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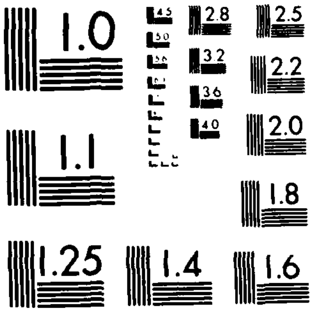

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IS HANDWRITING POSTURE ASSOCIATED WITH DIFFERENCES IN MOTOR CONTROL? AN ANALYSIS OF ASYMMETRIES IN THE READINESS POTENTIAL

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Levy and Reid's (1) hypothesis that persons who write using the inverted posture have ipsilateral control of distal limb movements, particularly those involved in handwriting, was tested in three experiments in which asymmetries in the readiness potential (RP) were measured. In the first experiment, each subject executed a self-paced repetitive squeeze. Contralaterally larger RPs were recorded from all subjects, irrespective of handwriting posture. In two other experiments, subjects performed the self-paced squeeze in one condition and write a single word repetitively in an analogous condition. Larger RPs were recorded over the contralateral cerebral hemisphere in most inverted-writing subjects in

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both conditions. Ipsilaterally larger RPs were recorded, however, from some left-handers while writing. These findings suggest that, although control of certain movements may originate from the ipsilateral motor cortex in a small proportion of left-handers, handwriting posture does not index this difference.

Is Handwriting Posture Associated With Differences in Motor Control?: An Analysis of Asymmetries in the Readiness Potential

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Abstract

Levy and Reid's (1) hypothesis that persons who write using the inverted posture have ipsilateral control of distal limb movements, particularly those involved in handwriting, was tested in three experiments in which asymmetries in the readiness potential (RP) were measured. In the first experiment, each subject executed a self-paced repetitive squeeze. Contralaterally larger RPs were recorded from all subjects, irrespective of handwriting posture. In two other experiments, subjects performed the self-paced squeeze in one condition and wrote a single word repetitively in an analogous condition. Larger RPs were recorded over the contralateral cerebral hemisphere in most inverted-writing subjects in both conditions. Ipsilaterally larger RPs were recorded, however, from some left-handers while writing. These findings suggest that, although control of certain movements may originate from the ipsilateral motor cortex in a small proportion of left-handers, handwriting posture does not index this difference.

Levy and Reid (1) have conjectured that the position of one's hand when writing may index differences in the organization of the motor system. Persons who write with the noninverted style (hand below the line and pencil tip pointed toward the top of the page) are thought to have larger crossed pyramidal pathways and contralateral control of handwriting movements, whereas those who write with an inverted posture (hand above the line and pencil tip pointed toward the bottom of the page) may have mainly uncrossed fibers and ipsilateral control of these movements (see Fig. 1).*** Although Levy and Reid did not test their

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insert Figure 1 About Here

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hypothesis, results from an analysis by Herron, Galin, Johnstone and Ornstein (2) of the relative alpha power recorded over the two hemispheres while subjects were writing suggest that these movements are contralaterally controlled in both inverted- and noninverted-writing persons.

A systematic test of the model using handwriting as the primary task has not been reported. Levy and Reid's model has been interpreted by some to include the control of other distal limb movements in addition to those involved in handwriting (e.g., 3-5). This interpretation has been assessed by measuring reaction time (RT). McKeever and Hoff (3) reported that the performance of noninverted-writing left-handers in a simple RT task was consistent with the inference that control of distal limb movements in this group originates from the contralateral motor cortex. Inverted-writing left-handers showed a complex interaction between responding hand and RT. Nevertheless, McKeever and Hoff concluded that in their subjects control was contralateral as well. In contrast, Moscovitch and Smith (4,5), who used a go/no go manual RT task, provided partial support for the inference that in inverted-writing left-handers movements other than those involved in the control of handwriting originate from the ipsilateral hemisphere in inverted-writing left-handers. Support for this inference was restricted, however, to a visuomotor response. Evidence was provided for contralateral control of manual responses in both handwriting posture groups to auditory or tactile stimuli.

Thus, analyses of distal limb movement control in the various handwriting posture groups using manual RT procedures have generated conflicting findings. It is noteworthy that in these studies inverted-writing subjects showed a response pattern that differed from the usual. The possibility exists therefore that in persons who write with the inverted posture the structure of the pyramidal system is such that certain limb movements are controlled by the ipsilateral hemisphere.

Currently, all techniques that can be used to identify those persons, if any, in whom the control of movements originates from the ipsilateral motor cortex are invasive. Development of measures to differentiate these modes of control would be of clinical value. Handwriting posture promises to provide such a test; however, the lack of consistent support for the model precludes confident use of of handwriting posture as an index of motor control. We report an attempt to obtain a more direct measure of this relationship by analyzing the readiness potential (RP) associated with the performance of self-paced squeezes and handwriting.**** Squeezes were selected as a reference movement for subsequent comparisons since previous work in our laboratory has established the reliability of the RP measured prior to squeezes, identified its asymmetry on the scalp, and isolated some factors that alter its amplitude and morphology (6-8).

The RP, originally described by Kornhuber and Deecke (9), is one of several movement-related potentials (MRP) that can be recorded from the human scalp in association with a voluntary motor act. It appears as a slowly rising negative potential whose onset can occur as much as 1000 msec prior to the execution of a voluntary movement and is always largest at central scalp sites contralateral to the responding limb (6-8,10-13). This pattern of asymmetry is consistent with the known locus of control in the pyramidal pathways and suggests that it reflects the direction of control in this system. If so, then a strict interpretation of Levy and Reid's model implies that the pattern of RP asymmetry associated with handwriting, but not with squeezing, should be different in inverted writers. If pyramidal control of handwriting is indeed ipsilateral in this group, then larger RPs should be observed over the ipsilateral rather than the contralateral sensorimotor areas. Noninverted handwriters, however, should have contralaterally dominant RPs when writing. Both groups would be expected to have contralaterally larger RPs when squeezing. Our analysis of the RPs associated with both squeezing and handwriting tested each of these predictions.

EXPERIMENT I

Methods

Subjects. Twenty-four males***** from the University community, ranging in age from 18 to 33 and including two of the authors (TRB and RC), participated in the experiment. With the exception of the two authors, all subjects were paid for their participation. These subjects were selected such that three handedness/handwriting posture groups were obtained with eight subjects in each group. The groups were noninverted-writing right-handers (RN), noninverted-writing left-handers (LN), and inverted-writing left-handers (LI). Four members of each group had a left-handed family member in their immediate family and four did not. Each subject completed the Edinburgh Inventory (14) of handedness, although degree of handedness was determined by using only the initial five items of the questionnaire (15). All of our subjects reported at least four preferences in one direction. Handwriting posture was assessed while the subject completed the handedness inventory, using the criteria of McKeever (16). Each noninverted-writing left-hander was also asked if he could remember being taught to write in the noninverted style. All of these subjects were then required to write a sentence with the bottom of the paper aligned with the edge of the table. One subject was eliminated because he was taught to write in the noninverted style. One person was eliminated on this basis. A subject could also be excused from participation in the study if he assumed the inverted posture when writing with the paper even with the edge of the table. No one was rejected on this basis. Thus, twenty-five persons were screened from whom twenty-four were selected as subjects for this experiment.

Electrode placements and recording apparatus. The electroencephalogram (EEG) was recorded from Fz, Cz, and Pz as well as from lateral electrodes placed 4 cm to the right and left of Cz along the interaural line (International (10-20) Électrode Placement System [17]). These sites were selected because they have been demonstrated in our laboratory to be the locations at which the largest RPs are recorded during execution of a squeeze (6,7). Additional electrodes were used to record referentially, and "bipolarly", the electrooculogram (EOG) from above and to the right of the right eye.

Ag/Ag-Cl electrodes, affixed with collodion, were used to record the EEG and EOG. The EEG and EOG were amplified by Grass amplifiers (model

7P122) with an upper cutoff of 35 Hz, and modified to have an 8.0 second time constant. The electromyogram (EMG) was recorded from the responding arm with Beckman biopotential electrodes, affixed with adhesive collars. One EMG electrode was placed a third of the distance from the lateral humeral epicondyle to the styloid process of the ulna, and the other approximately 7 cm in the distal direction along the same line. EMG was amplified by a Grass model 7B3B preamplifier and integrator combination (1/2 low frequency .15 and time constant .02). Electrode impedance for the EEG and EOG was below 5 kilohms (Grass Electrode Impedance Meter), and differences between the lateral scalp electrodes never exceeded 2 kilohms. The acceptable impedance level for EMG electrodes was 15 kilohms.

Data collection. Data were digitized on-line at 100 samples/sec for a total epoch of 2560 msec beginning 1280 msec prior to the onset of the squeeze. Data were stored on digital tape and averaged off-line using a Harris/7 computer. Trials in which gross eye movements occurred were excluded from any data analysis. Trials were rejected if the sum of the squared digitized values exceeded a criterion value established by visual inspection of a large sample of EOG traces and their corresponding digital values. Averaging of EEG and EOG was aligned by the initial deflection of the force transducer (Daytronic linear velocity force transducer, model 152A, with a conditioner amplifier, model 830A).

Procedure. Each subject sat in a reclining chair and was instructed to squeeze a dynamometer attached to a handle. All subjects were exhorted to restrict movement to the muscle groups directly involved in the squeeze and to make the response as forceful as possible. Maximum displacement of the dynamometer was 0.025 cm. The squeezes were self-paced. Each subject was encouraged, however, to establish an intersqueeze interval of 7-8 seconds. Prior to initiating a squeeze the subject was told to fixate a point (whose distance varied as a function of an individual's judgement of a comfortable distance; range from 60 to 100 cm) for approximately 3 seconds. One experimental session of approximately 2 hours was required in which each subject made 96 squeezes with the left hand and 96 with the right hand. Response hand order was determined randomly and was counterbalanced. Each subject performed four blocks of trials, alternating hands in each. The initial two blocks consisted of 64 trials and the last two of 32. Rejection of trials because of eye blink artifact was rare. The range of acceptance was from 85% to 100%.

Results and Discussion

The broad interpretation of Levy and Reid's model predicts that the ipsilateral RPs will be larger than the contralateral RPs in inverted-writers across all movements. We call such a pattern "ipsilateral dominance". Our data fail to support this prediction. All subjects, regardless of handwriting posture, produced RPs that were larger over the hemisphere contralateral to the response hand. Grand averages depicting these lateral asymmetries are shown in Fig. 2. This asymmetry, showing contralateral dominance, emerged between 600 and 800 msec prior to the squeeze and persisted throughout the pre-movement period.

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insert Figure 2 About Here

We calculated the area under the contralateral and ipsilateral RP curves for each subject by computing a baseline voltage for the initial 400 msec of the pre-movement period and measuring the change in voltage from this baseline value for each point in the 800 msec preceding response onset. These values were summed to provide an estimate of the area under the curve for this pre-movement period (i.e., the RP). An analysis of variance on these values confirmed that the RP was markedly larger over the hemisphere contralateral to the response hand (Response Hand x Electrode, $F(4,84)=22.18$, $p < .01$). The mean values for this pre-squeeze response hand by electrode interaction are: C1' (left hand, -2393; right hand, -3014) and C2' (left hand, -3161; right hand, -2018).

Further confirmation was obtained from an analysis of "difference waves". These waves were computed by subtracting the average voltage at C1' from that at C2' for each point prior to the movement. The difference wave represents the amplitude difference between the two lateral electrodes during the pre-movement period. An analysis of these pre-squeeze difference waves revealed a significant response hand effect ($F(1,21)=47.50$, $p < .01$) which indicates a contralateral asymmetry that differed as a function of the hand executing the squeeze (see Figure 3). The magnitude of the asymmetry, as indicated by the absolute difference wave (determined by reversing the sign of the values for all negative-going difference waves), did not differ between the three groups.

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insert Figure 3 About Here

To ensure that these asymmetries were not associated with response output differences among each of the three groups, we measured the amplitude and peak latency of the force applied to the dynamometer on every trial, and performed an analysis of variance on these data. No significant relationships between peak latency or between the amplitudes with which different subjects squeezed the dynamometer and any of the independent variables were found. Yet, left hand squeezes were more forceful in all groups ($F(1,21)=11.44$, $p < .01$). In contrast, Kutas and Donchin (6) reported a significant reduction in the forcefulness of left hand squeezes by right-handers.

It interesting to note that Kutas and Donchin (6) reported that the asymmetry of the RP was reduced in both right- and left-handers prior to execution of a squeeze by the left hand. Neither we nor Kutas and Donchin (7) found such a reduction. Further, Kutas and Donchin (6) observed a bilaterally symmetrical RP in left-handers prior to a squeeze with the left hand, suggesting bilateral control of this movement. We did not replicate this finding. Rather, we found no differences between handedness groups in the magnitude or direction of RP asymmetry. This variation cannot be attributed to force output differences since Kutas and Donchin (8) have shown that the degree of RP asymmetry is unchanged beyond some minimal force output. It may be relevant that we measured the RP produced in association with approximately 90 squeezes, whereas Kutas and Donchin records associated with 600 to 1000 squeezes per subject. By using a large number of trials, differences may have emerged that would not be apparent with fewer trials.

In summary, the pattern of RP asymmetry we observed prior to the execution of a self-paced squeeze was not correlated with the subjects' handwriting posture. Inverted writers did not differ from the noninverted writers; no subject in either left-handed group produced ipsilaterally dominant RPs. This finding cannot be interpreted, however, as conclusively indicating that inverted-writing persons do not have ipsilateral control of handwriting. The cerebral mechanisms that control the fine distal movements associated with handwriting may differ from those subserving a ballistic squeeze. A stricter test of Levy and Reid's conjecture can be accomplished by characterizing the RP generated in association with handwriting. Thus, in a second experiment we required that each subject perform a self-paced handwriting task in one condition and a self-paced squeeze in another.

EXPERIMENT II

Methods

Subjects. Twenty-three males from the University community, ranging in age from 18 to 32, were paid for their participation. They were selected according to the criteria used in Experiment I. However, only subjects without left-handed relatives were selected as the data of Experiment I indicated that when squeezing with the left hand the asymmetry is reduced for these subjects. Each subject had to write and throw with the dominant hand. This selection procedure produced three groups: RN (n=6), LN (n=6), LI (n=11).

Electrode placements and recording apparatus. The recording procedures used in this experiment were identical to those used in the first experiment, except that the EMG electrode placements differed. Bipolar recordings were made from two muscles involved in the control of handwriting (18), the extensor carpi ulnaris and the flexor carpi radialis. The signal averages of EEG and EOG data, in the squeeze condition, were synchronized with the initial deflection of the force transducer. In the handwriting condition by the initial application of pen pressure on a Computek Graphics Tablet (Series GT 50/10) served as the synchronizing trigger.

Procedure. Each subject was required to perform a number of movements in addition to handwriting and squeezing, however, in this analysis we restrict our discussion to only those two conditions. Each subject was tested over two experimental sessions of approximately 3 hours. Handwriting was always performed in the first session and squeezing in the second. The procedure varied in the squeeze condition from that used in the previous experiment. A block of trials consisted of 56 squeezes performed consecutively. Again, response hand order was determined randomly and was counterbalanced.

The handwriting condition was analogous to the squeeze condition; the task was self-paced with the subject instructed to write a word every 7-8 seconds. In one block of trials the subject wrote the word "he" 56 times in lower case script, and in another block of trials he wrote the word "hand" 56 times in lower case script. Half of the subjects began with "he" and half with "hand", the order of which was randomly determined.

The subject was instructed to hold his pencil approximately 2 cm from the writing surface. He was admonished to refrain from blinking for about 3 seconds prior to the initiation of writing and to maintain a quiescent EMG during this interval. At the end of this pre-writing period, he was instructed to move his pencil directly to the tablet and to write using his normal style and maintaining his usual pace (e.g., as when writing a letter). After finishing the word, he was told to smoothly lift his pencil off the tablet and to refrain from blinking for another 3 to 4 seconds. Following this sequence, he was instructed to initiate another trial within 7-8 seconds.

Data collection. Our data collection varied from that used in Experiment I in that we digitized on-line at 100 samples/second for a total epoch of 6120 msec beginning 1400 msec prior to the onset of the squeeze or the application of pressure to the writing tablet. Further, in addition to rejecting trials in the handwriting condition for EOG artifact, trials were also rejected on the basis of EMG variance. During data analysis, the EMG activity was sorted on the basis of variance and those trials were rejected whose variance was sufficient to disrupt the synchrony of the initial EMG onset and the application of pressure on the writing tablet. This selection criterion resulted in an acceptance rate in the handwriting condition that ranged from 25% to 95%. The mean number of trials accepted for each group in each handwriting condition are: RN (He=26, Hand=30); LN (He=44, Hand=44); LI (He=38, Hand=40). The range of acceptance in the squeeze condition was from 50% to 100%, with the mean number of accepted trials for each group being: RN (SR=45, SL=42); LN (SR=51, SL=49); LI (SR=46, SL=43).

Results and Discussion.

In Fig. 4 are presented grand averages, based on data acquired from 19 of the subjects, of the movement-related potentials (MRP) recorded from C1' and C2' during both movements for each group. The remaining four subjects showed a different pattern of activity and are discussed below. As is apparent, the pattern of RP asymmetry generated by the inverted-writing subjects when executing either movement is not consistent with the prediction we derive from Levy and Reid's model. In all groups of subjects, the area under the RP curve (determined for 600 msec prior to movement using a baseline of 500 msec) was larger over the hemisphere contralateral to the response hand in both the writing and squeezing conditions (Within group: Task x Electrode (RN, $F(3,15)=17.72$, $p < .01$); LN, $F(3,12)=15.27$, $p < .01$); LI, $F(3,21)=27.98$, $p < .01$)). Thus, the RN group had larger RPs over C1' during both handwriting tasks

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Insert Figure 4 About Here

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and when squeezing with the right hand; but dominance over C2' when squeezing with the left hand. In contrast, the LN and LI groups had larger RPs over C2' during both handwriting tasks and when squeezing with their left hand; dominance over C1' was apparent only when these subjects squeezed with their right hand (Between group: Group x Task x Electrode, F(6,48)=10.73, p < .01).

Our analysis also indicated that the area of the RP was significantly reduced in the RN group prior to writing "he" (Task, F(3,15)=8.44, p < .01). It is difficult to interpret this finding, however, given the small number of trials performed by these subjects and the variablility in the RP apparent across groups and tasks. Superaverages of the RP area and the associated standard deviations for each group are presented in Table 1. There is no obvious relationship between the subject's task and the area of the RP across the different groups. The direction of the asymmetry was consistent across these subjects, but the area of the RP and the degree of asymmetry did vary across subjects.

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insert Table 1 About Here

In Experiment I, we failed to replicate Kutas and Donchin's (6) finding that the RP, particularly in left-handers, was reduced prior to a squeeze with the left hand. Our analysis in this experiment of the difference waves associated with squeezing confirmed the area analysis and indicates that the RP is contralaterally larger prior to a squeeze with either hand (Response Hand, F(1,16)=81.32, p < .01). However, the degree of asymmetry, as revealed by the absolute difference score, varied between groups. The magnitude of the RP asymmetry in noninverted-writing subjects did not differ across response hands, whereas that of the inverters was larger prior to a left hand squeeze (Within groups, Response Hand: LI, $F(1,7)=8.44$, $p < .01$; Between groups, Group x Response Hand: $F(2,16)=3.17$, $p=.07$). Interestingly, although the area of the RP did not differ between groups and response hands when squeezing, left hand responses were more forceful in noninverted- but not in inverted-writing subjects (Within groups, Response Hand: RN, $F(1,5)=6.87$, $p < .05$; LN, $F(1,4)=20.17$, $p < .05$; Between groups, Response Hand, $F(2,16)=19.88$, $p < .01$; Group x Response Hand, $F(2,16)=3.15$, $p=.07$). This finding does not replicate that of Experiment I in which each group was observed to squeeze more forcefully with the left hand. These data, those from Experiment I, and those of Kutas and Donchin (6-8) suggest the relationship between response force and the size of the RP is rather complex. The form of this relationship remains to be identified.

Of particular interest in this experiment, however, is our finding that most inverted- and noninverted-writing subjects produced contralaterally dominant RPs in association with either movement. The direction of the RP asymmetry when squeezing replicates that seen in Experiment I; that is, contralaterally larger RPs were found for every subject in each group in the period preceding the execution of a squeeze. Furthermore, both noninverted- and inverted-writing subjects had the same pattern of RP asymmetry when writing. This observation does not support the prediction we derive from Levy and Reid's model that inverted-writing persons will have ipsilaterally dominant RPs.

Four of the left-handed subjects did show a pattern of RP asymmetry that suggests ipsilateral control of handwriting. These patterns are sufficiently variable, however, to preclude firm conclusions. For example, only two of the subjects had ipsilaterally dominant RPs in both handwriting conditions. The other two were difficult to characterize, both appearing ipsilaterally dominant in only the "he" condition. Unfortunately, none of these subjects was available for subsequent testing, and only two returned for the squeeze condition. Of the two subjects with ipsilateral dominance across handwriting conditions, we have a complete set of data for only one subject. This subject produced ipsilaterally dominant RPs prior to handwriting but contralaterally dominant RPs prior to squeezing. Interestingly, he writes with his hand in the noninverted posture. The RPs generated by this subject are shown in Fig. 5. The three other subjects are inverted-writing left-handers.

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insert Figure 5 About Here

These findings suggest that in some small proportion of left-handers control of handwriting may originate from the ipsilateral motor cortex but that handwriting posture may not be the important variable associated with this variation.

The findings from this experiment fail to provide general support for Levy and Reid's model. However, since a relatively small number of trials was used to generate the RPs in the handwriting conditions, we conducted a third experiment in which each subject was required to write the words "he" and "hand" two hundred times.

Experiment III

Methods

Subjects. Twenty-two males from the University community, ranging in age from 18 to 34 and including two of the authors (TRB and RC), participated in this experiment. All subjects, with the exception of the two authors, were paid. Subjects were selected using the criteria of

Experiment II. In this experiment, however, we were able to identify an inverted-writing right-handed male. This subject has a family history of left-handedness. Nevertheless, because of the difficulty in finding inverted-writing right-handers, particularly males, we tested him. Thus, our groups consisted of: RN=6, RI=1, LN=6, LI=9. Two of these subjects in both the RN and LN groups, and three in the LI group, had also been subjects in Experiment II. All recording and data collection aspects of this experiment were identical to those used in Experiment II though the procedure used varied. Each subject wrote the words "he" and "hand" 200 times in two separate blocks of self-paced trials and made 60 voluntary squeezes with the left and right hand in two other blocks of trials. The handwriting tasks were performed by each subject prior to the squeezes. The first word written in the handwriting condition (he or hand) and the first hand used in the squeeze condition (left or right) were counterbalanced. Each subject was tested in one experimental session that lasted three hours. Our instructions strongly emphasized the importance of maintaining a quiet EMG prior to touching down to write. Individual trials were rejected on the basis of both EOG and EMG variance. These selection criteria resulted in an acceptance level in the handwriting and squeeze conditions of from 50% to 100%, and in the following mean number of accepted trials: RN (He=168, Hand=166, SR=46, SL=48); LN (He=174, Hand=175, SR=51, SL=51); LI(He=157, Hand=159, SR=48, SL=47).

Results and Discussion

The findings in this experiment substantiate those reported in Experiment II. Fig. 6 presents the MRPs for each group in the four different conditions. Again, the contralateral dominance of the RP is

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Insert Figure 6 About Here

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clearly apparent in each of the handedness and handwriting posture groups. The touchstone of our test of Levy and Reid's conjecture is the relationship between RP asymmetry and handwriting posture as revealed in the within groups interaction, task by electrode, and the between groups interaction, group by task by electrode. Each was significant and indicated that the asymmetry (as determined by the area under the RP curve for the 600 msec prior to movement using a baseline of 500 msec) was contralateral in both noninverted- and inverted-writing subjects (Within groups: Task x Electrode (RN, $F(3,18)=23.38$, $p < .01$; LN, $F(3,15)=37.36$, $p < .01$; LI, $F(3,18)=16.38$, $p < .01$; Between groups: Group x Task x Electrode, $F(6,51)=15.19$, $p < .01$). When right-handed subjects wrote or squeezed with their right hand the RP was larger over the left cerebral hemisphere. Conversely, when they squeezed with their left hand the RP was larger over the right hemisphere. In contrast to the predictions of Levy and Reid's model, left-handers, both noninverted- and inverted-writing, were also observed to produce contralaterally dominant RPs when writing or squeezing with the dominant hand; and this asymmetry reversed when a squeeze was initiated by the right hand. Thus, these findings replicate those of Experiment II and argue against Levy and Reid's hypothesis.

The mean areas and the associated standard deviations of the RPs for each group are shown in Table 2. As is the previous experiment, there is

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individual variation in the degree, but not the direction, of the RP asymmetry. In addition, we computed difference waves to demonstrate the magnitude of this asymmetry between groups, subjects, and tasks. The mean difference waves for each group in each condition are displayed in Fig. 7. The magnitude of the asymmetries revealed in the difference waves for each task did not vary between groups. As expected, however, the direction of the polarity differed between left- and right-handers when writing, and for all groups when squeezing with the left hand (Within groups, Task: RN, $F(3,18)=30.93$, $p < .01$; LN, $F(3,15)=31.32$, $p < .01$; LI, $F(3,18)=15.71$, $p < .01$; Between groups: Group, $F(2,17)=31.94$, $p < .01$; Task, $F(3,51)=41.19$, $p < .01$; Group x Task, $F(6,51)=14.36$, $p < .01$). In other words, when right-handers wrote, the RP was more negative at C1' (i.e., the difference wave was negative) and when left-handers wrote the RP was more negative at C2' (i.e., the difference wave was positive).

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insert Figure 7 About Here

When squeezing, difference waves were the opposite polarity for the two hands and in the same direction for each group. It is apparent in Fig. 7, however, that the degree of asymmetry was reduced across subjects when squeezing with the left hand (absolute difference wave, Response Hand, $F(3,51)=15.04$, $p < .01$). There were no differences between groups in the force exerted when squeezing and more forceful squeezes were made by all groups with the left hand (Response Hand, within groups: RN, $F(1,6)=6.44$, $p . < 05$; LN, $F(1,5)=11.98$, $p < .01$; LI, $F(1,6)=10.74$, $p < .05$; Between groups, Response Hand, $F(1,17)=24.67$, $p < .01$). The reduction in RP asymmetry with a left hand squeeze replicates the Kutas and Donchin (6) finding with right-handers and the force output is consistent with our first experiment. These findings do vary, however, from those in our second experiment and from those of Kutas and Donchin (7, 8) for left hand squeezes. The variability across experiments in RP asymmetry and response force associated with left hand squeezes suggests that the control of left hand movements may differ across individuals in both left- and right-handers.

Recall that only the RN group in Experiment II showed a reduction in the RP when writing. We expressed little confidence, however, in the reliability of this finding given the small number of trials on which it was based. With a larger number of trials and presumably more reliable data, we found evidence in this experiment that whereas the RP differs for noninverters when writing or squeezing, in inverters it is equivalent in size prior to both movements. That is, the area under the RP curve was significantly reduced for the noninverted-writing but not for the inverted-writing subjects when writing (Within groups, Task: RN, $F(3,18)=7.60$, $p < .01$; LN, $F(3,15)=3.29$, $p < .05$; Between groups, Group X Task: $F(6,51)=3.60$, $p < .01$).

It is interesting to note that the one inverted-writing male we tested produced dramatic contralaterally dominant RPs in both handwriting conditions and when squeezing with his right hand. The asymmetry of the RP was greatly attenuated, however, when he squeezed with his left hand. The RPs generated by this subject are shown in Fig. 8. Recall that he

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Insert Figure 8 About Here

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had a history of familial left-handedness. Interestingly, this finding is consistent with the trend we found in Experiment I for subjects with left-handed relatives.

Two of the inverted-writing left-handers generated RPs that deviated from the pattern observed in the other left-handed subjects. One subject had ipsilaterally dominant RPs when writing and squeezing with his left hand but contralaterally dominant RPs when squeezing with his right hand. The other produced weakly contralateral RPs when writing, strong contralateral dominance when squeezing with the right hand, and an unusual pattern when squeezing with the left hand. This latter pattern was characterized by a slight contralateral asymmetry about 500 msec prior to the squeeze and a large ipsilateral asymmetry at the time of the squeeze. Since this pattern was so different from that seen in other subjects, we had the subject return and produce one hundred squeezes with each hand. The pattern persisted.

Two additional subjects were tested in the handwriting conditions only. These subjects, both males, are predominantly right-handed but, nevertheless, write with their left hand in the inverted posture. Contralaterally larger RPs were manifest in each subject prior to writing.

General Discussion

According to the predictions that we derive from Levy and Reid's hypothesis, ipsilaterally larger RPs should be generated in inverted-writing persons prior to initiating a distal limb movement. We tested this prediction in three experiments by measuring asymmetries in the RP prior to squeezing or writing. In each experiment, contralaterally dominant RPs were observed in association with either movement in both inverted- and noninverted-writing persons. We conclude that in most people distal limb movements mediated by the pyramidal system are controlled from the contralateral motor cortex. However, ipsilaterally larger RPs were manifest in some left-handers prior to writing. These data suggest that handwriting may be controlled from the ipsilateral motor cortex in a small proportion of left-handers.

Levy and Nagylaki (19) hypothesized that handedness and cerebral lateralization are determined by two diallelic genes, one of which controls the hemisphere that is dominant for speech and manual skill, and the other of which whether movement is controlled from the contralateral or ipsilateral motor cortex. The dominant alleles are considered to produce left hemisphere mediation of speech and contralateral control of movement. In discussing Levy and Nagylaki's theory, Morgan and Corballis (20) wrote that "the idea that control of the hand could be ipsilateral rather than contralateral in some recessive minority is, at best, debatable. It is generally thought that motor control of the extremities is largely if not exclusively contralateral" (p. 274). Our data indicate that a small proportion of left-handers may indeed have ipsilateral control of certain distal limb movements. The factors associated with this control variation remain to be isolated, although our findings do argue against using handwriting posture as an index of this difference. We controlled sex, degree of handedness, and family history of left-handedness, variables widely recognized as contributing to differences in cerebral laterality. Consequently, no variable obvious to us is associated with the observed differences.

Our findings differ from those reported in RT investigations of Levy and Reid's model in that we failed to find any systematic differences in inverters suggestive of common variation in motor system organization. As described above, McKeever and Hoff's (3) findings did not support the inference that distal limb movements are controlled from the ipsilateral motor cortex in inverters, whereas Moscovitch and Smith (4, 5) reported directional differences in RT suggestive of ipsilateral control only in the visuomotor pathways of these persons. This variability across RT paradigms raises questions about the validity of these procedures as tests of motor control. With the exception of simple RT procedures, the validity of more complex RT tasks in the assessment of hemispheric engagement is yet to be established (21). Thus, although our failure to find any consistent evidence for organizational differences in the pyramidal system of inverted-writing persons may result from the engagement of different muscles in the tasks we employed, any comparison between the various paradigms is premature until replications of the RT analyses and characterization of the MRPs associated with a variety of movements have been accomplished.

Nevertheless, a common observation in the different studies is that inverters vary in some way from noninverters. Our finding in Experiment III that these subjects generated RPs of equal area when writing or squeezing suggests that the mechanisms controlling handwriting may be activated differently in inverters. This variation may represent the engagement of cerebral hemispheres with different functional capabilities or with differences in motor control organization (22). One expression of these cerebral differences may be, of course, use of the inverted posture when writing. Other differences in, for example, acquisition of a skilled movement, may obtain as well. Since inverted-writing persons do seem to differ in the movements thus far studied, a significant problem for future research is characterization of the behavioral and physiological processes associated with this writing posture.

It is interesting to note that in this series of experiments and in the work of Kutas and Donchin (6-8), there is considerable variability in both the degree of RP asymmetry and response force differences associated with left hand squeezes. Thus, left hand responses were observed to be less forceful, more forceful, or equally forceful in the various experiments; and the magnitude of the RP asymmetry associated with left hand squeezes was found to be smaller than, equivalent to, or greater than that for right hand squeezes. Comparable variability is not apparent when right hand squeezes are executed. Recent attention has focused on differences in neural organization between left- and right-handers (22). Our data suggest that control of left hand movements may differ in both handedness groups, and that identification of these control differences poses a problem worthy of subsequent research.

The objection can be raised that RPs may not reflect the organizational properties of the motor system and, therefore, failure to find the predicted asymmetries does not demonstrate whether control is ipsilateral or contralateral. Although there is controversy regarding the precise significance of the RP (23-25), there are strong indications that it is a manifestation, at the scalp, of preparatory processes associated with the initiation of a voluntary motor response.****** This conclusion is supported by the observation that the amplitude of the RP preceding the initiation of movements of different parts of the body varies in a manner consistent with the somatotopic organization of primary motor cortex (13), and that the largest changes are apparent over central scalp sites contralateral to the responding hand (6-8, 9-13, 26).

Further, an analysis of squeezing under conditions which allowed different degrees of preparation prior to the response revealed that the onset latency and lateral distribution of the RP are determined by the extent to which the subject is aware of when the response is to be made and, as a result, can prepare to respond (7).

Intracranial recordings in neurological patients (27, 28) and nonhuman primates (29-32) have also isolated slow negative shifts that precede a voluntary movement and are comparable to those obtained from scalp recordings. For example, Arezzo and Vaughan (33) recorded MRPs from epidural electrodes in rhesus monkeys trained to initiate repetitive wrist movements and found the RP to be absent in recording sites ipsilateral to the responding hand. Arezzo and Vaughan also reported that the largest potentials were found in the hand area of the contralateral primary motor cortex. Investigations of single unit activity in the precentral gyrus of monkeys (34-36) and cats (37) have identified a population of neurons in the contralateral sites whose firing patterns are altered as early as 500 msec prior to a movement. Although the relationship between changes in single neuron activity and the RP is unknown, the fact that they occur within the same time period allows for the possibility that both measures are manifestations of the same control system.

The evidence cited above supports the assumption that asymmetries in the RP reflect the direction of control in the pyramidal system. We conclude, therefore, that our data and those of Herron et al. (2) strongly indicate that in most people control of distal limb movements originates from the contralateral motor cortex. Further, although these movements may be controlled from the ipsilateral motor areas in a small number of left-handers, handwriting posture does not index this difference.

TABLE 1

AREA UNDER RP CURVE FOR SIGNIFICANT THREE-WAY INTERACTION--EXPERIMENT II

Group by Task by Electrode

	RN		LN		LI	
	C1'	C2'	C1'	C2'	C1'	C2'
He	-401 (712)	180 (568)	-1317 (899)	-2145 (696)	-659 (1534)	-1831 (1855)
Hd	-2389 (789)	-1453 (730)	-621 (1158)	-1527 (1699)	-286 (1100)	-1119 (2160)
SR	-1659 (1038)	-848 (612)	-2194 (1254)	-1437 (482)	-1299 (1057)	-822 (1087)
SL	-1579 (706)	-2326 (835)	-1460 (1187)	-1899 (882)	-1314 (876)	-2218 (1625)

TABLE 2

AREA UNDER RP CURVE FOR
SIGNIFICANT THREE-WAY INTERACTION--EXPERIMENT III

Group by Task by Electrode

	RN		LN		LI	
	C1'	C2'	C1'	C2'	C1'	C2'
He	-2136 (1121)	-865 (783)	-263 (717)	-1064 (688)	-1397 (866)	-2253 (1296)
Hd	-2130 (1031)	-799 (805)	-566 (917)	-1386 (1059)	-1412 (817)	-2381 (1365)
SR	-3786 (1376)	-2635 (1504)	-2583 (1313)	-1667 (1254)	-1616 (930)	-1218 (865)
SL	-3090 (1527)	-3528 (1481)	-1530 (1644)	-2006 (1716)	-1118 (1386)	-1884 (1664)

Footnotes

*** Levy and Reid (1, 38) argue that "there are variations among individuals in the proportion of crossed and uncrossed pyramidal fibers and that people in whom the uncrossed bundle is larger control the writing hand from the language hemisphere via the ipsilateral pyramidal tract" (1, p. 122). They estimate that approximately 60% of left-handers write with the inverted style and 40% with the noninverted posture, whereas 99% of right-handers use the noninverted posture and only 1% the inverted. Noninverted-writing right-handers and inverted-writing left-handers are postulated to have speech mechanisms in the left hemisphere, whereas noninverted-writing left-handers and inverted-writing right-handers are hypothesized to have speech mechanisms in the right hemisphere. Levy and Reid's estimate of the percentage of left-handers in the population who write with the inverted posture approximates that of those persons found to have larger uncrossed pyramidal pathways (4-8%), and in the left-handed population (60%) of those reported by Hecaen et al. (39) to have an agraphia associated with an aphasia produced by damage to the left hemisphere. Levy and Reid's inference derives in large part from these coincidental proportions. Thus, 60% of left-handers and 1% of right-handers are hypothesized to have larger uncrossed pyramidal bundles and ipsilateral motor control. Estimates of the proportion of inverted- and noninverted-writing left-handers vary (40), however, as does the proportion of each hand posture among left-handed males and females (3, 16). It should be noted that a recent review of Levy and Reid's model challenged their estimate of the incidence of uncrossed pyramidal pathways (41).

**** Since our concern is with global asymmetries in the cerebral macropotentials that are measured prior to the execution of a movement rather than with specifying the morphological characteristics of this activity, we have chosen to use the term readiness potential to refer to the entire complex of premovement activity. We are aware of the controversy that exists concerning the various components of the movement-related potential, however, our experiment is not designed to address these issues.

***** We decided to use only males in this series of experiments to eliminate one other source of variance from the data, sex. Differences between the sexes in cerebral laterality are well-documented (42) and for our purposes restriction of the sample to males seemed appropriate in testing Levy and Reid's model. Further, their model makes no distinction between the sexes in motor system organization. The variable of significance is handwriting posture and the organizational differences are presumed to characterize both males and females.

****** The fact that increases in pre-movement negativity are apparent at both contralateral and ipsilateral scalp sites should not be taken as an indication of a strong bilateral component in movement. Recordings of individual pyramidal neurons in motor cortex of nonhuman primates (34-38) and of humans (43) reveal that the ipsilateral motor cortex is generally silent prior to and during movement, although some small proportion of cells are active. The source of the ipsilateral RP in scalp recordings is unknown, but it may be produced by volume conductance at the scalp.

Acknowledgements

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Figure Captions

Figure 1. Diagrammatic representation of Levy and Reid's model (adapted from Levy and Reid (5), p. 122).

Figure 2. Experiment I: MRPs recorded at C1' and C2' from subjects identified on the basis of handedness and handwriting posture during execution of a self-paced ballistic squeeze. Movement onset is indicated in this and all other figures by a vertical line; the activity recorded at C1' is represented by a solid line and at C2' by a dashed line; and right-noninverters are identified as RN, left-noninverters as LN, and left-inverters as LI. The total recording epoch is 2560 msec with a pre-movement period of 1280 msec. EMG activity is not displayed in this figure because of a problem in the time constant setting that produced a signal which did not resolve during the recording epoch.

Figure 3. Difference waves calculated for each group. The solid and dashed lines identify the differences waves for left and right hand squeezes, respectively. The duration of the recording epoch is shown on the horizontal line at the bottom of the figure. Initiation of the squeeze is indicated by the vertical line which extends from 0 on the time axis. The pre-movement time is shown in msec as a negative value. In all subsequent figures the length of the recording epoch is displayed at the bottom of the figure and the time is shown in msec, with time 0 indicating initiation of the movement and negative values identifying the pre-movment period.

Figure 4. Experiment II: Grand average MRPs for each group in each condition. "HE" and "HAND" identify the two writing conditions; SR and

SL, the squeeze right and squeeze left conditions, respectively. The MRPs in each condition are displayed in the upper plot and the associated EMG is shown in the lower plot. The calibration mark for the MRPs is 10 uV and that for the EMG is 50 uV. In all subsequent graphs, when the calibration marks for the MRP and EMG are not labeled, the respective values are 10 and 50 uV. It should be noted that the large amplitude of the MRP apparent in the RN group in the SL condition was produced by unusually large activity generated by two subjects when making a left hand squeeze.

Figure 5. Example of an ipsilaterally larger RP in a noninverted-writing left-hander. Note that while the RP is largest over the contralateral hemisphere prior to squeezing with either the left or right hand, it is ipsilaterally larger before writing.

Figure 6. Experiment III: Grand average MRPs for each group in each condition. As was the case in Experiment II, two of the RN subjects produced unusually large MRPs in the SL condition and this is reflected in the amplitude of the grand average.

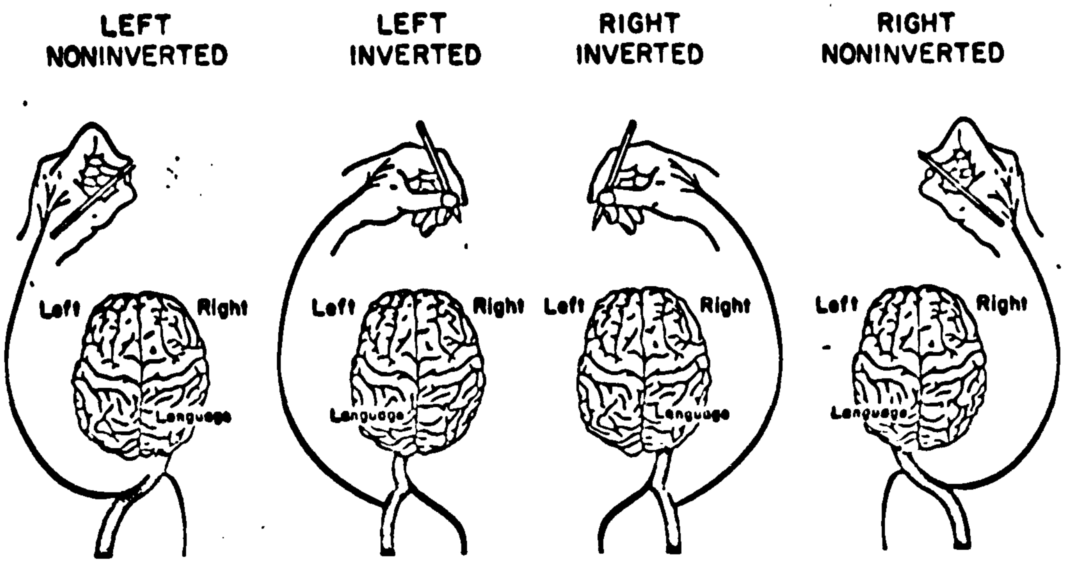
Figure 7. Difference waves for each group in each condition. In this figure the difference waves for each group are superimposed within a condition so that both the direction and degree of asymmetry between groups can be compared.

Figure 8. Grand average MRPs for the inverted-writing right-hander tested in Experiment III.

Table Captions

Table 1. Area measures for the significant Group x Task x Electrode interaction in Experiment II. Numbers in parentheses indicate the standard deviations; RN, LN, and LI designate the three handedness/handwriting posture groups.

Table 2. Area measures for the significant Group x Task x Electrode interaction in Experiment III.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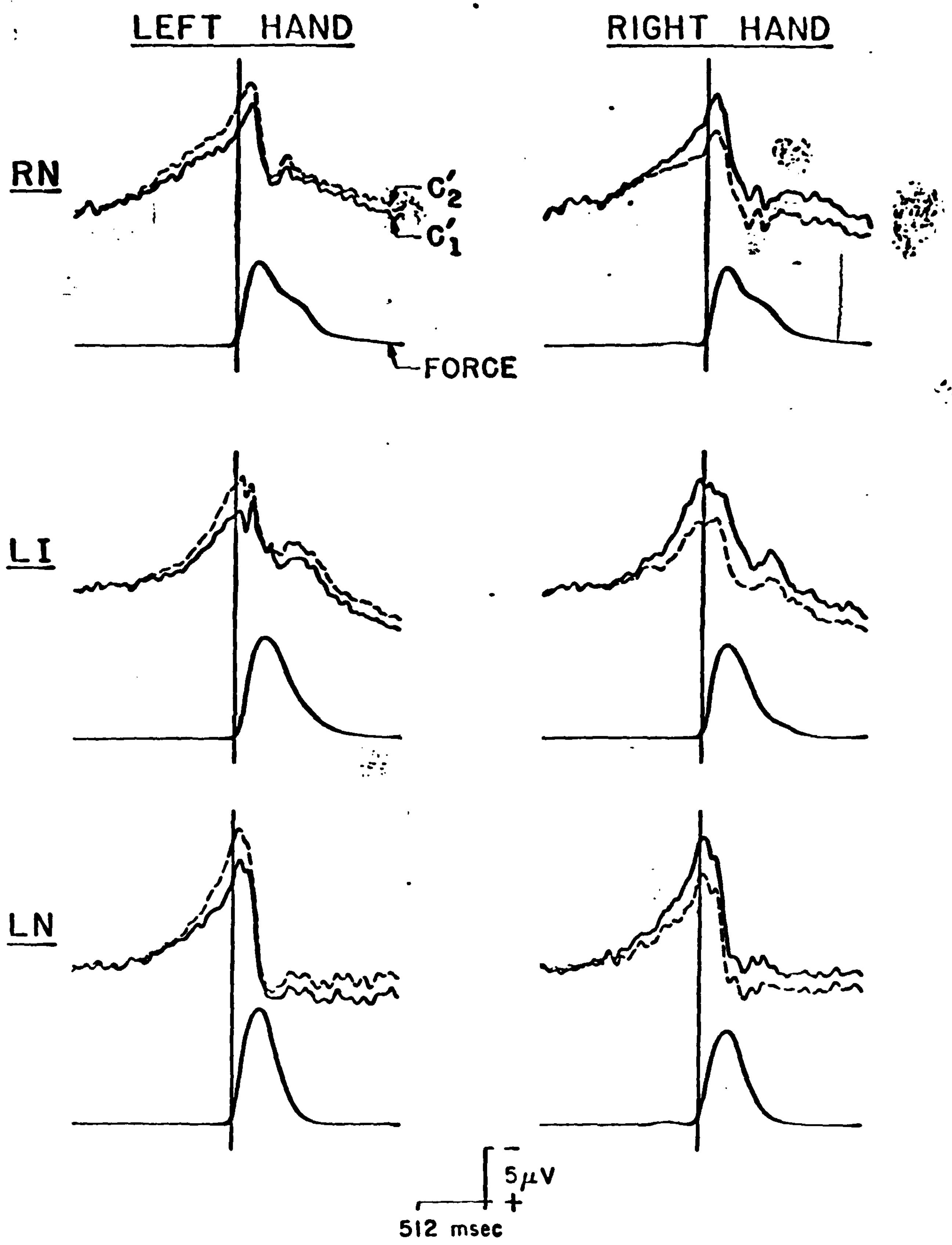
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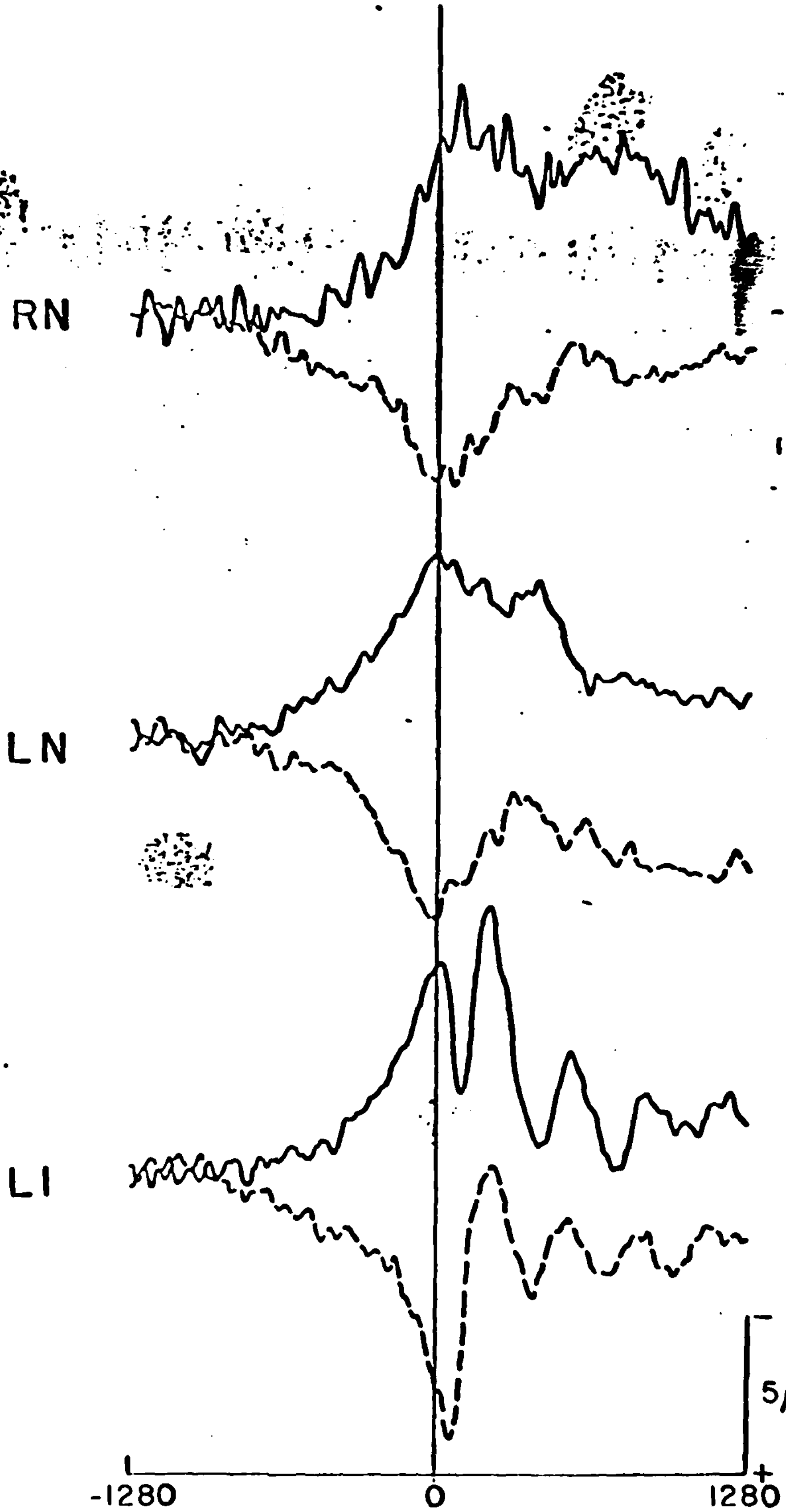
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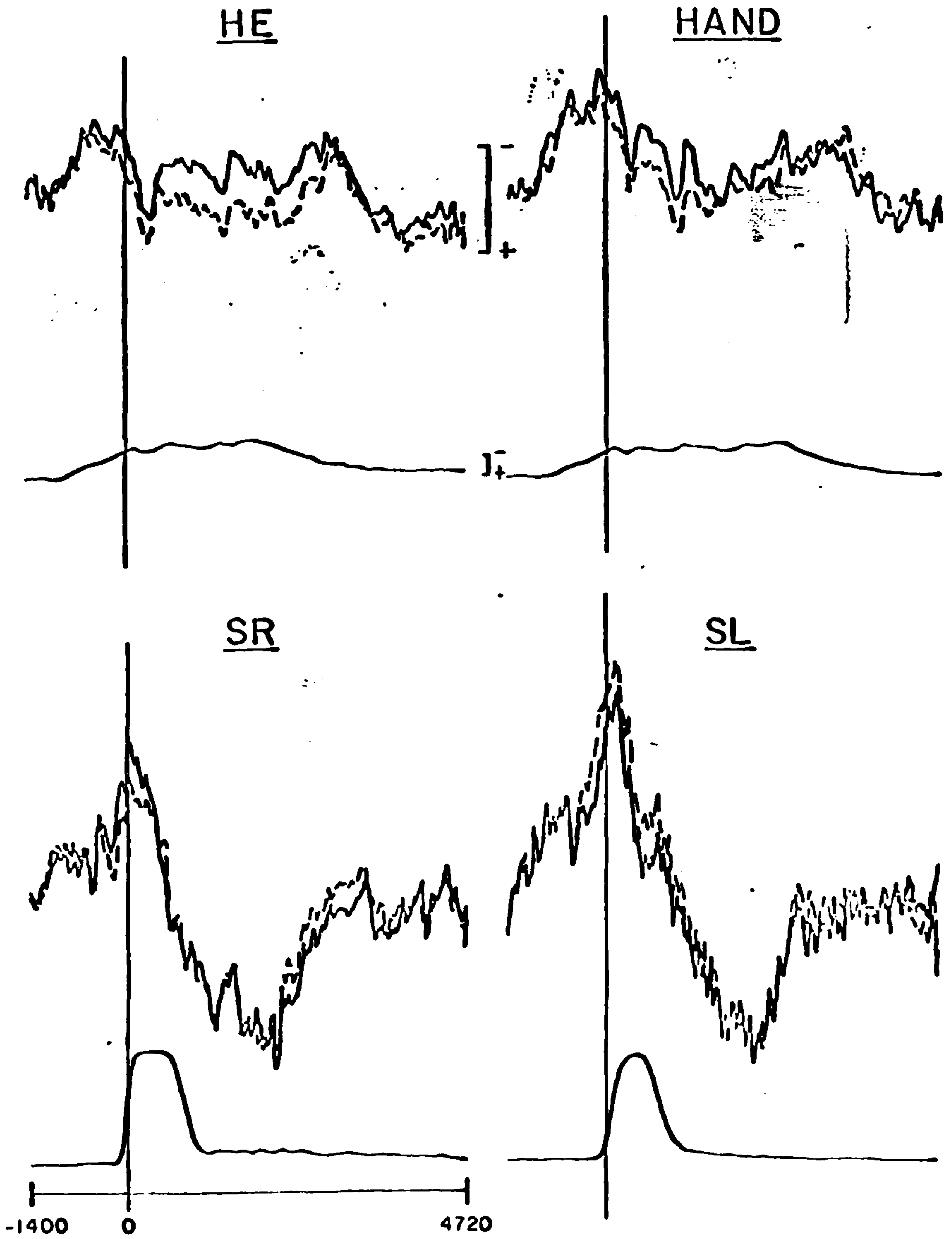
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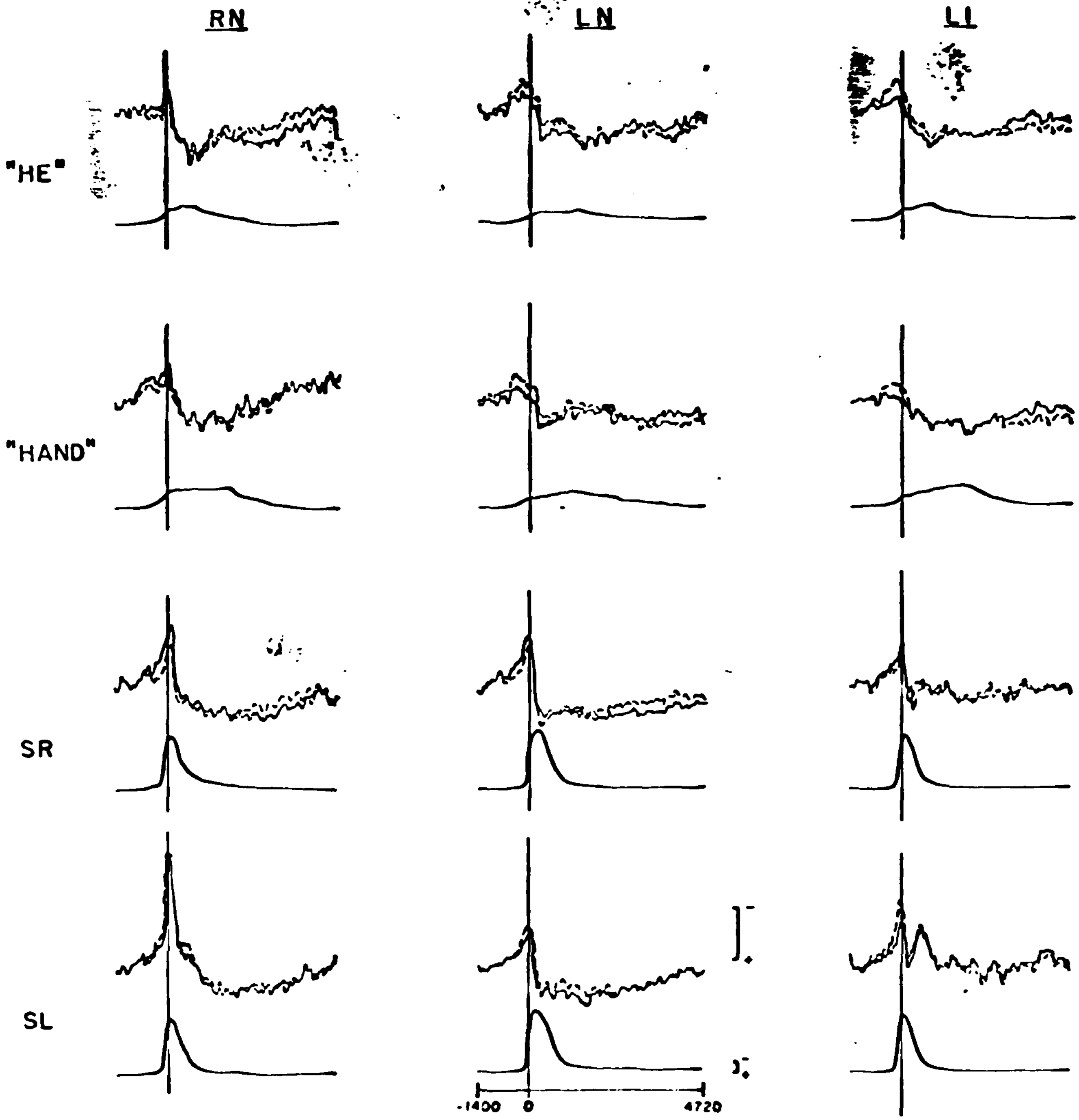
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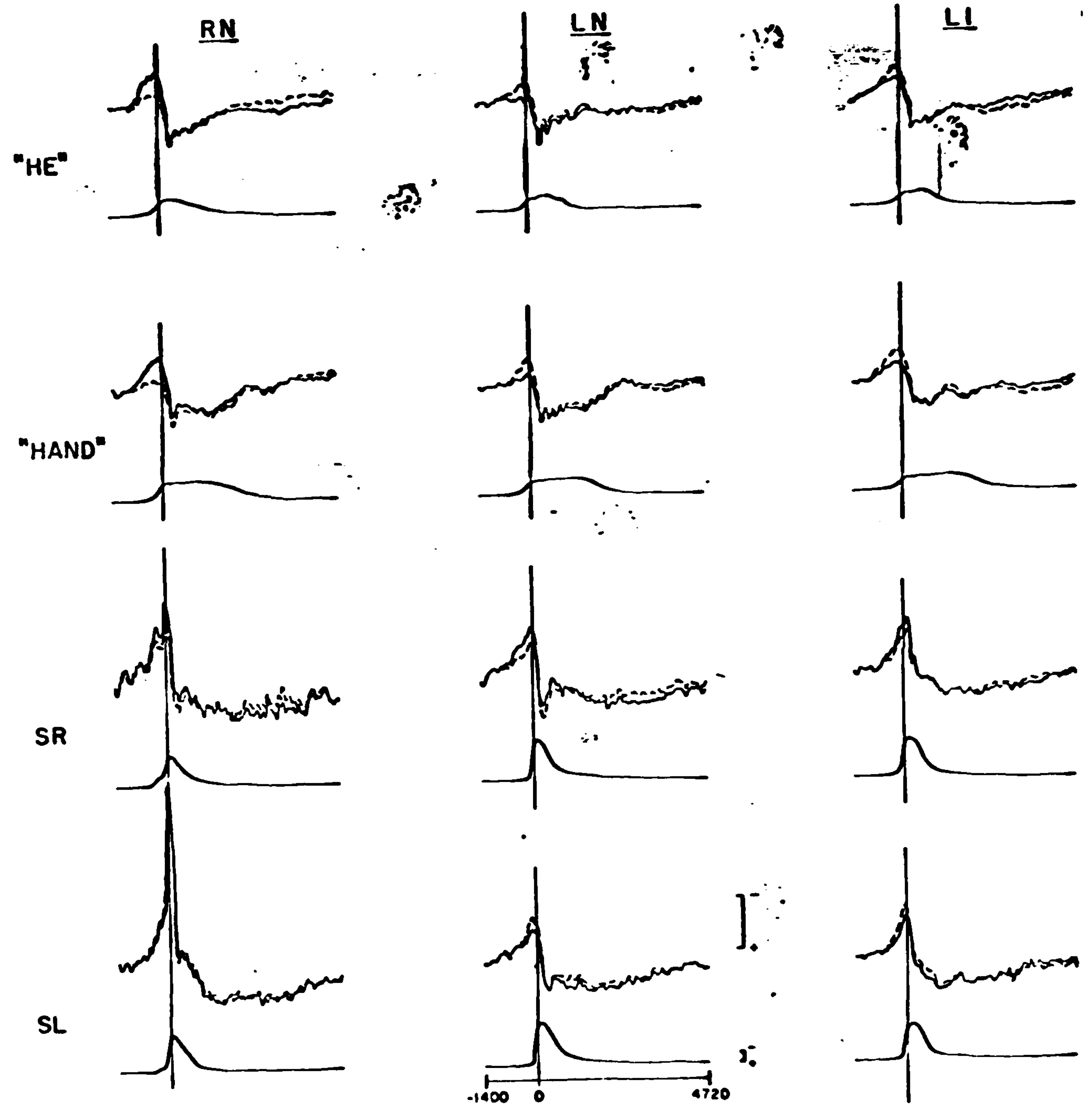
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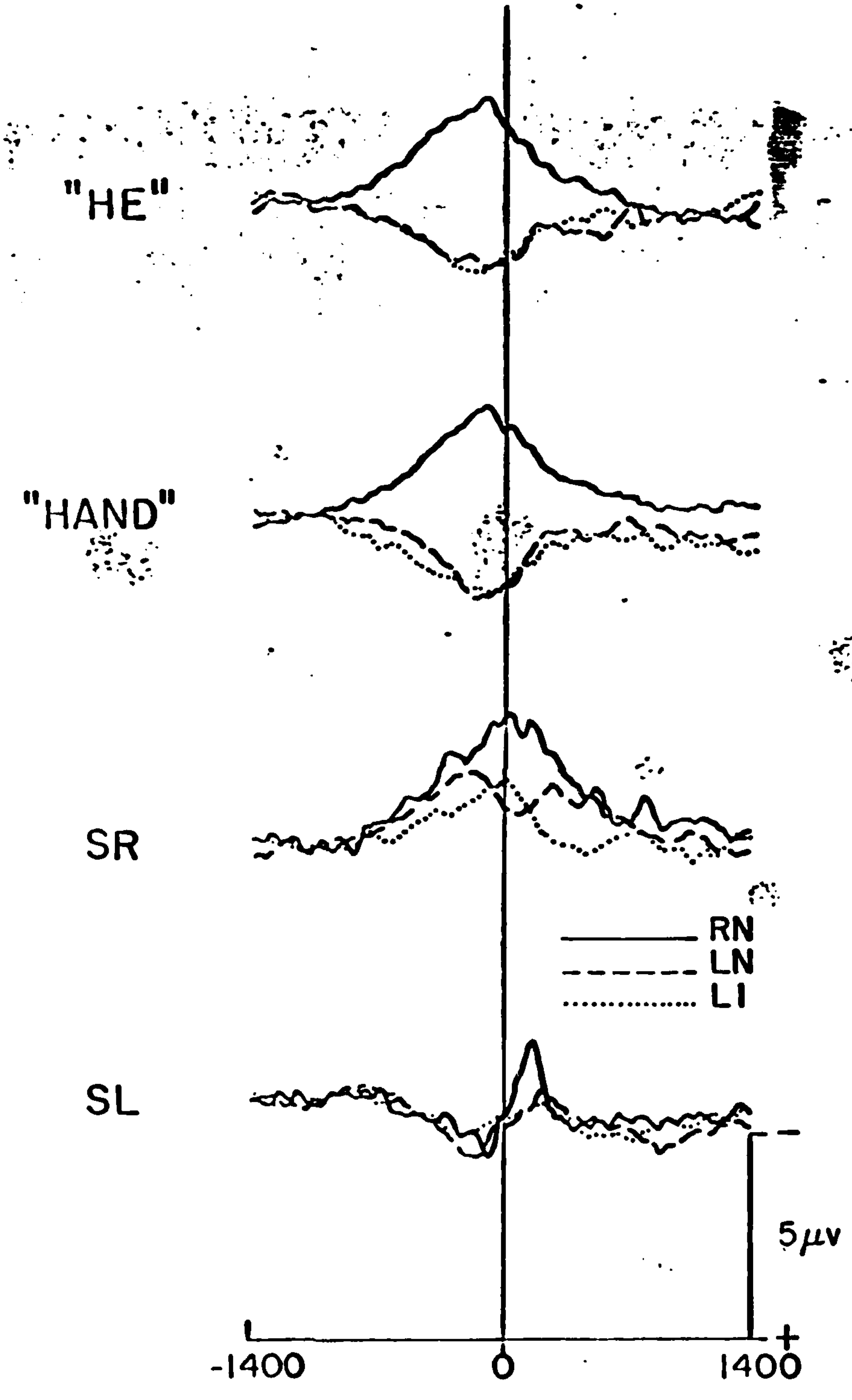
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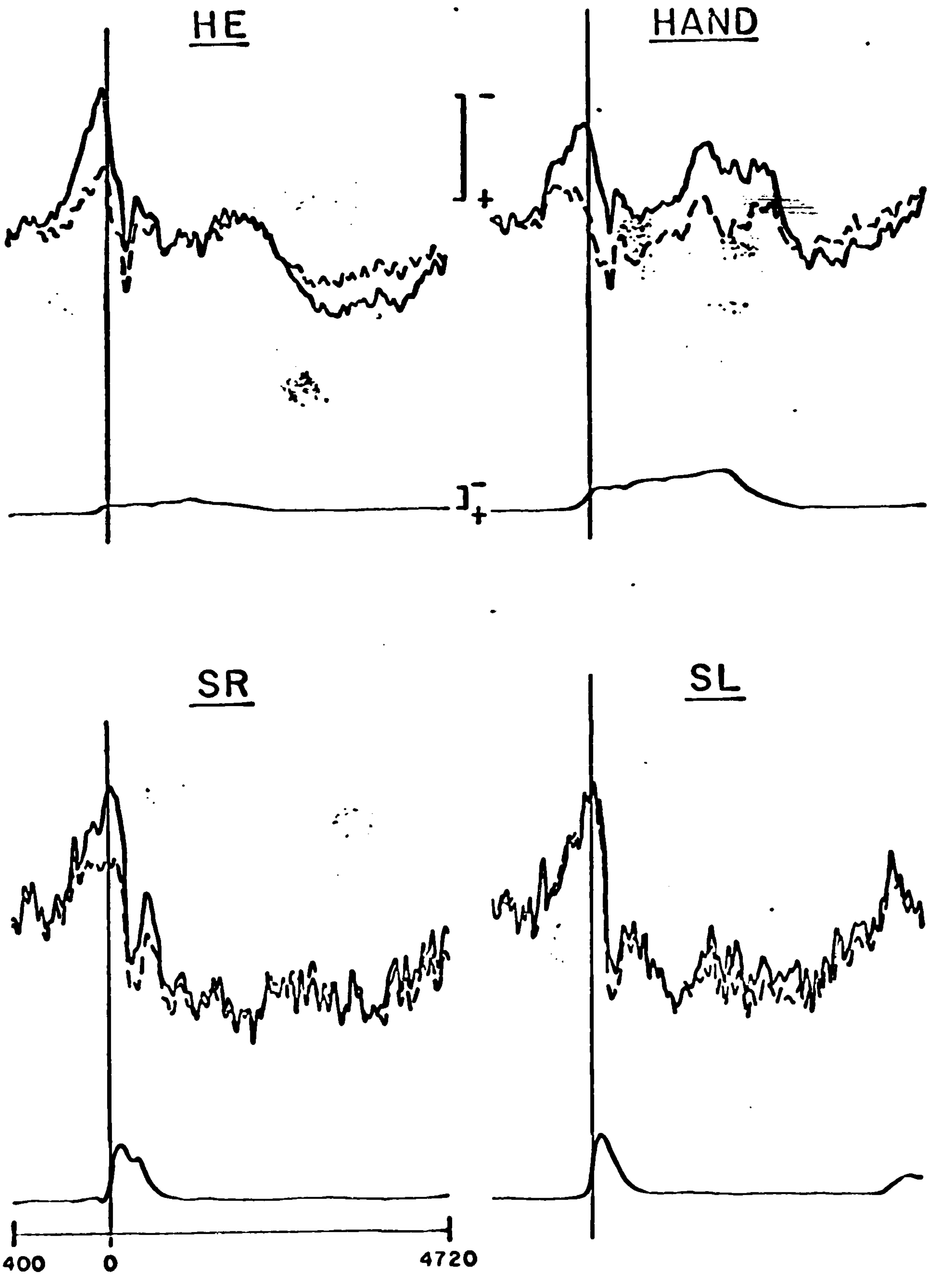
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