilloscope situated at eye level directly in front of the subject. The oscilloscope sweep (approximately 0.08 foot-lamberts) was triggered by the onset of the dynamometer movement.

Recording system

The electroencephalogram (EEG) was recorded from 6 electrodes, each referred to the linked mastoids. The electrodes were placed according to the International 10-20 convention²⁸ for frontal (F3 and F4) and parietal (P3 and P4) locations. The precentral electrodes (C3' and C4') were placed 4 cm lateral to the vertex along the interaural line. We have found that these placements yield the largest potentials preceding the squeeze.

Six non-polarizable Ag-AgCl electrodes were secured to the subject's scalp with collodion. Electrode impedance did not exceed 3 k Ω . Right supraorbital and canthal electrodes were used to record the difference electrooculogram (EOG). The electromyogram (EMG) was recorded with a bipolar arrangement, one electrode a third of the distance from the lateral epicondyle to the styloid process of the ulna and the other 2 inches in the distal direction along the same line³⁵. The EMG was recorded from the responding and non-responding arms. The subject was grounded at the forehead.

The EEG and EOG were amplified with Grass 7P122 amplifiers modified for a time constant of 8 sec and an upper half amplitude frequency of 35 Hz. The EMG was recorded by means of a Grass 7P3 preamplifier and integrator combination (time constant = 0.02 and half amplitude low frequency = 0.3 Hz).

Data collection

The experiment was controlled by a Lab 8/E computer through digital logic. The EEG, EOG, EMG, output of the force transducer and the codes associated with the tones were recorded, at 1 7/8 ips, on a 14 channel FM tape recorder. For each trial the computer squared and summed all the values on the EOG channel (at a 10 msec sampling rate). If this sum of squares exceeded a preselected criterion value, the trial was marked for rejection during subsequent averaging. Analog to digital conversion was performed by an IBM 1800 computer. Three seconds of EEG data, sampled at a rate of 10 msec per point, were stored for each trial on magnetic tape. Each 3 sec epoch consisted of 1650 msec preceding and 1350 msec following movement initiation as measured by dynamometer output. The averaging and most of the data analysis were carried out on a Harris/7. The data analyses, using the SOUPAC statistical package⁷, were done at the Computer Services Office of the University of Illinois, Urbana.

Procedure

The subject sat in a lounge chair inside an electrically-shielded, dimly-lit room. In each condition, subjects were instructed to squeeze a dynamometer constructed from a force transducer attached to a handle. The displacement of the dynamometer was 0.25 cm at all applied force levels. At the start of each session, subjects were given approximately 20 min experience in manipulating the handles and relating their squeezes to the dynamometer output displayed on an oscilloscope. This display was available throughout the session. Subjects were asked to practice so that their movements were of relatively constant duration and amplitude. The emphasis was on quick, abrupt movements.

In the first session each subject participated in 3 different experimental conditions, always in the following order:

(1) *Voluntary (VOL)*. The subjects were instructed to generate a series of squeezes with response characteristics similar to those learned during the training segment. The subjects were allowed to proceed at their own pace with the stipulation that the interval between consecutive responses was at least 6.5 sec.

(2) *Signalled (SIG)*. A series of tones of the same frequency, either 1000 Hz or 1500 Hz were presented. The interstimulus interval was varied irregularly between 6 and 15 sec. The subjects were required to squeeze the dynamometer as quickly as possible in response to each tone.

(3) *Warned (WARN)*. The subjects were asked to squeeze the dynamometer as quickly as possible after the second of two tones, separated by 1000 msec. The warning stimulus was always a 1000 Hz. All the imperative stimuli in the series were of the same frequency, either 1000 Hz or 1500 Hz. The intertrial intervals were varied randomly between 6 and 14 sec.

Each of these 3 conditions was presented 4 times during the first session, twice with each hand. Hand usage was alternated from run to run. Each series lasted approximately half an hour, during which the subjects generated 60 to 80 movements. Several minutes of rest were allowed between runs.

In subsequent sessions 5 different experimental conditions were used. Six of the runs were replicates of VOL, SIG, and WARN conditions described for the first session. The other runs were variants of these conditions, in which the imperative stimulus indicated which hand was to squeeze, as follows:

(4) *Choice Signalled (CHOICE SIG)*. The subjects were to respond to half the tones in a given series (1000 or 1500 Hz) with the right hand and to the other half (1000 or 1500 Hz) with the left hand.

(5) *Choice Warned (CHOICE WARN)*. The imperative stimulus was either a 1000 Hz or 1500 Hz tone requiring a response with either the right or the left hand. For both conditions, the imperative stimulus tones were presented in an irregular, random sequence. The probability that a high or low tone would be presented on any trial was 0.5 and was independent of the outcome of the previous trial. The relationship between tone frequency and the responding hand was held constant within each subject over conditions and days, but was counterbalanced across subjects.

On the average, subjects participated in 4 test sessions, generating approximately 450 movements per session.

Data analysis

Amplitude, latency and area measurements were carried out by a computer. The measures and subsequent analyses are based on individual subject's waveforms. The statistical analyses utilized a 3 factor repeated measures ANOVA design (hand \times condition \times electrode) and a 2 factor repeated measures ANOVA design (hand \times electrode) for each condition separately and a few planned comparisons.

RESULTS

Potentials associated with self-paced movements (VOL)

The ERPs and the average EMG recorded when the subject squeezed with the

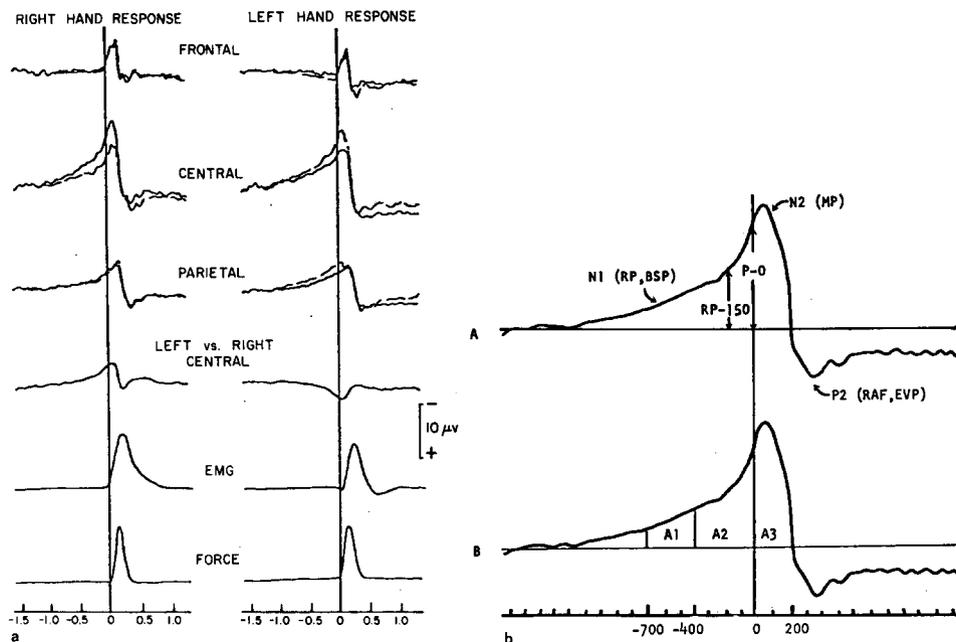


Fig. 1a. Scalp-recorded potentials preceding voluntary right and left hand movements. In the upper 3 records, 'grand mean' ERPs (averaged over 10 subjects) from homologous locations over the frontal, central and parietal regions (referred to linked mastoids) are superimposed. Left hemisphere recordings are indicated by solid lines. The fourth tracing represents a recording between left and right central electrodes. Time is indicated on the abscissa in seconds, zero time representing the onset of the dynamometer squeeze. Below the ERP waveforms are plotted the integrated EMG from the responding arm and the output of the force transducer averaged over the same trials used in computing the ERPs. Negativity at the scalp electrodes is indicated by an upwards deflection in this and all subsequent figures. Fig. 1b. A: typical waveform of the potential recorded from the central leads accompanying voluntary movement. Note the slowly incrementing negative shift (N1, RP-readiness potential, BSP-Bereitschaftspotential) prior to movement onset which gives way to a sharp negativity (N2, MP-motor potential) followed in turn by a post-movement, predominantly positive complex (P2, RAF-reafferent potential, EVP). The manner in which base-to-peak amplitude measurements were derived is indicated. RP-150 is the amplitude measured with respect to a pre-potential baseline at 150 msec prior to onset of dynamometer movement. P-O is the amplitude at movement onset. B: the boundaries of the segments of the epoch used in the analyses of the pre- and post-movement negativity are shown. The data were obtained by integrating the values over each segment, measured relative to a baseline defined as the midmean of the initial 300 msec of the record.

right or the left hand in the VOL condition, averaged over the 10 subjects, are depicted in Fig. 1. The averages are based on 40–195 movements per subject. Each pair of superimposed traces represents the 'grand' average ERPs over the left (solid line) and right (dashed line) hemispheres.

The configuration of these waveforms is generally consistent with that reported by other investigators^{3,54}. Three different segments can be readily identified in association with voluntary squeezes: (a) a slow negativity developing prior to the movement (RP-N1); (b) an abrupt acceleration in the negativity around the time of movement (N2 or MP); and (c) a positive going complex following movement onset. The P1 or premotion positivity (PMP), described as a small positive potential appearing 60–80 msec before movement initiation, was difficult to identify.

The RP (NI). Visual inspection of these ERPs reveals that the RP appears largest over the central and parietal regions and that it is either absent or slightly positive at the frontal electrodes, as reported previously^{3,4,21,51}.

A prominent feature of these data is the difference in magnitude between the negativity recorded from the right and left central electrodes. The potential recorded from the side contralateral to the responding hand is larger than that recorded over the ipsilateral hemisphere. The onset of this contralateral dominance begins, in some subjects, as early as 1000 msec prior to the movement. These data are in accord with previous reports from this laboratory^{33,34} but are at variance with the results of Kornhuber and Deecke. While these researchers agree that the RP can begin as early as 1500 msec prior to movement onset, they believe it to be symmetric in the parietal and central leads until 400 msec prior to movement³. They report that the lateralization of the potentials is not statistically significant until approximately 150 msec before movement onset. Several investigators^{4,19,20} have, in fact, noted that in the 150 msec immediately preceding the initial EMG activity, the RP in the central leads may be obscured by the superimposition of the P1 and N2 components so that measurements taken in this interval exaggerate RP asymmetry. The waveforms presented in Fig. 1,

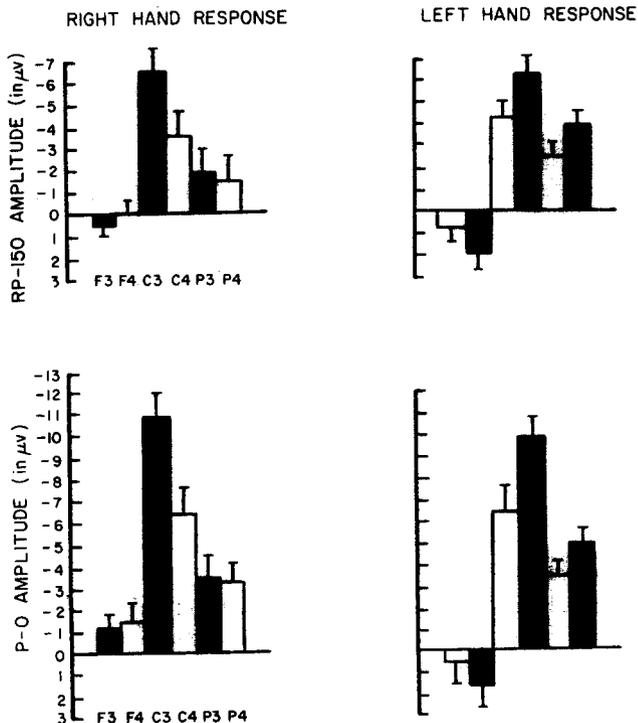


Fig. 2. Base-to-peak amplitude measurements (mean and S.E.) for RP-150 and P-O over 6 electrode sites. Measurements at sites contralateral to movement are shown as unfilled bars, ipsilateral measurements by shaded bars. P-O and RP-150 amplitudes are largest over central locations contralateral to the response. Similar, reciprocal interhemispheric differences in both measures are seen at parietal sites, but the differences are smaller. An inverse relation is seen at the frontal sites; P-O and RP-150 measures are more positive over contralateral sites.

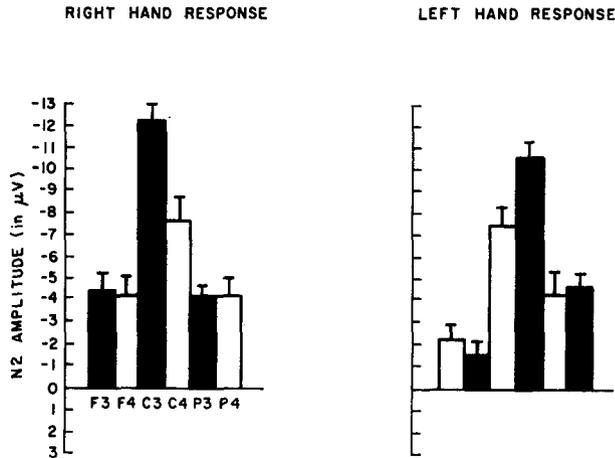


Fig. 3. N2 amplitude measurements (mean and S.E.) over 6 electrode sites. Measurements at sites contralateral to movement are shown as unfilled bars, ipsilateral site measurements by shaded bars. The values represent Deecke's estimate of the motor potential (P-O minus RP-150). This is a pre-movement onset measure.

however, demonstrate that the onset of RP asymmetry occurs substantially earlier than the 400 msec prior to the response.

To assess the reliability of these conclusions, we obtained measures of areas under selected portions of the movement-related curves (see Fig. 1b). To facilitate comparisons with the reports of other investigators, peak amplitude measures were also obtained. The means of the RP-150 and P-O amplitudes at the different electrode sites are presented in Fig. 2.

These base-to-peak measures corroborate that the RP is consistently more negative over the sensorimotor area contralateral to the squeezing hand than over the homologous ipsilateral sensorimotor area (for the RP-150 measure, right hand $F_{1,9} = 25.99$ and left hand $F_{1,9} = 12.18$; for the P-O measure, right hand $F_{1,9} = 40.27$ and left hand $F_{1,9} = 28.72$). Area measures over the 700 msec interval preceding movement onset confirm these findings (for segment A1, right hand $F_{1,9} = 8.59$ and left hand $F_{1,9} = 4.29$; for segment A2, right hand $F_{1,9} = 26.98$ and left hand $F_{1,9} = 14.75$)*.

The RP shows a similar, but smaller, contralateral predominance in the parietal leads (based on the area of the left minus right difference for the 700 msec preceding movement onset, $F_{1,9} = 5.85$ vs $F_{1,9} = 41.44$ for the same measure at

* This finding holds whether the ANOVA and subsequent t -tests are based: (1) on the area of the entire 700 msec interval preceding the response (for segment A1 + A2 in Fig. 2, hand by electrode interaction $F_{5,45} = 11.22$, for central location $t = 6.43$, $df = 9$); or (2) on the area over the 300 msec interval preceding the 400 msec which immediately precede movement onset (for segment A1 in Fig. 2, hand by electrode interaction $F_{5,45} = 4.21$, for central location $t = 3.92$, $df = 9$); or (3) on the RP-150 measure (hand by electrode interaction $F_{5,45} = 15.51$, P-O measure (hand by electrode interaction $F_{5,45} = 22.97$, for central location $t = 8.01$, $df = 9$); or (4) on the P-O measure (hand by electrode interaction $F_{5,45} = 22.97$, for central location $t = 8.01$, $df = 9$).

central locations). Potentials recorded at the frontal electrodes, on the other hand, are characterized by an inverse relation, with the contralateral electrode showing slightly more positivity than the ipsilateral one (for L-R difference for 700 msec preceding movement, $F_{1,9} = 7.32$).

The N2 (MP). The N2 or MP component refers to the additional negativity generated within the 200 msec immediately preceding movement onset. Its peak

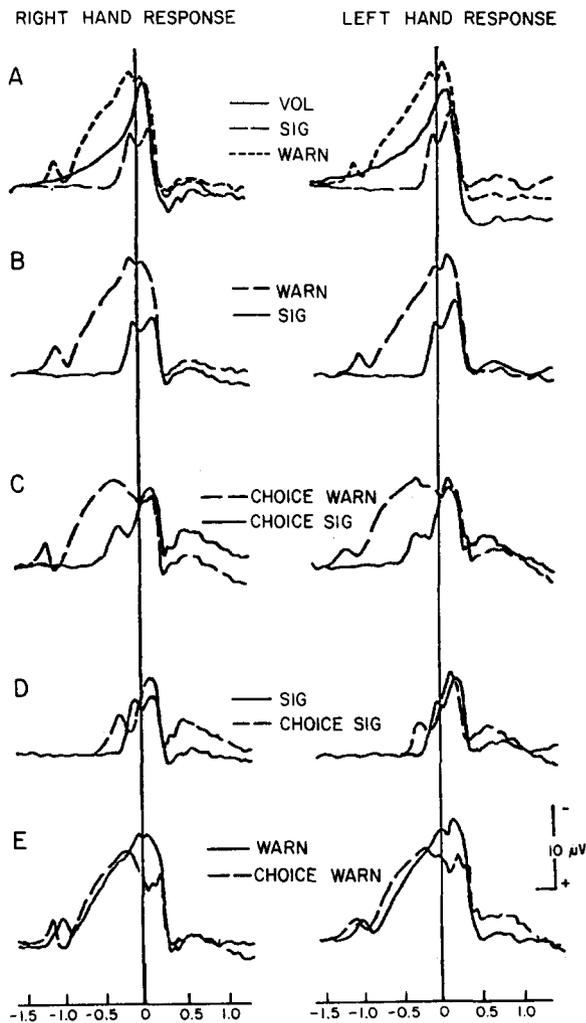


Fig. 4. Comparisons of the grand mean ERPs from the contralateral central locations for right and left hand squeezes in the 5 experimental conditions. Similar physical responses were performed in each condition. The comparisons in A (VOL vs SIG vs WARN), B (SIG vs WARN), and C (CHOICE SIG vs CHOICE WARN) demonstrate the effect of temporal uncertainty on the onset time of the pre-movement negativity. The comparisons in D (SIG vs CHOICE SIG) and E (WARN vs CHOICE WARN) show the influence of prior knowledge of the responding hand on the pre-movement potential waveform. Calibrations: 250 msec; 10 μ V. The ERPs extend over a 3 sec epoch, 1650 msec preceding and 1350 msec following movement onset.

latency relative to movement is highly controversial. The discord may be due partly to the different types of movements which have been studied or to the possibility that the MP (measured premovement) and the N2 (generally peaking post-movement) are two different components (see refs. 19 and 53).

The amplitude of the N2 measured as the most negative peak around movement onset at each of the electrode sites is graphed in Fig. 3. A second measure of N2, called MP, by Deecke and his collaborators^{3,4,32} is based on the difference between the voltage at movement onset (P-O) and that at 150 msec premovement onset (RP-150). As the N2/MP is a centrally-located asymmetric process it is reportedly best seen in a bipolar derivation (left vs right precentral). MP amplitudes in the central bipolar derivation averaged $-1.7 \pm 0.4 \mu\text{V}$ for right hand responses and $1.6 \pm 0.4 \mu\text{V}$ for left hand responses; this represents a significant reversal in direction with responding hand ($F_{1,9} = 16.74$).

Response preparation time and the RP

The onset latency of the RP. The experimental conditions varied in the extent to which the subject was forewarned as to the moment (Fig. 4A, B, C) or the hand (Fig. 4D, E) of the upcoming movement. When response onset could be anticipated with fair precision as it could when the squeeze was self-paced or the subject forewarned, the EPN emerged well in advance of the movement (as early as 800 msec). However, when the exact moment of movement initiation could not be anticipated, as when the subject squeezed in response to a randomly occurring imperative stimulus, the EPN was restricted to the 200–400 msec interval immediately preceding movement onset (Fig. 4D). These effects are particularly evident in the central leads (see Fig. 5).

As can be seen in Fig. 5, where the grand average waveforms from the contralateral anterior–posterior (A-P) locations have been superimposed, the pre-movement negativity was predominantly central in the simple response conditions (30–40% of maximum at frontal and parietal sites) and fronto-central in the corresponding choice reaction conditions. Despite these slight differences in A-P distribution, onset time of the centrally-located premovement negativity was influenced by the subject's knowledge of when the response would be required. Varying the time at which the subject knew which hand was to respond, however, did not alter the onset time of the central premovement negativity.

The asymmetry of the movement-related negativity. As mentioned above the response-locked ERPs were larger at the electrode contralateral to the responding hand for the central locations. These asymmetries are evident in Fig. 6, in which are shown the ERPs, averaged over the 10 subjects, recorded when the subjects were using their right or their left hand in each of the 5 experimental conditions. The same data for individual subjects are presented in Fig. 7.

The premovement negativity at the central location is consistently larger on the side contralateral to the responding hand. The onset, or mean latency, of this premovement asymmetry appears to depend on the time at which the subject could begin the differential mobilization of the hemispheres demanded by a unimanual response. This is best seen in the waveforms (Fig. 8) obtained by point by point

subtraction of the ERPs recorded from the left and from the right sensorimotor areas.

When information about the responding hand was provided early enough to be incorporated into the sequence of preparatory activities already underway, the potentials from homologous central locations began to diverge appreciably before movement onset. The onset latencies of the lateral amplitude asymmetries which reversed direction with the responding hand for the VOL (717 \pm 94 msec for right hand squeezes and 725 \pm 119 msec for left hand squeezes) and WARN conditions (891 \pm 60 msec and 783 \pm 85 msec for right and left hand responses, respectively) were not significantly different. However, when the time available for differential preparation was limited, as in the SIG and CHOICE SIG conditions, the amplitude

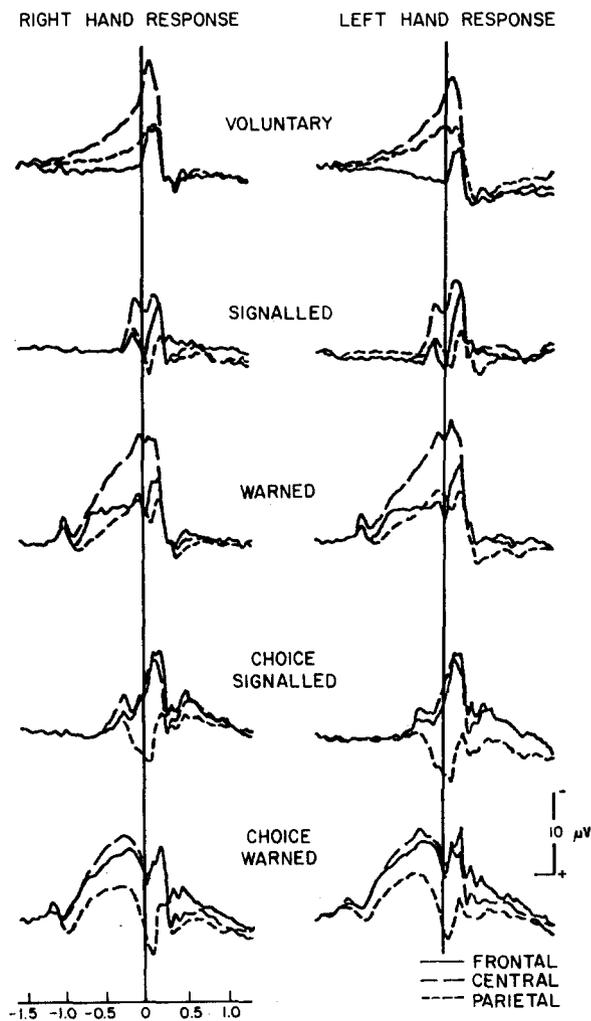


Fig. 5. Superimpositions of the response-locked grand mean ERPs from the contralateral frontal, central and parietal locations for right and left hand responses in each of the 5 conditions. The vertical line separates pre- from post-squeeze activity. Calibrations: 250 msec; 10 μ V.

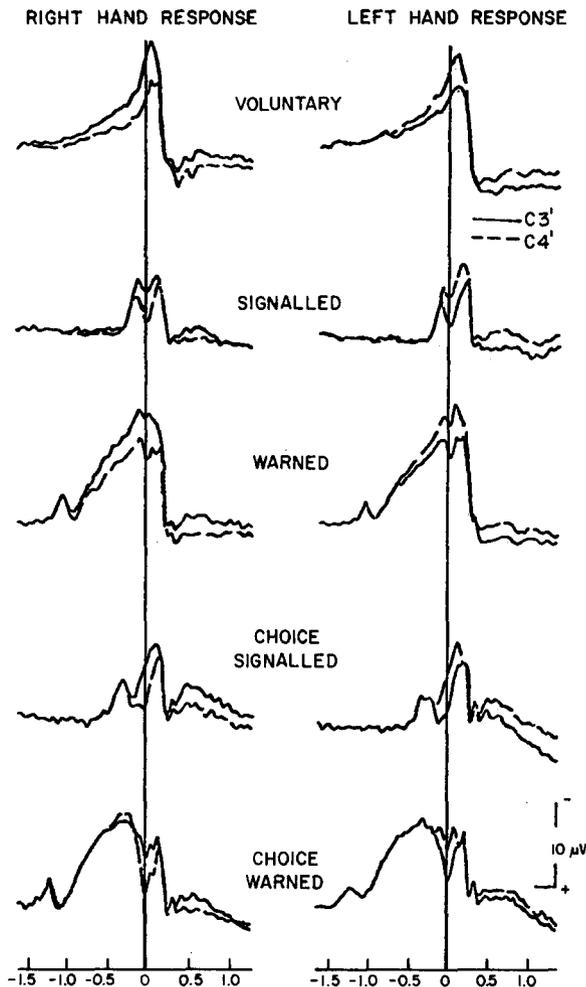


Fig. 6. A comparison of the response-locked grand average ERPs recorded at electrodes placed at left central (C3', solid line) and right central (C4', dashed line) loci for right and left hand squeezes in the 5 experimental conditions. The vertical line separates pre- from post-squeeze activity. Calibrations: 250 msec; 10 μ V.

asymmetry was restricted to the few hundred msec immediately preceding movement onset (281 ± 31 msec for right hand squeezes and 326 ± 44 msec for left hand squeezes for the SIG condition, and 347 ± 104 msec for right hand squeezes and 337 ± 34 msec for the left hand squeezes in the CSIG condition). The measurement of the onset of the asymmetry in the CWARN condition was complicated by the fact that 6 of the subjects showed an early asymmetry (3 with left hemisphere more negative than the right and 3 vice versa) in the EPN which did not reverse its direction as a function of the responding hand (969 ± 101 msec). Taking this into account, the latency of the onset of that portion of the asymmetry which reversed as a function of the responding hand averaged 240 ± 14 msec.

A summary of the F ratios for the hand \times electrode interactions from the

ANOVAs of the areas over 100 msec segments of the 700 msec interval preceding movement onset for the different experimental conditions is provided in Table I. These data also indicate the differential onset times for the amplitude asymmetry at the central locations which reversed as a function of the responding hand, lasting throughout the 700 msec premovement epoch for the VOL and WARN conditions and only in the last 100–200 msec for the SIG, CHOICE WARN and CHOICE SIG conditions.

Stimulus-locked difference waveforms. The movement-related asymmetries previously described for the response-locked differences averages are also evident in the stimulus-locked representations (see Fig. 9). It is somewhat reduced in amplitude because the stimulus-locked average is not as well synchronized to movement onset as is the response-locked average. There are significant bilateral asymmetries related to the responding hand at the central locations in all conditions; the extent and latency of the asymmetries, however, vary across conditions. Only the simple WARN condition waveforms show a significant asymmetry during the S1–S2 interval. The asymmetry in

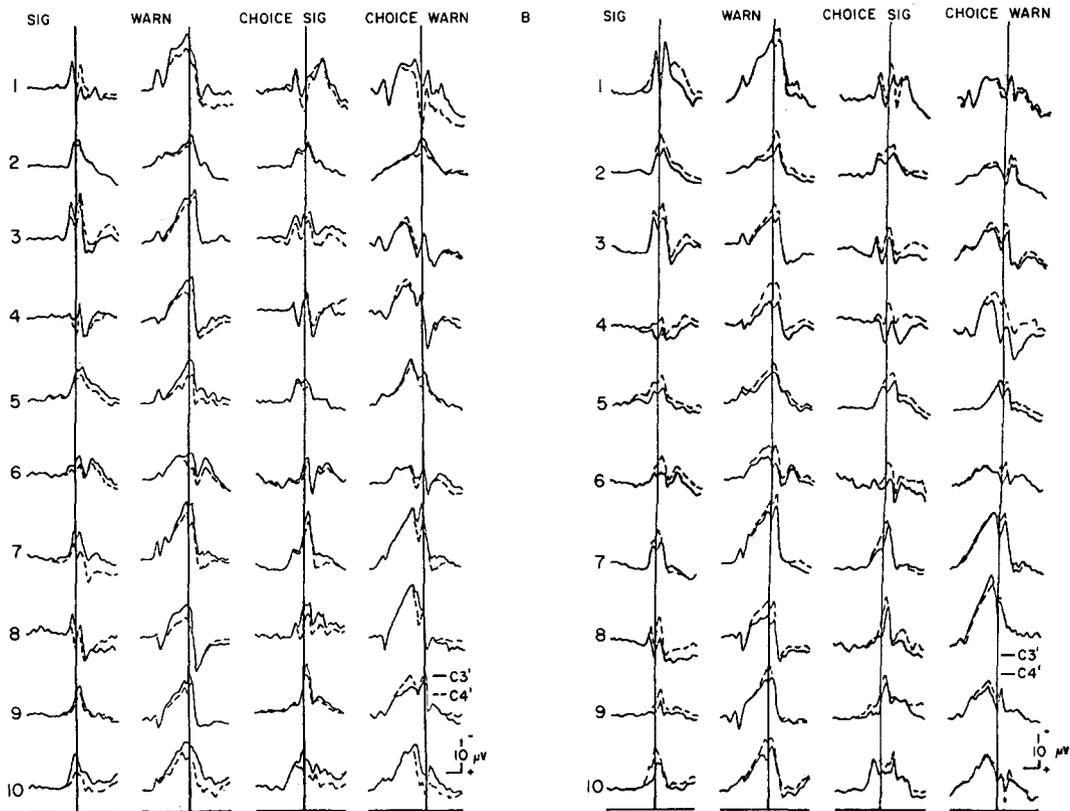


Fig. 7. A comparison of the response-locked ERPs recorded at left central (C3', solid line) and right central (C4', dashed line) loci for the 10 subjects in 4 of the experimental conditions. The vertical line separates pre- from post-squeeze activity. ERPs associated with right hand squeezes are shown in part A, those with left hand squeezes in part B. Subjects no. 3 and no. 9 were left-handed. Calibrations: 500 msec; 10 μ V.

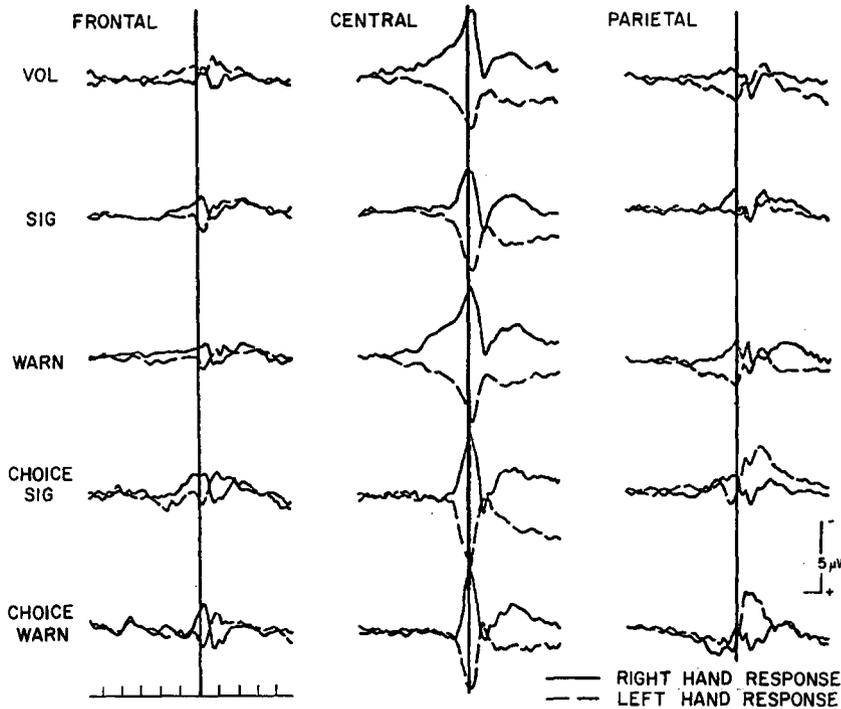


Fig. 8. A comparison of interhemispheric differences in the response-locked ERPs recorded at the frontal, central and parietal electrode locations. Each waveform was obtained by point by point subtraction of the ERPs recorded at the right hemisphere loci from the ERPs recorded at the homologous left loci. This difference is negative if the left hemisphere potential is larger and positive if the right hemisphere potential is larger. Each curve represents the difference calculated for each subject and averaged over subjects. The difference curves obtained when subjects were squeezing a dynamometer with the right (solid line) and left (dashed line) hands are superimposed for each of the 5 experimental conditions. The vertical line separates pre- from post-squeeze activity. Calibrations: 250 msec; 5 μ V. Note that a centrally dominant asymmetry, which reverses with the responding hand, is present in curves associated with each experimental condition; this asymmetry begins well in advance of the movement for the VOL and WARN conditions only.

TABLE I

F ratios for significant hand by electrode interactions ($df = 5,45$) for pre-movement area measures in the 5 experimental conditions

The intervals refer to msec pre-movement onset (0 msec) in the response-locked averages.

	700-500	500-400	400-300	300-200	200-100	100-0
Voluntary	3.33*	5.86**	7.41§	10.76§§	16.10§§	23.71§§
Warned	3.79**	6.18***	7.61§	9.45§§	14.57	20.50§§
Signalled	—	—	—	—	3.56**	17.24§§
Choice warned	—	—	—	—	—	9.67§§
Choice signalled	—	—	—	—	5.49***	15.47§§

* $P < 0.01$; ** $P < 0.008$; *** $P < 0.0005$; § $P < 0.00004$; §§ $P < 0.000001$.

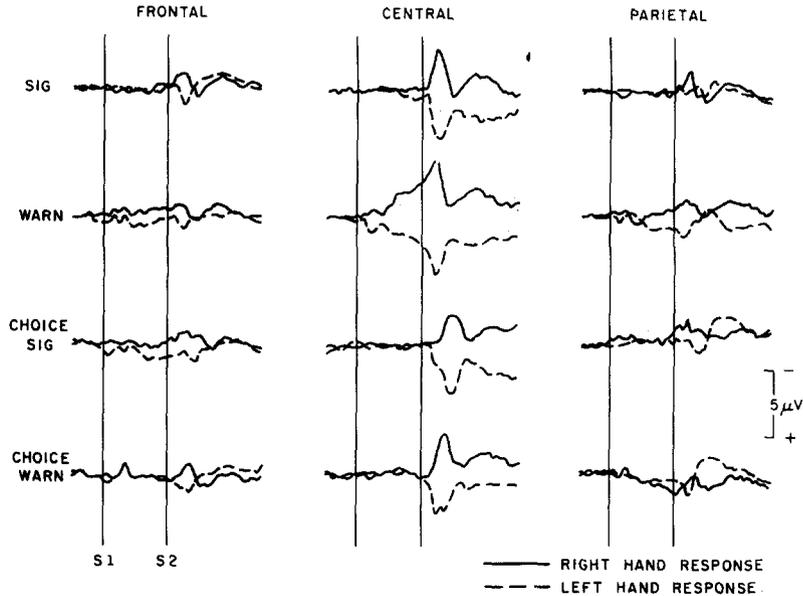


Fig. 9. A comparison of interhemispheric differences in the stimulus-locked ERPs at the frontal, central and parietal electrode locations. Each waveform was obtained by point by point subtraction of the ERPs recorded at right hemisphere loci from ERPs recorded at the homologous left hemisphere loci. Each curve represents the difference calculated for each subject and averaged over subjects. The difference curves obtained when subjects were squeezing a dynamometer with the right (solid line) and left (dashed line) hands are superimposed for each of the experimental conditions. The two vertical lines, separated by 1000 msec, demarcate the foreperiod interval. Calibrations: 250 msec; 5 μ V. Note that a centrally dominant asymmetry, which reverses with the responding hand, is present in the curves associated with each condition. The latency of the peak asymmetry from the imperative stimulus varies with the condition, being shortest in the WARN waveform and longest in the CHOICE SIG waveform.

the other series is restricted to the postimperative region. Prior knowledge of both the responding hand and the time of response appear to influence the timing of the asymmetry.

On the whole, the ordering of the peak asymmetry latencies shows a correspondence with the ranking of the mean RTs for the various conditions. Peak detection was performed by a computer program within an epoch 190–660 msec following the imperative stimulus. Consistent reversible asymmetries were restricted to the central locations. The mean and S.E. of the peak asymmetries measured in the difference waveforms from the central locations were 245 ± 13 and 274 ± 25 msec for signalled, 207 ± 7 and 209 ± 7 msec for warned, 445 ± 30 and 443 ± 21 msec for choice signalled and 355 ± 19 and 328 ± 39 msec for choice warned conditions for the right and left hand responses, respectively. The latencies of these peak asymmetries at the central site were highly correlated ($r = 0.85$, $F = 98.00$, $P < 0.00001$ for right hand and $r = 0.81$, $F = 72.53$, $P < 0.00001$ for left hand responses) with the reaction times from the different conditions. The correlations between standard scores for the RTs and the latencies of the peak asymmetries at the frontal and parietal sites were insignificant ($r = 0.12$ – 0.30).

An analysis of response parameters. Basic to the argument that the waveshape

and topography of these response-related ERPs reflect various stages of differential preparation for movement is the assumption that the responses generated in the different experimental conditions remain relatively constant. While this assumption cannot be validated with certainty, some support for its validity derives from an analysis of the data available on the response.

Analysis of the dynamometer output. Three parameters of the squeeze were measured: peak amplitude, peak latency, and the total duration of the squeeze. Neither the peak latency of the response (130 ± 23 msec) nor the total squeeze duration (262 ± 40 msec) bore a systematic relation to any of the experimental variables. However, an ANOVA of these response measures revealed that the peak force amplitude varied significantly with the experimental conditions ($F_{4,36} = 4.23$, $P < 0.05$). The movements generated during the simple reaction conditions (VOL = 47 ± 10 lbs; SIG = 47 ± 10 lbs; WARN = 46 ± 7 lbs) were executed with slightly more force than movements produced during the choice reaction conditions (CSIGN = 43 ± 7 lbs; CWARN = 43 ± 7 lbs).

Whereas such results indicate that the squeezes did vary with the conditions, several lines of evidence suggest that the differences in force levels do not account for the ERP differences. Although the force associated with simple and choice reactions differed, within each response type the force levels developed during warned and unwarned responses were equivalent. The presence of a negativity preceding warned movements and its absence prior to unwarned responses is not attributable to differences in force. Similarly, variations in force are insufficient to explain why unimanual response preparation is associated with response-related lateral ERP amplitude asymmetries and bimanual response preparation is not. Kutas and Donchin³⁴ have shown that beyond some minimal output, the extent of RP asymmetry is unaffected by the amount of force output. Furthermore, the differences in the lateral asymmetries between the WARN and CWARN condition ERPs are in agreement with the findings of Sydulko and Lindsley⁵⁵, who required subjects to respond with simple index finger extensions.

An analysis of reaction times. The extent to which the different experimental conditions demanded, and allowed, different degrees of preparation to respond is reflected in the corresponding reaction times (RTs). A two factor ANOVA and subsequent *t*-tests indicated that the mean RTs from all 4 experimental conditions are significantly different from each other ($F_{3,27} = 140.20$). The shortest RTs were obtained in the WARN conditions (right hand = 217 ± 30 msec; left hand = 216 ± 39 msec) and the longest in the CHOICE SIG conditions (right hand = 526 ± 23 msec; left hand = 494 ± 53 msec) with the RTs in the SIG condition (right hand = 311 ± 41 msec; left hand = 318 ± 41 msec) being shorter than those in the CHOICE WARN condition (right hand = 413 ± 45 msec; left hand = 415 ± 81 msec).

In general, when the responding hand was not cued until the imperative stimulus, a cost of nearly 200 msec in the RT was incurred compared to the condition in which the information was given at the beginning of a trial block ($t = 9.33$, $df = 36$ for the warned conditions and $t = 9.10$, $df = 36$ for the signalled conditions). On the other hand, whether or not the responding hand was known well in advance, the

benefit of decreased uncertainty about the timing of the response provided by the warning signal was a 95 msec reduction in RTs relative to those observed during conditions when the moment of response was unpredictable ($t = 4.59$, $df = 36$ for simple reactions and $t = 4.36$, $df = 36$ for choice reactions).

DISCUSSION

Our intent in this investigation was to ascertain the extent to which the readiness potential reflects neural processes underlying preparation for the execution of a unimanual motor response. To this end we required subjects to squeeze a dynamometer while varying the degree to which they could anticipate and prepare the response. On the basis of previous findings, we reasoned that if the RP represents primarily motor preparation its amplitude should be larger over the hemisphere contralateral to the responding hand. Furthermore, this asymmetry should appear only if the subject could anticipate and prepare the response. The data indicate that this is the case.

We have demonstrated that (a) the onset latency of the RP was influenced by subjects' knowledge about response timing and that (b) the lateral distribution of the EPN was affected by the degree to which the subject could differentially prepare for the upcoming movement. Voluntary and warned movements were preceded by centrally maximal negative shifts. Unwarned movements were not. When people were allowed to prepare in advance either a right or a left hand response, the RP was larger in amplitude over the contralateral sensorimotor area. On the other hand, when bimanual response preparation was required, no consistent asymmetries were obtained. Thus, the data indicated that at least a portion of the RP is a manifestation at the scalp of neural activity related to the preparation for a motor response.

It is clear, however, that the readiness potential does not account for all the recordable event-preceding negative activity. It would appear that the EPNs include the activity of several distinct intracranial processes only some of which are 'motor' in function. This view is consistent with the suggestion that the contingent negative variation is a composite of several distinct slow potentials arising from different brain regions. Several investigators have noted that if a 4–8 sec interval is allowed between the warning and imperative stimuli (the 'foreperiod'), the CNV that develops between them appears to consist of an 'early' CNV, which they considered an orienting response, and a 'late' CNV reflecting preparatory processes^{18,30,31,36,37,51,63}. McCarthy and Donchin⁴¹ have shown that the CNV can be decomposed into multiple components even when the foreperiod is 1000 msec long. However, their data indicate that the 'early' CNV depends on the information conveyed by the warning stimulus.

The data reported here also indicate that at least one additional negative component appears in the foreperiod that is a manifestation of processes other than orientation to the warning stimulus and preparation to move. The differences between the frontal and parietal distributions of the EPNs in the WARN and CHOICE WARN conditions imply the existence of this component, as do the studies showing that CNVs are generated in the absence of motor engagement^{9,62}. It seems reasonable,

therefore, to conceive of the CNV as a generalized negativity upon which are superimposed task and modality specific slow waves such as the RP²⁶. This general event-preceding negativity obtained in the WARN and CHOICE WARN conditions probably reflects sensory-perceptual or cognitive processes rather than purely motor activities. Whatever the number of distinct components comprising the CNV and the RP, it seems reasonable to assume that the portion of the response-locked EPN over the sensorimotor region which is asymmetrically distributed on the scalp and reverses as a function of the responding hand does represent activity specific to motor preparation. This inference is strengthened by the high correlation obtained between the peak latency of the asymmetry in the central sites of the stimulus-locked ERPs and the reaction times in the different experiment conditions.

Further understanding of the RP as an index of movement-related preparatory activity depends on identification of its cerebral sources and the underlying neural activities. Slow negative shifts have been recorded from intra-cranial electrodes in both man and animals in experimental situations comparable to those employed with scalp-recordings. Event- and movement-preceding potentials have been investigated in patients with intracerebral electrodes implanted for therapeutic purposes^{21,25,39,40,44,45} and in primates with indwelling electrodes^{9,24,42,43,45,48-50}. Like the scalp-recorded EPNs, the waveform and topographic distribution of these cortical and subcortical EPNs have been shown to be sensitive to variations in task demands.

Johnson²⁹ observed that some components of the premovement potential in the Rhesus were synchronized to the movement, responsive to variations in force and larger over the hemisphere contralateral to the responding arm. Arezzo and Vaughan¹ recorded movement-related potentials from an array of up to 60 epidural electrodes in Rhesus monkeys trained to perform repetitive wrist movements. The largest RP and N2 components were obtained from the hand area of the precentral motor cortex and the RP (N1 in their terminology) was found to be 'completely absent' in recordings from areas ipsilateral to the responding limb. Arezzo and Vaughan suggested that these potentials could be related to movement-related single unit activity in the cortex reported by Schmidt et al.⁵². They noted the similarities (a) between the RP and the gradual increase in the firing of some precentral neurons which participate in phasic premovement discharge and (b) between the N2 and time course of precentral unit activity which arises from the same cortical sites.

Investigators of single neuron activity related to movement in various animals (refs. 5, 6, 12-17, 52, 56-60) have reported that some cells, situated throughout the motor system, discharge in a fixed temporal relationship to movement initiation. Evarts¹⁴ recorded single unit activity in monkey cortex in association with a movement in response to a photic stimulus whose time of occurrence was unpredictable. Pyramidal tract neurons in the precentral motor cortex discharged 100 msec prior to a hand flexion or extension. The behavior of these neurons was in marked contrast to those in the postcentral gyrus which tended to fire only after movement onset.

When Evarts and Tanji¹⁷ recorded neuronal activity in a paradigm in which monkeys were forewarned as to the type of movement required, they noted modifications in the precentral neuronal firing patterns as early as 500 msec preceding the

movement. Furthermore, the recordings revealed that the pattern of neuronal activity between the warning signal and the movement varied with the information provided by the cue as to the type of movement which would be subsequently required. Evarts and his associates further observed that the neuronal changes which precede movement are coupled with the monkey's differential response to the instructions. Thus, if the neuronal response to a cue calling for a 'pull' was the pattern that was normally associated with a push, the monkeys would actually push rather than pull the lever⁵⁶.

Clearly, then, there are neural populations with temporal patterns of activity quite similar to that of the RP. However, it cannot be inferred from this that the RP is the manifestation on the scalp of the activity of the neurons studied in single unit investigations. The similarity between the processes is intriguing and the elucidation of this relationship is an important challenge. If EPNs and single unit firings reflect the same processes, then it may well be possible to study physiological concomitants of voluntary action, as has been suggested by Eccles¹¹.

The data described above also have implications for the interpretation of ERP experiments where it is necessary to obtain ERPs and performance measures on the same trials. Requiring subjects to execute a motor response to a stimulus produces overlapping stimulus- and response-related potentials which are difficult to disentangle. One approach to this problem is to use the voluntary, movement-related ERPs as estimates of the 'pure motor' contribution to scalp recordings which can be subtracted from the ERPs obtained in the task of interest. The residual ERP would then be considered free of contamination by movement-related potentials. This procedure, however, assumes that the movement-related potentials recorded in self-paced responding are identical to those recorded during the stimulus-response experimental task. The results of the present investigation reveal that this is not always the case. The potentials obtained during the voluntary movement conditions differ appreciably from ERPs recorded in response to stimuli whose time of occurrence is unpredictable. Subtraction under such circumstances would clearly be inappropriate.

ACKNOWLEDGEMENTS

The work described here was supported, in part, by DARPA through Contract N00014-76-C-0002 with the Office of Naval Research.

The authors wish to thank Steven A. Hillyard, Jack Isreal, and Gregory McCarthy for their helpful comments on the manuscript.

REFERENCES

- 1 Arrezo, J. and Vaughan, H. G., Jr., Comparative analysis of motor potentials in man and monkey. *Paper presented at the International Symposium on Evoked Potentials in Man, Brussels, April, 1974.*
- 2 Butler, S. R. and Glass, A., Asymmetries in the CNV over left and right hemispheres while subjects await numeric information, *Biol. Psychol.*, 2 (1974) 1-16.
- 3 Deecke, L., Grozinger, B. and Kornhuber, H. H., Voluntary finger movement in man. Cerebral potentials and theory, *Biol. Cybernetics*, 23 (1976) 99-119.
- 4 Deecke, L., Scheid, P. and Kornhuber, H. H., Distribution of readiness potential, pre-motion

- positivity, and motor potential of the human cerebral cortex preceding voluntary finger movements, *Exp. Brain Res.*, 7 (1969) 158–168.
- 5 DeLong, M. R., Motor functions of the basal ganglia: single unit activity during movement. In F. O. Schmitt and F. G. Worden (Eds.), *The Neurosciences*, MIT Press, Cambridge, 1974, pp. 319–325.
 - 6 DeLong, M. R. and Strick, P. L., Relation of basal ganglia, cerebellum and motor cortex units in ramp and ballistic limb movements, *Brain Research*, 71 (1974) 327–335.
 - 7 Dickman, K. W., *SOUPAC program descriptions, DCL Report No. UICDS-R-72-370-4*, University of Illinois, 1972.
 - 8 Donald, M. W., Preliminary report in discussion of CNV and human behavior. *Electroenceph. clin. Neurophysiol.*, (Suppl.) 33 (1973) 241–242.
 - 9 Donchin, E., Gerbrandt, L. K., Leifer, L. and Tucker, L., Is the contingent negative variation contingent on a motor response?, *Psychophysiol.*, 9 (1972) 178–188.
 - 10 Donchin, E., Otto, D., Gerbrandt, L. K. and Pribram, K. H., While a monkey waits: electrocortical events recorded during the foreperiod of a reaction time study, *Electroenceph. clin. Neurophysiol.*, 31 (1971) 115–127.
 - 11 Eccles, J. C., *The Understanding of the Brain*. McGraw-Hill, New York, 1977, p. 110.
 - 12 Evarts, E. V., Pyramidal tract activity associated with a conditioned hand movement in the monkey. *J. Neurophysiol.*, 29 (1966) 1011–1027.
 - 13 Evarts, E. V., Relation of pyramidal tract activity to force exerted during voluntary movement. *J. Neurophysiol.*, 31 (1968) 14–27.
 - 14 Evarts, E. V., Contrast between activity of precentral and postcentral neurons of cerebral cortex during movement in the monkey, *Brain Research*, 40 (1972) 25–31.
 - 15 Evarts, E. V., Motor cortex reflexes associated with learned movement, *Science*, 179 (1973) 501–503.
 - 16 Evarts, E. V., Precentral and postcentral cortical activity in association with visually triggered movement, *J. Neurophysiol.*, 37 (1974) 373–381.
 - 17 Evarts, E. V. and Tanji, J., Reflex and intended responses in motor cortex pyramidal tract neurons of monkey, *J. Neurophysiol.*, 39 (1976) 1069–1080.
 - 18 Gaillard, A. W. K., The late CNV wave: preparation versus expectancy, *Psychophysiology.*, 14 (1977) 563–568.
 - 19 Gerbrandt, L. K., Analysis of movement potential components. In J. E. Desmedt (Ed.), *Attention, Voluntary Contraction and Event-Related Cerebral Potentials. Vol. I*, Karger, Basel, 1977, pp. 174–188.
 - 20 Gerbrandt, L. K., Goff, W. R. and Smith, D. B., Distribution of the human average movement potential, *Electroenceph. clin. Neurophysiol.*, 34 (1973) 461–474.
 - 21 Gilden, L., Vaughan, H. G., Jr. and Costa, L. D., Summated human EEG potentials associated with voluntary movements, *Electroenceph. clin. Neurophysiol.*, 20 (1966) 433–438.
 - 22 Groll-Knapp, E., Ganglberger, J. A. and Haider, M., Voluntary movement-related slow potentials in cortex and thalamus of man, In J. E. Desmedt (Ed.), *Attention, Voluntary Contraction and Event-Related Cerebral Potentials. Vol. I*, Karger, Basel, 1977, pp. 164–173.
 - 23 Grunewald, G., Grunewald-Zuberbier, E., Homberg, V. and Netz, J., Cerebral potentials during smooth goal-directed hand movements in right-handed and left-handed subjects, *Pflüger's Arch. ges. Physiol.*, in press.
 - 24 Hablitz, J. J., Operant conditioning and slow potential changes from monkey cortex, *Electroenceph. clin. Neurophysiol.*, 34 (1973) 399–408.
 - 25 Haider, M., Ganglberger, J. A. and Groll-Knapp, E., Computer analyzed thalamic potentials and their relation to expectancy waves in man, *Acta Neurol. Latinoamerica*, 14 (1968) 132–137.
 - 26 Hillyard, S. A., The CNV and human behavior. In W. C. McCallum and J. R. Knott (Eds.), *Event-related Slow Potentials of the Brain*, Elsevier, New York, 1973, pp. 161–171.
 - 27 Jarvilehto, T. and Fruhstorfer, H., Differentiation between slow cortical potentials associated with motor and mental acts in man, *Exp. Brain Res.*, 11 (1970) 309–317.
 - 28 Jasper, H. H., Report of the committee on methods of clinical examination in electromyography, *Electroenceph. clin. Neurophysiol.*, 10 (1958) 370–375.
 - 29 Johnson, R. E., Jr., *Movement-related Slow Potential Activity in the Rhesus Monkey*, Unpublished Masters Thesis, University of Illinois, 1975.
 - 30 Klorman, R. and Bentsen, E., Effects of warning-signal duration on the early and late components of the contingent negative variation, *Biol. Psychol.*, 12 (1975) 609–617.
 - 31 Kok, A., The effect of warning stimulus novelty on the P300 and components of the contingent negative variation, *Biol. Psychol.*, 6 (1978) 219–233.

- 32 Kornhuber, H. H. and Deecke, L., Hirnpotential nderungen bei Wilkurbewegungen und passiven Bewegungen des Menschen: Bereitschaftspotential und Reafferente Potentiale. *Pflügers Arch. ges. Physiol.*, 284 (1965) 1–17.
- 33 Kutas, M. and Donchin, E., Studies of squeezing: handedness, responding hand response force and asymmetry of the readiness potential, *Science*, 186 (1974) 545–548.
- 34 Kutas, M. and Donchin, E., The effect of handedness, of responding hand, and of response force on the contralateral dominance of the readiness potential. In J. Desmedt (Ed.), *Attention, Voluntary Contraction and Event-related Cerebral Potentials. Progress in Clinical Neurophysiology, Vol. 1*. Karger, Basel, 1977, 189–210.
- 35 Lippold, O. C. J., Electromyography. In P. H. Venables and I. Martin (Eds.), *A Manual of Psychophysiological Methods*. Elsevier, New York, 1967.
- 36 Loveless, N. E. and Sanford, A. J., Slow potential correlates of preparatory set, *Biol. Psychol.*, 1 (1974) 304–314.
- 37 Loveless, N. E. and Sanford, A. J., The impact of warning signal intensity on reaction time and components of the contingent negative variation, *Biol. Psychol.*, 2 (1975) 217–226.
- 38 Marsh, G. R. and Thompson, L. W., Effect of verbal and non-verbal psychological set on hemispheric asymmetries in the CNV. In W. C. McCallum and J. R. Knott, (Eds.), *Event-related Slow Potentials of the Brain*, Elsevier, New York, 1973, pp. 195–200.
- 39 McCallum, W. C. and Papakostopolous, D., Anticipatory potentials associated with motor acts. *Paper presented at the International Symposium on Cerebral Evoked Potentials in Man, Brussels, April, 1974*.
- 40 McCallum, W. C., Papakostopolous, D., Gombi, R., Winter, A. L., Cooper, R. and Griffith, H., Event-related slow potential changes in human brain stem. *Nature (Lond.)*, 242 (1973) 466–467.
- 41 McCarthy, G. and Donchin, E., Brain potentials associated with structural and functional visual matching. *Neuropsychol.*, 16 (1978) 571–585.
- 42 McSherry, J. W. and Borda, R. P., The intracortical distribution of the CNV in rhesus monkey, *Electroenceph. clin. Neurophysiol.*, (Suppl.) 33 (1973) 69–74.
- 43 McSherry, J. W., Borda, R. P. and Hablitz, J. J., Analysis of event-related slow potentials in primates. In J. E. Desmedt (Ed.), *Attention, Voluntary Contraction and Event-related Cerebral Potentials Vol. 1*, Karger, Basel, 1977, pp. 231–241.
- 44 Papakostopolous, D. and Crow, H. J., Electroencephalographic studies of the Contingent Negative Variation and P300 in man. In W. C. McCallum and J. R. Knott (Eds.), *The Responsive Brain*, John Wright, Bristol, 1976, pp. 201–204.
- 45 Pieper, C. F., Goldring, S., Jenny, A. B. and McMahon, J. P., Comparative study of cerebral cortical potentials associated with voluntary movements in monkey and man, *Electroenceph. clin. Neurophysiol.*, 48 (1980) 266–292.
- 46 Poon, L. W., Thompson, L. W., Williams, R. B., Jr. and Marsh, G. R., Changes of anterior-posterior distribution of CNV and late positive component as a function of information processing demands, *Psychophysiol.*, 11 (1974) 660–673.
- 47 Popper, K. R. and Eccles, J. C., *The Self and its Brain*. Springer, Berlin, 1977, pp. 282–286.
- 48 Rebert, C. S., Cortical and subcortical slow potentials in the monkey's brain during a preparatory interval, *Electroenceph. clin. Neurophysiol.*, 33 (1972) 389–402.
- 49 Rebert, C. S., Slow potential changes in the monkey's brain during reaction time foreperiod. In W. C. McCallum and J. R. Knott (Eds.), *The Responsive Brain*. John Wright, Bristol, 1976, pp. 191–194.
- 50 Rebert, C. S., Intracerebral slow potential changes in monkeys during the foreperiod of reaction time. In J. E. Desmedt (Ed.), *Attention, Voluntary Contraction and Event-related Cerebral Potentials, Vol. 1*, Karger, Basel, 1977, pp. 242–253.
- 51 Rohrbaugh, J. W., Sydulko, K. and Lindsley, D. B., Brainwave components of the contingent negative variation in humans, *Science*, 191 (1976) 1055–1057.
- 52 Schmidt, E. M., Jost, R. G. and Davis, K. K., Cortical cell discharge patterns in anticipation of a trained movement, *Brain Research*, 75 (1974) 309–311.
- 53 Shibasaki, H., Barrett, G., Halliday, A. M. and Halliday, E., Scalp topography of movement-related cortical potentials. In H. H. Kornhuber and L. Deecke (Eds.), *Proceedings of the 5th International Symposium on Electrical Potentials Related to Motivation, Motor and Sensory Processes of the Brain*, in press.
- 54 Simson, R., Vaughan, H. G., Jr. and Ritter, W., The scalp topography of potentials in auditory and visual go/no-go tasks, *Electroenceph. clin. Neurophysiol.*, 43 (1977) 864–875.

- 55 Syndulko, K. and Lindsley, D. B., Motor and sensory determinants of cortical slow potential shifts in man. In J. Desmedt (Ed.), *Attention, Voluntary Contraction and Event-related Cerebral Potentials*. Karger, Basel, 1977, pp. 97–131.
- 56 Tanji, J. and Evarts, E. V., Anticipatory activity of motor cortex neurons in relation to direction of an intended movement, *J. Neurophysiol.*, 39 (1976) 1062–1068.
- 57 Thach, W. T., Discharge of cerebellar neurons related to two maintained postures and two prompt movements. II. Purkinje cell output and input, *J. Neurophysiol.*, 33 (1970) 537–547.
- 58 Thach, W. T., Discharge of cerebellar neurons related to two maintained postures and two prompt movements. I. Nuclear cell output, *J. Neurophysiol.*, 33 (1970) 527–536.
- 59 Thach, W. T., The behavior of Purkinje and cerebellar nuclear cells during two types of voluntary arm movement in the monkey. In W. S. Fields and W. D. Willis, Jr. (Eds.), *The Cerebellum in Health and Disease*. Warren H. Green, St. Louis, 1970, pp. 217–230.
- 60 Thach, W. T., Cerebellar output: properties, synthesis, and uses, *Brain Research*, 40 (1972) 89–97.
- 61 Vaughan, H. G., Jr., Costa, L. D. and Ritter, W., Topography of the human motor potential, *Electroenceph. clin. Neurophysiol.*, 25 (1968) 1–10.
- 62 Walter, W. G., Cooper, R., Aldridge, V. J., McCallum, W.C. and Winter, A.L., Contingent negative variation: an electric sign of sensorimotor association and expectancy in the human brain, *Nature (Lond.)*, 203 (1964) 380–384.
- 63 Weerts, T. C. and Lang, P. J., The effects of eye fixation and stimulus and response location on the contingent negative variation (CNV), *Biol. Psychol.*, 1 (1973) 1–19.