The Effect of Handedness, of Responding Hand, and of Response Force on the Contralateral Dominance of the Readiness Potential

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Preliminary Note on Nomenclature

In this paper we will identify movement-related potentials with labels proposed by VAUGHAN *et al.* [1968]. While this system is not consistent with the recommendations of the Methodology Committee (this volume) in that the components will be identified ordinally, we feel that there will be no ambiguity in our usage when applied to movement-related potentials. The nomenclature recommended by the Methodology Committee is appropriate for naming potential peaks, either positive or negative, but not for naming slopes, for which latency cannot be meaningfully specified. Some writers refer to the components in question with labels like 'readiness potentials' (RP), 'reafferent potentials', etc. Such labels which of course imply a certain theoretical position concerning the origin and functional significance of the potentials should be avoided. In this report, therefore, the term RP is used to refer to a theoretical process underlying pre-response negativity which we shall call N_1. Whether N_1 is a manifestation of a RP is the central issue of our study.

Introduction

It has been reliably established that, during the foreperiod of a reaction time task, a slow negative cerebral potential develops which peaks just before the presentation of the imperative stimulus whereupon it gives place to a rapidly changing, positive-going cortical potential. WALTER [1964] labelled this negative shift, the contingent negative variation (CNV). The CNV has been reported to reflect psychological constructs

such as expectancy [WALTER et al., 1964], conation [LOW et al., 1966], motivation [IRWIN et al., 1966; REBERT et al., 1967], and attention [MCCALLUM, 1969; WEINBERG, 1973]. While the CNV is currently assumed to be primarily a manifestation of cognitive/perceptual activity, there is no consensus on its functional significance. The interpretation of the CNV has been complicated when KORNHUBER and DEECKE [1965] as well as VAUGHAN and co-workers [GILDEN et al., 1966; VAUGHAN et al., 1968; VAUGHAN, 1969] reported that self-paced voluntary activity was also preceded by a slow cerebral potential having both a slow pre-response negative component and post-response positivity. The positive post-response potential had originally been described by BATES [1951] and DONCHIN and LINDSLEY [1966], but the pre-response potentials had not been previously reported. These movement-related potentials have been differentiated into four components: (1) a ramp-shaped negative potential which begins to develop 800–1000 msec prior to the movement (N_1); (2) a rapid acceleration at the end of N_1 (N_2); (3) a rapid, small amplitude positive wave (P_1) reported to occur between N_1 and N_2, and (4) a large positive wave (P_2) which follows N_2. Whereas GILDEN et al. [1966] referred to this entire complex as 'motor potentials', implying that they are indicators of '... physiological correlates of preparatory motor sets and readiness for movement', DEECKE et al. [1969] consider only the P_1 and N_2 components to be 'motor' potentials and consider N_1 a 'Bereitschaft' or 'readiness' potential (RP), thus pointing to some similarity between the CNV and the RP. Other investigators have also suggested that the CNV and N_1 may be related. Some have said the CNV might be a RP [GILDEN et al., 1966; LOW et al., 1966], others that the RP might be a CNV [DEECKE et al., 1969; COHEN, 1969]. VAUGHAN viewed the CNV as an index of a response-related readiness associated with control processes in the pyramidal system rather than with global mobilization in anticipation of some external stimulus. More recent formulations proposed that N_1 may be a sum of several independent event-related slow potentials [HILL-YARD, 1973] and the nature of the N_1-CNV relation remains unclear.

In most CNV studies, subjects were to respond to the imperative stimulus (S2), with a movement (e.g. a button press). In fact, the close association of the CNV with the subject's intention to make a response contingent on S2 was emphasized by WALTER and led him to postulate a response-priming function for processes underlying the CNV. However, the slow cortical negativity is not dependent upon the execution of a motor response after the imperative stimulus [COHEN and WALTER, 1966; LOW

et al., 1966; DONCHIN et al., 1972, 1973]. Yet, while CNVs can be elicited in the absence of a motor response, the execution of a response after S2 increases the amplitude of the CNV [WALTER, 1964; IRWIN et al., 1966; LOW et al., 1966; PETERS et al., 1970]. IRWIN et al. [1966] have pointed out that the enhancement of CNV magnitude by a subsequent motor response is of the same order (10–15 μV) as the N_1 produced prior to a voluntary movement. Further, this slow surface negativity is significantly larger when a large amount of force, or muscular effort, is required as the response to S2 [LOW and McSHERRY, 1968; REBERT et al., 1967].

Another attempt at the dissection of the motor from the non-motor aspects of pre-response potentials has been made by studying the scalp distribution of the potentials. The CNV's distribution is reportedly symmetric around a peak at the vertex, somewhat smaller in the frontal areas and smallest in the posterior region [LOW et al., 1966]. The cortical distribution of N_1 depends according to VAUGHAN et al. [1968] on the responding limb and is somatotopically related to the muscles involved in the movement. While these data suggest that N_1 and CNV are distinct, there are reports [OTTO and LEIFER, 1973; SYNDULKO and LINDSLEY, this volume] that in a forewarned unimanual task the pre-response negativity is greater over the sensorimotor area contralateral to the responding hand. Of course, an asymmetric distribution of the potential is most consistent with the notion that it reflects activity of the motor cortex associated with preparation for movement.

The present study was an attempt to determine the degree to which parameters of the motor response determine the waveform, amplitude, and hemispheric distribution of the N_1 component. The N_1 features were chosen for study because there is some question as to whether the later components of the motor potential occur before or after the motor response [cf. DEECKE and KORNHUBER, this volume; RITTER et al., this series]. The response variables manipulated were response force and the responding hand. Since the motor cortex is directly involved in the control of muscle force [EVARTS, 1967], it could be expected that some cerebral motor preparation specific to one hand would be maximal over the contralateral pre-rolandic area. This problem cannot yet be clarified from published data and possible differences related to the subject's handedness should also be considered. The present experiment was designed to determine the distribution of N_1 over the motor areas when both left and right- handed subjects responded with either hand, using three different force levels to respond.

Method

Subjects: Eleven University students (7 right-handed and 4 left-handed) were paid for participating in the experiment. Handedness was determined by self-report, subsequently verified by the Edinburgh Inventory [OLDFIELD, 1971].

Recording procedures: Beckman biopotential electrodes (No. 6509) filled with Beckman electrode paste were secured to the subject's scalp with collodion at C_z, C_4, and C_3 and were referred to a linked mastoid electrode. Electrode impedance, measured with a Grass E-Z-M impedance meter, did not exceed 10 kΩ. Right supraorbital and canthal electrodes (fastened with adhesive collars) were used to record the electrooculogram (EOG). The electromyogram (EMG) was recorded from the responding arm, one electrode at a third of the distance from the lateral humeral epicondyle to the styloid process of the ulna and the other approximately 1.5–2 inches in the distal direction along the same line. Signals were amplified with Brush amplifiers (No. 13-4218–00) with bandwidth setting of 0.1–30 Hz (6 dB/octave roll-off, i.e. the time constant was 1.51 sec). EMG activity was recorded by means of a Grass Model 7P3 preamplifier and integrator combination (1/2 amplitude low frequency = 0.3, time constant = 0.02). Data were recorded on a Hewlett-Packard 3955 FM tape recorder at $1^7/_8$ ips and averaged off-line with either a PDP/8E or an IBM 1800. All trials in which detectable, gross eye movements occurred were not used in averaging. Trials were included if the sum of squares of digitized EOG voltages did not exceed a criterion value.

Procedure: The subject sat in a comfortable chair inside of an electrically shielded, darkened room fixating a dim square displayed continuously in a scope. Subjects were instructed to rapidly squeeze a Dynamometer constructed by attaching a Daytronic model 152A, LDVT force transducer to a grip-handle. The displacement of the dynamometer was 0.25 mm at all applied force levels. We determined for each subject a maximal force level for each hand by asking the subject to rapidly squeeze the dynamometer several times as hard as he could. The force levels the subjects generated during test series were defined as 0.25, 0.50, and 0.75 of their maximal force. The actual force levels used were 0.25 = 5 kg, 0.5 = 10 kg, and 0.75 = 15 kg for the non-dominant hand, and 0.25 = 7 kg, 0.5 = 12.5 kg, and 0.75 = 20 kg (± 1 kg) for the dominant hand.

To provide the subjects with feedback concerning their emitted force, a transilluminated circle was superimposed on the fixation square. Subjects were told to find the squeeze force level that would just extinguish the circle. The circle, once extinguished, was reilluminated after 1 sec. The electronics made it possible to arrange the extinction of the stimulus at any preset force level. Subjects were cautioned against overpressing. Within each session there were two separate runs. In the first, the subjects generated a series of 50–100 similar squeezes, each extinguishing the feedback circle for a short period. In the second run, subjects were instructed to continue squeezing the dynamometer at the same level that previously extinguished the light, without the visual feedback. Except for two test cases, in any one session, voluntary movements were performed using one hand only at each of the three force levels, and always in the order 0.25, 0.50, and 0.75. Each subject participated in a minimum of six sessions, three with each hand. The order of hand usage was counterbalanced across different subjects.

Results

Pattern of motor responses of the subjects. The output of the dyna-
mometer served to time-lock the averaging of ERPs recorded at C_3 and
C_4 scalp locations and it was continuously recorded, along with the EMG
of forearm flexors. Analysis of these data served to assess the relationship
between the nominal force requested in the instructions and the actual
force produced. Figure 1A presents the force traces for a series of succes-
sive trials at one nominal force. The course of the traces is reasonably un-
iform from onset to peak, but is variable after dynamometer release. A
study of confidence limits of average force curves per series showed this
to be the common pattern. In the early part of a session, subjects
squeezed the dynamometer at rather irregular intervals, but they gradual-
ly shifted to a more regular squeezing rate; interspersed with rest periods.
The minimum interval was 3 sec and the maximum 8 sec (fig. 1B). Figure
2 presents the means and SD for peak force measurements in right- and
left-handed subjects, in all experimental conditions. An analysis of the
variance of these data showed that: (a) the actual peak force is a mono-
tonically increasing function of the nominal force levels, with the distribu-
tions of actual force exhibiting only minimal overlap; (b) the mean peak
values are consistently smaller for the non-dominant hand, and (c) in the
condition without feedback, the response force always exceeds that gener-
ated during the corresponding feedback condition. These data suggest that
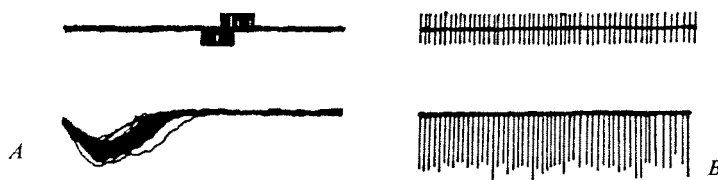on the whole the subjects behaved as instructed.

Fig. 1. A Superposition of traces of movement force obtained in a series of
successive trials at one nominal force level in one subject. *B* The force responses
shown in *A* are displayed on a slower time base to indicate the variability of the in-
tervals between successive trials and of the force amplitude. The upper traces are
the trigger pulses used to mark events, the lower traces represent the output of the
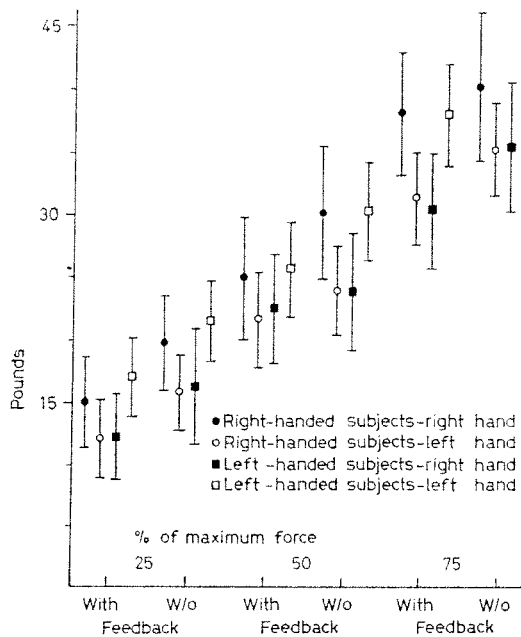force transducer. The horizontal sweep represents 800 msec in *A* and 20 sec in *B*.

Fig. 2. The means and standard deviations of the peak mean force measurements plotted as a function of the subjects' handedness and the responding hand in all experimental conditions.

Waveform of average ERP. There was a considerable similarity between the waveforms recorded from C_3 and C_4 scalp electrodes in all subjects. The right-handed subjects showed substantially less variability (fig. 3, 4). In view of this consistency between subjects, we used in subsequent figures the grand ('over-subject') averages for right-handed and left-handed subjects, respectively (fig. 5), thus comparing ERPs from C_3 (solid line) and C_4 (dashed line) locations when responding with either the right or the left hand, at the three chosen levels of squeeze force. The average integrated EMG (dashed line) and force output (solid line) are presented below the ERP records in figure 5.

In agreement with previously published data, a slow negativity developed prior to movement (N_1), and this accelerated at about the time of the movement (N_2) and was followed by a positive-going wave (P_2). The P_1 component, called pre-motion positivity by DEECKE and KORNHUBER [cf. this volume], was difficult to identify in our records.
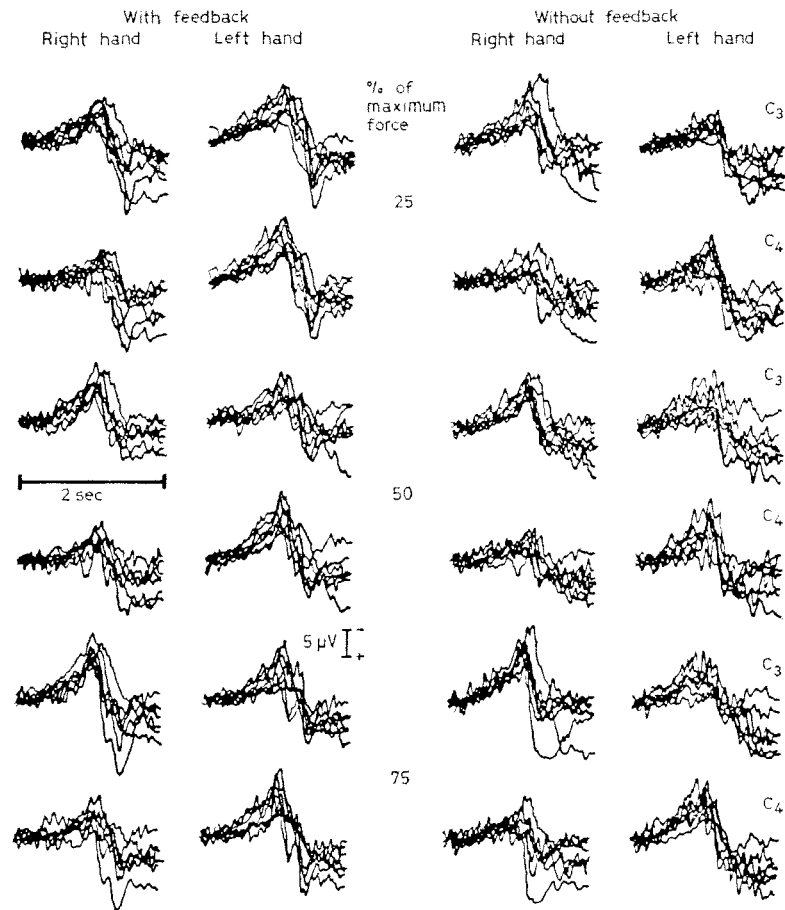
Fig. 3. Superposition of event-related potentials (ERPs) obtained from each of the 7 right-handed subjects at the C_3 and C_4 electrodes, for each responding hand at each force level for each feedback condition. Avarages were obtained over all subjects after the elimination of trials in which the EEG was contaminated by EOG activity. Number of trials per ERP ranges between 100 and 400.

When right-handed subjects perform a self-paced voluntary movement, the premotion negativity (N_1) is consistently larger over the sensorimotor location contralateral to the hand used. This asymmetry is evident (in some cases) as early as 500 msec before the initiation of the movement, as defined by EMG onset. The hemispheric difference in N_1 is smaller for left-hand responses. Contralateral dominance is apparent
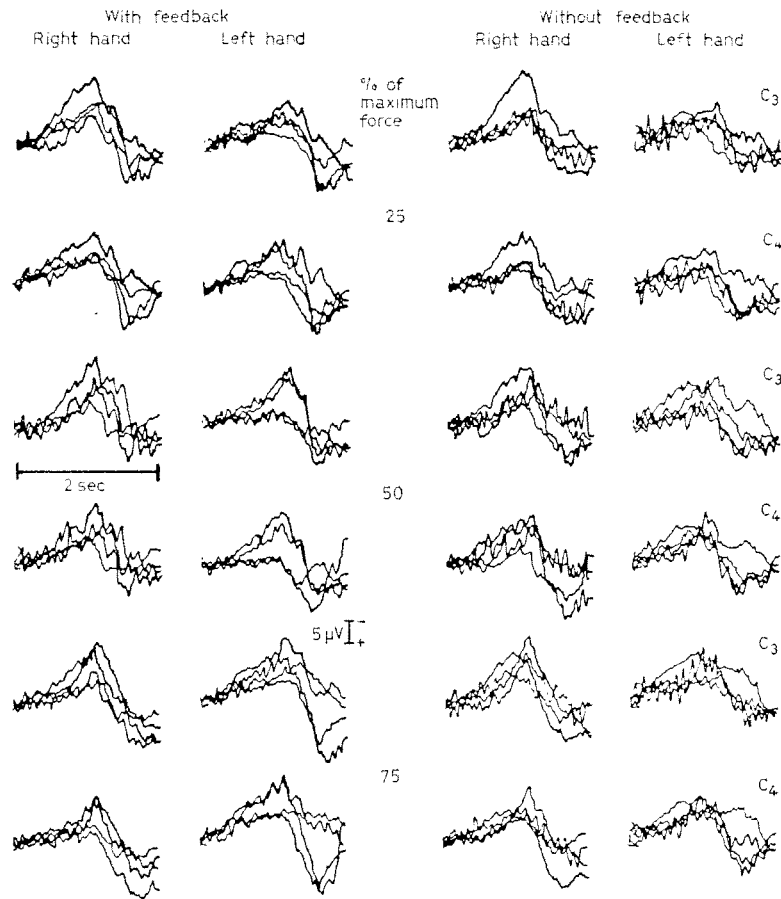
Fig. 4. Superposition of ERPs obtained from each of the 4 left-handed subjects at the C_3 and C_4 locations, for each responding hand at each force level and feedback condition.

(though reduced) in the left-handed subjects when they respond with their right hand (fig. 5). Thus, N_1 is maximal over the hemisphere contralateral to the responding hand for right hand responses, independent of subject handedness. This is *not* the case for left hand responses. While left-handed subjects show contralateral dominance when using their right hand, they generally show bilaterally symmetric waveforms when responding with their left hand. Occasionally, a left-handed subject would show a slight degree of contralateral dominance preceding left-hand squeezes.
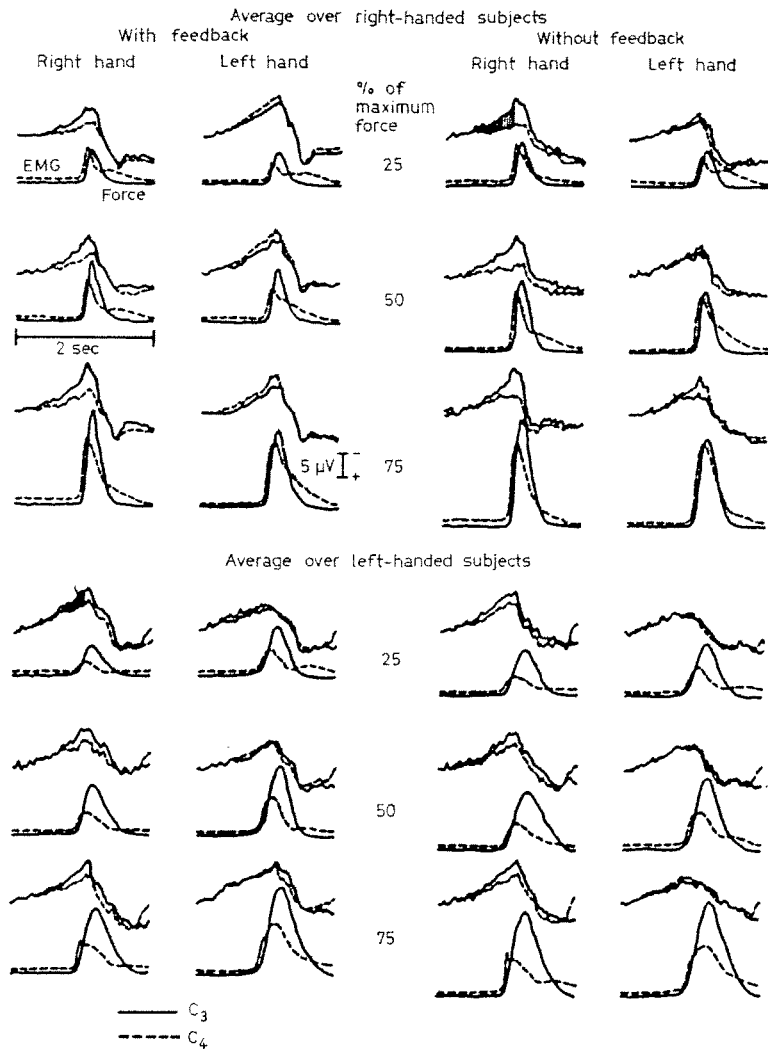
Fig. 5. A comparison of ERPs recorded at electrodes placed at left central (C_3, solid line) and right central (C_4, dashed line) loci during voluntary squeezes. Under each pair of superimposed ERPs, we plot the integrated EMG (dashed line) and the output of the force transducer (solid line) averaged over the same trials over which the ERP was averaged. Comparisons are presented as a function of the subject's handedness (right vs left), nominal force output (25, 50, and 75% of subject's maximal force), responding hand (right vs left) and feedback (with vs without). Number of trials per ERP ranges between 600 and 1,050. The cross-hatched areas in two of the comparison illustrate the areas measured for the purpose of the quantitative data analysis.

Analysis of area of ERP. For each subject, the ERPs at each experimental condition were averaged over all replications of the condition and the number of trials per such grand averages ranged between 150 and 300. In general, the within-subject wave forms recorded on different days for similar conditions did not vary greatly, as shown by figure 6 for 3 right- and 3 left-handed subjects recorded under feedback condition at force level of 0.75 maximum. The degree of hemispheric asymmetry remained relatively invariant over the different sessions in any one subject.

To obtain a measure of hemispheric asymmetry, we subtracted, point by point, the C_3 from C_4 ERP curves and integrated this difference curve over an interval beginning 500 msec prior to and 25 msec following the onset of EMG deflection. The integrated area obtained has been cross-hatched in figure 5. The values obtained for all subjects and for all experimental conditions are listed in table I. The analysis of variance of these data corroborates the impressions based on visual inspection of the ERPs. Statistically significant effects were obtained for the responding hand, with the hemispheric asymmetry being larger for the right- than left-hand movement, independently of the subjects' handedness. The hemispheric asymmetry is larger for right- than for left-handed subjects, but significance is not obtained because of variability between subjects.

It has been suggested that in the last 150 msec before the first EMG response, the N_1, P_1, and N_2 components are superimposed in certain leads so that measurements which include this area would exaggerate N_1 asymmetries [DEECKE et al., 1969; GERBRANDT et al., 1973]. It has been recommended therefore that measurements of N_1 should not extend beyond 150 msec before EMG onset [DEECKE and KORNHUBER, this volume]. We have thus integrated N_1 up to that -150 msec point and compared these results with the previous data. The results corroborate the statement above that in some cases, the asymmetry occurred as early as 500 msec prior to EMG onset. For those cases which show *any* asymmetry, the asymmetry at the -150 msec point between C_3 and C_4 was evident in 83% of the right-handed subjects using their right hand, in 76% of the same subjects using their left hand, in 70% of the left-handed subjects using their right hand, and in 90% of the left-handed subjects using their left hand.

The ERP analysis also indicated that response force had no statistically significant effect on the hemispheric asymmetry. An analysis of the effect of the response force on the area under the ERP recorded at vertex (C_z), at C_3 and at C_4 for the 500 msec preceding and the 25 msec follow-
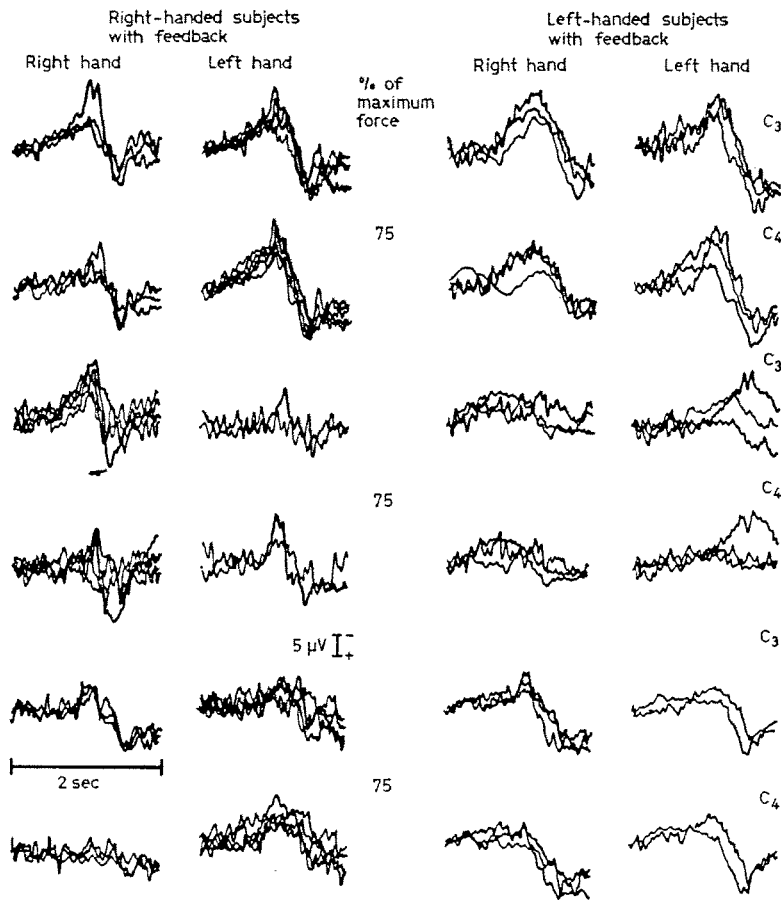
Fig. 6. Superposition of ERPs recorded at C_3 and C_4 locations during voluntary squeezes with the 75% nominal force and with feedback conditions. Each set of comparisons for right- and left-hand response conditions are made with data recorded from one subject at various recording sessions (i.e. different days). Records are provided for 3 right-handed and 3 left-handed subjects.

ing EMG onset showed that the force had a slight effect at all electrode sites. However, there was no significant force $\times$ electrode interaction and the degree of contralateral dominance seemed independent of the force produced.

The force output and the EMG were quite similar in their initial segments. In general, the EMG onset preceded that of force by 50–80 msec. The EMG onset always followed the appearance of asymmetry of N_1, but

Table I. Areas of pre-response negativity in difference curves (C₄–C₃)

		Right-handed subjects							Left-handed subjects			
		J.E.	C.G.	J.H.	D.L.	D.T.	T.T.	M.C.	T.E.	R.S.	C.T.	G.W.
Right hand												
25%	w	696	1,691	3,492	−417	2,197	5,518	1,516	3,077	3,529	1,143	108
	w/o	2,937	2,588	2,448	2,328	3,603	5,638	2,453	3,701	464	2,641	250
50%	w	2,744	1,688	2,628	−1,002	2,990	1,602	3,489	1,244	3,055	3,843	952
	w/o	1,135	4,497	14,879	1,289	2,958	3,005	3,626	2,352	1,226	629	495
75%	w	3,296	1,038	2,685	2,141	3,919	2,200	1,792	2,826	1,829	2,083	−838
	w/o	5,396	4,373	2,672	2,341	3,949	5,332	1,317	2,464	1,463	2,348	−295
Left hand												
25%	w	−640	958	192	−2,226	−1,677	−1,603	843	−804	−1,785	−2,675	879
	w/o	106	−112	4,134	−2,456	−1,755	−490	−1,643	−85	−586	−1,483	−1,548
50%	w	−1,292	−1,168	−2,755	−1,026	−2,218	−2,565	−11	−293	−807	−1,639	−1,206
	w/o	−2,615	665	613	1,339	−1,333	−37	−1,608	196	−1,892	−2,320	1,880
75%	w	−621	233	−1,172	−3,361	−1,713	−2,622	814	503	−491	−2,199	−354
	w/o	−2,259	1,310	−4,493	−2,345	−1,482	−4,105	−169	454	−1,635	948	−645

it occurred either before, during, or after the peak negativity (called N_2), depending unsystematically on subject and condition. On the whole and to the extent that P_1 can be identified in our records, it appears that P_1 (and also N_2) would coincide with or follow the movement onset, peaking at or slightly before the EMG peak.

Post-movement potentials. The other major component of the motor potential, P_2, was recorded consistently in all subjects as a relatively large and complex positive-negative wave occurring after the movement; a marked difference in the sharpness of the positive peak can be observed for data obtained during the with- and without feedback conditions. P_2 peaks on the average 290–340 msec after the feedback stimulus in the feedback condition, whereas it is usually broader and flatter in the without feedback condition. This finding is again most consistent in the right-handed subjects.

Principal component analysis. The above analyses were based on either visual inspection or on the somewhat arbitrarily chosen area measure for each ERP record. As there has been some question as to the proper measure of N_1 independent from N_2 and of P_2 as well, we performed a factor analysis on the actual evoked response waveforms in the manner discussed by DONCHIN [1966]. All the ERPs were condensed to arrays of 50 points (40 msec per point). The principal axes of the entire 50×132 matrix were obtained, and a varimax rotation performed. In figure 7B, we plot the factor loadings of the five principal axes (accounting for 92.6% of the variance). The waveform averaged over all 132 ERPs is also plotted, for reference, in fig. 7A. The first factor (which accounted for 31% of the variance) appears heavily loaded on variables associated with the overall waveform. The second factor (25%) clearly represents points associated with the baseline, the third (19%) with N_1, the fourth (13%) with the transition points from N_2 to P_2, and the fifth (5.8%) primarily with P_2.

The factor scores obtained by applying the loadings for each of the 50 variables to the standardized matrix of raw data used in producing the factors were then subjected to an analysis of variance. The analysis was performed on all of the factor scores associated with each of the factors for each of the 132 evoked responses obtained from the eleven subjects for the six experimental conditions. Much of the variance is accounted for by the waveform factor which is significantly affected by the electrode position (C_3, C_4 and C_z) and various electrode interactions (electrode $\times$ responding hand and electrode $\times$ force). On the whole, these analyses simply confirm the results reported above.

Table II. Anova summary table of factor scores with dependent variable (factor 5 or component P_2)

Source	d.f.	SS	MS	MS error	f	p
Handedness (A)	1/9	4.5678	4.5678	F	0.36	0.55892
Responding hand (B)	1/9	1.6909	1.6909	B × F	0.51	0.49168
Force (C)	2/18	0.6938	0.3469	C × F	0.4979	0.61592
Feedback (D)	1/9	49.3711	49.3711	D × F	8.24	0.01845
Electrode (E)	2/18	0.8472	0.4236	E × F	0.95	0.40367
Handedness × responding hand	1/9	0.0680	0.0680	B × F	0.01	0.89487
Handedness × force	2/18	1.8438	0.9219	C × F	1.32	0.29101
Handedness × feedback	1/9	16.8839	16.8839	D × F	2.81	0.12747
Handedness × electrode	2/18	0.8040	0.4020	E × F	0.90	0.42188
Responding hand × force	2/18	4.5986	2.2993	B × C × F	2.29	0.12924
Responding hand × feedback	1/9	1.3203	1.3203	B × D × F	1.28	0.28596
Responding hand × electrode positions	2/18	2.1775	1.0887	B × E × F	3.41	0.05524
Force × feedback	2/18	1.1033	0.5516	C × D × F	0.73	0.49134
Force × electrode	4/36	0.7431	0.1857	C × E × F	3.61	0.01415
Feedback × electrode	2/18	0.7740	0.3870	D × E × F	3.99	0.03663
Handedness × responding hand × force	2/18	3.0563	1.5281	B × C × F	1.52	0.24405
Handedness × responding hand × feeback	1/9	0.0061	0.0061	B × D × F	0.01	0.94021
Handedness × responding hand × electrode	2/18	0.2532	0.1266	B × E × F	0.39	0.67788
Handedness × force × feedback	2/18	3.0563	1.5280	C × D × F	1.52	0.24405
Handedness × force × electrode	4/36	0.1405	0.0351	C × E × F	0.6835	0,60798
Handedness × feedback × electrode	2/18	0.4299	0.2149	D × E × F	2.21	0.13753
Responding hand × force × feedback	2/18	0.0346	0.0173	B × C × D × F	0.01	0.98860
Responding hand × force × electrode	4/36	1.3921	0.3480	B × C × E × F	10.52	0.00001
Responding hand × feedback × electrode	2/18	0.1104	0.0552	B × D × E × F	0.83	0.45122

|						
Force × feedback × electrode	4/36	0.6279	0.1569	C×D×E×F	4.00	0.00872
Handedness × responding hand × force × feedback	2/18	1.2765	0.6382	B×C×D×F	0.42	0.66145
Handedness × responding hand × force × electrode	4/36	0.1753	0.0438	B×C×E×F	1.32	0.27891
Handedness × responding hand × feedback × electrode	2/18	0.6709	0.3354	B×D×E×F	5.05	0.01814
Handedness × force × feedback × electrode	4/36	0.2978	0.0744	C×D×E×F	1.89	0.13205
Responding hand × force × feedback × electrode	4/36	0.1480	0.0370	B×C×D×E×F	1.11	0.36654
Handedness × responding hand × force × feedback × electrode	4/36	0.1278	0.0319	B×C×D×E×F	0.95	0.44133
Subjects (F)						
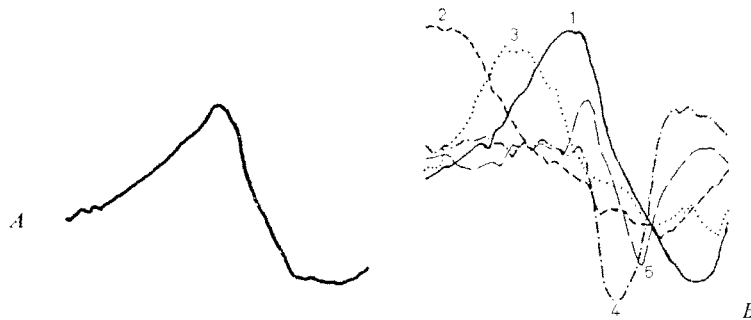
Fig. 7. *A* Grand average wave form obtained over all experimental conditions and all subjects (sum of 132 ERPs). *B* Factor loadings for each of the five factors extracted from a factor analysis of the ERP. The factors are labeled. Factor 1 is heavily loaded on variables associated with the overall wave form, factor 2 with the baseline, factor 3 with N_1, factor 4 with the N_2-P_2 transition points and factor 5 with component P_2.

The factor analysis is especially interesting in the light of the new information that it reveals concerning the late positive component (P_3) of the ERP. Table II presents an analysis of variance of factor scores on factor 5 (P_3) as the dependent variable. Both the presence and the absence of feedback have a significant effect on this factor. In fact, the factor scores for the two different feedback conditions are of equal amplitude but opposite polarity, positive and negative for the with and without feedback conditions, respectively. This provides a more direct assessment of the effect of feedback on the late positive component (P_3) which has too wide a range of latencies to be reduced to one characteristic measure. The responding hand $\times$ force $\times$ electrode interaction also has a significant effect ($p < 0.00001$) on the P_3 factor. Figure 8 shows a plot of these factor scores for C_3 and C_4 for right- and left-hand responses in each of the three force conditions. It is clear that the P_3 factor is asymmetric at higher force levels; the degree of asymmetry increasing as a function of increasing force. For right-handed responses, the post-response positivity (P_3) is consistently larger over the left sensorimotor condition while for left hand responses this holds true for all but the 0.25 force condition. This relation holds for both the with and without feedback conditions. We note that several of the third-order interactions are significant, but these will not be discussed in greater detail here.
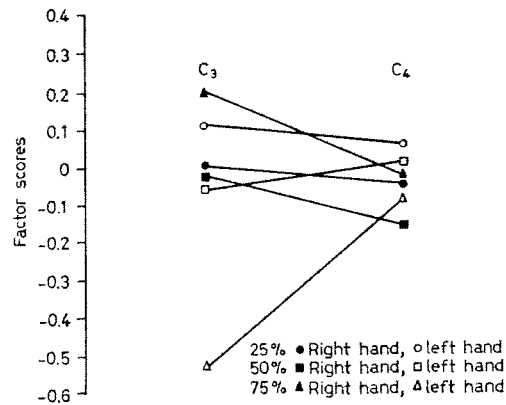
Fig. 8. Factor scores for the factor 5 or the P_2 component represented graphically for the C_3 and C_4 electrode positions for right- and left-hand responses, in each of the three force conditions.

Discussion

Handedness and contralateral dominance of N_1. Movement-related potentials were recorded from eleven subjects squeezing a dynamometer, at three different force levels, with their right or left hand. The presence or absence of hemispheric asymmetry and the degree of such asymmetry appear to depend on the subject's handedness, the hand used for response and response force.

On the whole, the clearest degree of contralateral dominance appears in right-handed subjects, for whom the pre-motion cortical negativity (N_1 and part of N_2 as well) is significantly larger over the contralateral sensorimotor location. The asymmetry is reduced for left (non-dominant) hand responses. Left-handed subjects are not mirror image right handers. The left-handers studied here demonstrate contralateral dominance for right (non-dominant) hand responses and a greatly reduced sensorimotor asymmetry for left (dominant) hand responses. The large differences between right- and left-handed subjects is not without precedent in both the electrophysiological and behavioral literature. All investigators are in agreement that the left-handed population tends to be quite heterogeneous and can best be characterized as highly variable whatever the reported measure. Thus, while it is not surprising that the results of the left-

handers in this study are different from those of the right-handers in that they show a reduced degree of hemispheric motor asymmetry preceding left-hand movements, an explanation for the right-hand contralateral dominance in left-handers is not readily apparent. We propose that a more extensive sampling of the left-handed population may provide several subgroups with different interhemispheric relations and a better estimate of the range of the left-handedness continuum.[1] Such data would also be more interpretable and informative when collected concurrently with several different measures (dichotic listening, inverted handwriting, horizontal scanning direction, orientation of drawn human profile, etc.) of the degree of cerebral dominance.

An especially interesting note concerning the data in both right- and left-handed subjects is that the absolute magnitude of the ipsilateral potential (N_i) is quite substantial. Uncrossed fiber systems of the brain allow a certain degree of bilateral sensory representation and motor control within each hemisphere. It has not only been shown that loss of ipsilateral function results in some sensorimotor deficits even when the contralateral hemisphere is intact, but also that although the majority of pyramidal cells fire with contralateral movement, some discharge only with ipsilateral movement [EVARTS, 1967]. It is difficult to disregard the size of the ipsilateral N_i yet its amplitude is difficult to reconcile with the interpretation that the activity in the contralateral system may suppress or cancel the activity in the supposedly weaker ipsilateral system. A pattern of voluntary movements performed by one hand is often involuntarily altered when another movement has to be carried out simultaneously by the contralateral arm (or in fact any other part of the body) [COHEN, 1970]. Although there is an observed interaction between the limbs during bimanual voluntary activity, the cortical mechanism be it bilateral excitation or unilateral inhibition remains unknown for both the uni and bi-manual conditions.

Force of response and N_i. While response force does accentuate N_i asymmetry, the absolute right-left asymmetry does not change with increasing force levels. Pilot data in our laboratory indicated that some minimal amount of force is necessary in order for the motor asymmetry to develop and be readily observable.

Our results are in accord with earlier reports (based on vertex data)

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[1] Note added in proof: In the time since this paper was submitted, 25 additional sinistral subjects were tested. These new data essentially confirm this statement.

that increasing the force required to accomplish a response results in an increased CNV preceding the response [REBERT et al., 1967; LOW and MCSHERRY, 1968]. As N_1 does not become more asymmetrical as a function of increased response force, our data are consistent with HILLYARD's [1973] two-component hypothesis which suggests that two sources contribute to the observed negativity: a lateralized slow negative wave specific to response-initiation and a relatively large, bilateral component, like the CNV, reflecting preparatory activity independent of the specific movement. Such a proposition is consistent with the notion that there is a family of task-related slow negative waves [DONCHIN et al., 1972] of which the N_1 is but one member.

Post-response components. In this experiment, the force of response also has a significant effect on the P_2 component of the motor potential. Like N_1, P_2 is larger at the motor cortex contralateral to the activated limb, with the degree of asymmetry increasing as a function of increasing force. These findings are consistent with the suggestion that P_2 represents activity resulting from kinesthetic feedback (proprioceptive and somatosensory impulses) produced by the movement [BATES, 1951; VAUGHAN et al., 1968; DEECKE et al., 1969]. Part of the P_2 complexity reported by various investigators is probably a result of the confounding effect of a feedback associated with the completion of a movement or the achievement of a given output level. Our data indicate that with a more explicit feedback manipulation, there are substantial changes in the shape of P_2. The more peaked positivity seen in the feedback condition can be attributed either (1) to a possible superposition of various EP components onto the motor potential P_2 or (2) to the generation of a potential similar to the P300 resulting from the resolution of response parameter uncertainty provided by the feedback stimulus.

Summary

We report an experiment designed to assess the degree to which premovement negativity (N_1) is associated with the preparation to execute a response by determining the degree to which parameters of the response determine its waveform, amplitude, and distribution over the motor area. Eleven subjects were asked to perform self-paced, voluntary squeezes on a dynamometer at six to eight recording sessions. There were four independent variables: (1) the self-reported handedness of the subject (right or left); (2) the hand used in responding (right or left); (3) the amount of force required for any particular series of squeezes – each subject responded at

three different force levels, preset at 25, 50, and 75% of his maximum determined separately for each hand, and (4) the presence or absence of an illuminated circle the extinguishing of which served to inform the subject when he has squeezed up to the required force level.

In right-handed subjects, N_1 was larger over the hemisphere contralateral to the responding hand. Left-handed subjects showed contralateral dominance when responding with the right hand and very little when responding with the left. Furthermore, while response force did accentuate N_1, the absolute right-left asymmetry did not change with increasing force levels.

These conclusions are supported by visual inspection, analysis of variance of N_1 area measures and a principal component analysis of the data. Our data are most consistent with a two-component hypothesis for the observed negativity: (1) a lateralized slow negative wave specific to response-initiation, and (2) a relatively large, bilateral component like the contingent negative variation, reflecting preparatory activity independent of the specific movement.

Acknowledgments

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