8 Report of Panel III: Preparatory Processes

Panel chair: W. Ritter

Panel members: S. Kelso

M. Kutas R. Shiffrin

8.1 SURVEY OF EVENT PRECEDING NEGATIVITIES

RITTER: After a brief survey of ERP components such as the CNV and the readiness potential, I shall outline recent changes in thinking about these potentials. Marta Kutas will then comment on the view that there are several subcomponents to the CNV. Then Scott Kelso will present an analysis of the process of movement control.

The CNV is usually studied while subjects are assigned a warned reactiontime task, in which two stimuli, S1 and S2, are presented and the interval between S1 and S2 is constant. The S1 is the "warning" stimulus, and S2 is a target or "imperative" stimulus to which the subject must somehow respond. Figure 8.1 illustrates the ERPs that are recorded in this situation (note that in my figures, negative is "down"). These data were reported by Simson, Vaughan, and Ritter (1977). The interval between S1 and S2 was 1 sec, and the interval between successive presentations of the pair (trials) was 8 sec. S1 was identical on all trials of a given condition and served only as a warning cue. On the other hand, one of two stimuli, chosen randomly, were presented as S2. The subject was instructed to respond to one of these stimuli and to ignore the other (this is often called a "Go-No-Go" task). The two ERPs in the left column of the figure were recorded in a condition in which S1 and S2 were auditory. The waveforms in the right column were elicited by a visual S1 and S2. All these ERPs are recorded at a vertex electrode. The S1 elicited an ERP with a sequence of components. It is clear that auditory and visual stimuli elicit

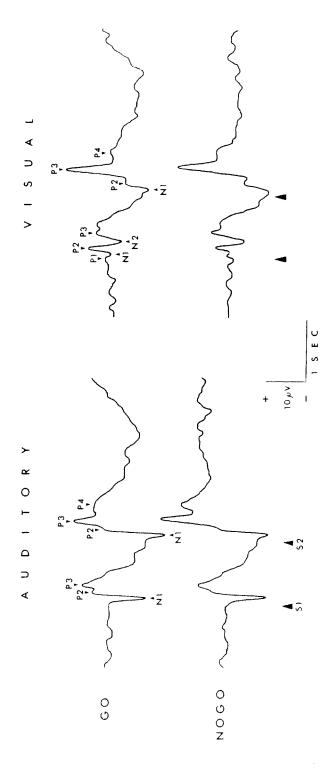


FIG. 8.1 Averaged event-related potentials at the vertex for one subject in the auditory and visual conditions. Reproduced from Simson et al. (1977),

ERPs that differ in morphology. These early components are followed by a prominent negative shift that continues until S2 is presented. This negative shift was called by Grey Walter (1964) the "contingent negative variation" (CNV). Unlike the early components, whose shapes vary with the modality of the stimuli, similar shaped CNVs were elicited by the auditory and the visual stimuli. It has been commonly assumed that the CNV's waveform is independent of the modality of the eliciting stimuli. This conventional view needs to be qualified in light of new data I shall discuss in the following.

The CNV was first discovered by Walter, Cooper, Aldridge, McCallum, and Winter (1964). They assumed that this negative variation (the term the English sometimes use for "potential") can be recorded only when a contingency is established between two stimuli. It was suggested, in the early reports, that the CNV reflected brain activity related to anticipation, preparation, or attention to the task.

At about the same time, in other laboratories, a different experimental procedure was being employed. The subjects were instructed to make a repetitive movement. They were told, for example, to lift a hand repeatedly. No stimuli were presented and the subjects were instructed to respond at their own pace. The averaging computer was triggered by the myographic activity at the responding muscles. Note that in this case we are averaging the EEG recorded before and after the myographic trigger. A slow negativity that begins 500 to 1000 msec prior to the movement can be observed. Slightly before the actual response the slope of the wave increases and a new negative component appears. This later negativity has been shown in studies of monkeys to reflect pyramidal tract discharge from precentral gyrus (Arezzo, Vaughan, & Koss, 1977). Figure 8.2 illustrates these potentials. The ERPs in this figure from Vaughan, Costa, and Ritter (1968) were recorded from the scalp of a human subject, and the brain outline in the figure shows the estimated location of the electrodes with respect to the precentral gyrus. The arrows indicate the triggering point.

The slow negative shifts obtained in these two different ways were assumed to reflect different functions and anatomical substrates. One was labeled the *Bereitschaft* potential, or the readiness potential, by Kornhuber and Deecke (1964). Vaughan et al. (1968) referred to it as the N1 because it is the first negative wave that is observed in the "motor" potential. The other was called the CNV.

The readiness potential is asymmetric over the two cerebral hemispheres. If the subject makes a movement with a right limb, then the potential is larger over the left hemisphere and vice versa (Kutas & Donchin, 1974). In our laboratory, subjects were instructed to move their feet, hands, tongue, etc., on different runs (Vaughan et al., 1968). As different muscles were moved, the maximal amplitude of the readiness potential varied in a way that is consistent with the known distribution of motor control along the precentral gyrus. In

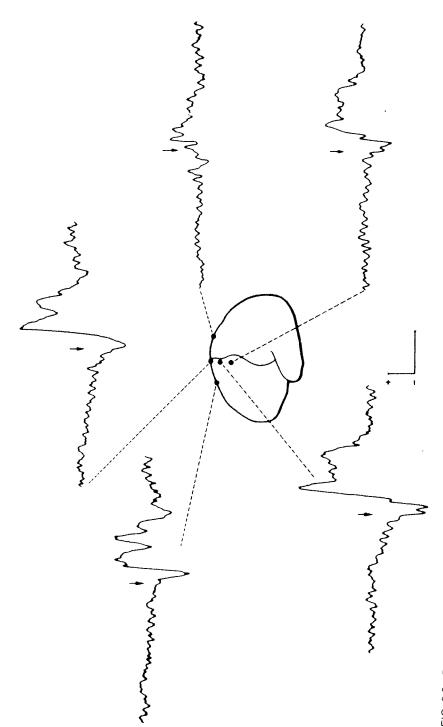


FIG. 8.2 Event-related potentials associated with dorsiflexion of the right foot. Calibration 500 msec, 2.5 l.c.GK mu. Reproduced from Vaughan et al. (1968).

Fig. 8.2, for example, the ERPs were recorded while the subject flexed his right foot backward. The readiness potential was largest in the vicinity of the most dorsal portion of the left precentral gyrus, that is, the area from where the leg is "controlled." By contrast, according to most reports, the CNV is symmetric over the two sides of the head. So these two different experimental paradigms apparently yield two different types of slow negative activity; yet, both seem to have something to do with preparation. In the case of the readiness potential, it is preparation to perform a skeletal movement, whereas the CNV is associated with preparation of a more psychological nature related to the task assigned to the subject. Furthermore, the CNV is called forth by an external warning stimulus whereas the readiness potential appears to be elicited by the internal pacing of the subject's responses.

OSCAR-BERMAN: What's the response required in the warned reaction-time tasks that causes a CNV to appear?

RITTER: You mean what responses were required at S2?

OSCAR-BERMAN: Yes. You said that the CNV is contingent on some kind of task given to the subject. Is it motor or covert? Must the subject speak? Press a key?

RITTER: Often a key press is required, but a purely perceptual task requiring no immediate motor response on each trial can also be used. For example, a signal detection task in which S2 is near-threshold and occurs on only 50% of the trials can be employed, and the subject's task is subsequently to report verbally if S2 was presented.

Recently, this neat and simple view of the preparatory potentials has been challenged (see Gaillard, 1978, for review). Impetus for the challenge was provided by experiments in which the interval between S1 and S2 was longer than usual. When S1 and S2 are separated, for example, by a 3-sec interval instead of the 1-sec interval used in the classical CNV paradigms, the S1 elicits the usual ERP that is followed by a negativity that reaches a peak somewhere between 600 and 800 msec. But unlike the "classical" CNV, the negativity is not sustained until S2. Rather the voltage may return to the baseline some 1200 or 1500 msec after S1. About a second or so prior to S2, a second negativity appears and is maintained until S2. If a motor response is required following S2, this "late" slow wave is asymmetric across the head as is the readiness potential. If the EEG is triggered from the key press, or from the EMG burst, then the late negativity is larger in amplitude; this implies that it is time-locked to the motor response rather than to S2. Furthermore, the late negativity becomes more asymmetric when averaged with respect to the motor response. The earlier slow wave, however, is not asymmetric. These results led to the suggestion that the original, "classical" CNV consists of at least two kinds of slow negativity: the early slow negative wave that appears in the vicinity of S1 and a later slow negativity, which is "nothing but" a readiness potential. It may be that the early negativity continues well beyond the traditional 1000-msec interval between S1 and S2; therefore, it persists into the period immediately prior to S2, and as it is not asymmetric, it obscures the asymmetry of the readiness potential. The failure in the past to observe an asymmetry of the CNV with a 1-sec interval between S1 and S2, even for warned, simple reaction-time tasks, could be accounted for by a combination of two factors: first, an overlap in time between the early and late slow negativities; second, triggering the EEG only from the stimuli rather than also triggering the EEG from the motor response.

Let us return now to the experiment from which the waveforms of Fig. 8.1 were obtained. In that study there were two conditions, one in which S1 and S2 were auditory and a second in which S1 and S2 were visual. Both conditions used a 1-sec interval between S1 and S2, and S2 in each condition was one of two possible stimuli that provided the basis for a go-no-go task. Although the slow negative shifts in Fig. 8.1 appear similar for the auditory and visual conditions, this similarity is somewhat deceptive. We recorded ERPs at 13 recording sites in order to examine the scalp distribution of different ERP components. In Fig. 8.3, the two columns of waveforms in the center are grand averages pooled across all subjects. The numbers to the left of the waveforms designate the recording sites indicated on the outline of the head in the upper right-hand corner. Immediately below the 13 waveforms are arrows that specify the occurrence of S1 and S2. The waveforms stop shortly after S2, so the ERP components elicited by S2 are not seen in this figure. Notice that after the sharp deflections which follow S1, there is a slow negativity that is most prominent for electrode 3 (the vertex) at the time of S2. The isopotential maps of the far left and far right columns are to be read in the following manner. The line with the 90 on it means that the particular component depicted was 90% or more of maximum voltage within its confines. The lines with 70 and 50 on them mean that the voltage of that component within their confines were 70% and 50% of maximum, respectively.

Until the S2 appears, the slow negativity has a similar scalp distribution on the go and the no-go trials within the auditory condition, and within the visual condition. That makes sense because the subject did not know which S2 would be presented on any trial. The go and no-go trials for each condition were averaged together in Fig. 8.3. The ERPs associated with the two S2s differed, of course, as the stimuli called forth different responses.

The three lower isopotential maps in the left column of Fig. 8.3 depict the scalp distribution of the slow negativity 500, 700, and 900 msec after S1 in the auditory condition. The three corresponding maps of the right column depict similar data for the visual condition. It can be seen that in response to the au-

ditory condition there is a progressive shift in the slow negative wave from a more frontal to a more central distribution from the 500- to 700- to 900-msec latency measurements. By contrast, in the visual condition there is a double focus 500 msec after S1, one frontocentral and another in the vicinity of the occipital area. The visual maps at 700- and 900-msec latency exhibit a decrease in the amplitude of the posterior focus and a change in the frontocentral focus to a more central focus. These results suggested to us that an early portion of the CNV (the "early slow negative wave") is modality-specific. There is also a later portion of the CNV whose attributes do not depend on the modality of the stimulus. This later negativity appears to be mainly a readiness potential, as discussed previously. Figure 8.1 provides support for this interpretation. The subjects were instructed to withhold their responses to the "go" stimuli for about a second. Note that in the upper two waveforms (go trials) the negative shift persists well beyond the instant at which S2 is presented, whereas in the other two waveforms (no-go trials) the negative shift returns to baseline shortly after S2. The readiness potential appears to be maintained until the response is executed.

Unfortunately, this study did not provide data needed to determine whether the modality specificity of the early negativity was in response to S1 or in anticipation of S2. Both stimuli were always of the same modality. We therefore ran another study (Ritter, Rotkin, & Vaughan, 1980) in which the interval between S1 and S2 was 3000 msec. We could thus examine the early negativity in more detail. There were four conditions. In one condition, S1 and S2 were both auditory. In another condition, S1 was auditory and S2 was visual. In a third condition S1 and S2 were both visual. And in a fourth condition, S1 was visual and S2 was auditory. In all cases, the subject was instructed to respond to S2 by pressing a button.

Grand averages from the four conditions are shown in Fig. 8.4. The modality of the stimulus is indicated by Vis (for visual) and Aud (for auditory). The small triangles at the bottom of the figure indicate the time of occurrence of the stimuli. When S1 was auditory (the upper panels), the sharp deflections associated with S1 are followed by the early slow negative wave that peaks roughly 600 to 800 msec after S1 and is largest at the vertex (Cz) and next largest at the frontal recording site (Fz). There is little or no negativity in this latency range at the temporal (T5) or occipital (Oz) recording sites, whether the sensory modality of S2 was auditory or visual. About 1 sec prior to S2 a late slow negativity appears. Its amplitude gradually increases until the presentation of S2. The maximum amplitude of this component is recorded at the vertex. When S1 was visual (the lower two panels), the sharp deflections associated with S1 are again followed by an early slow negativity, also largest in amplitude at the vertex and with a peak latency about 600 to 800 msec after S1, except that in these conditions a negative process can be seen at T5 and Oz (compare the upper and lower panels at these recording sites). As with the

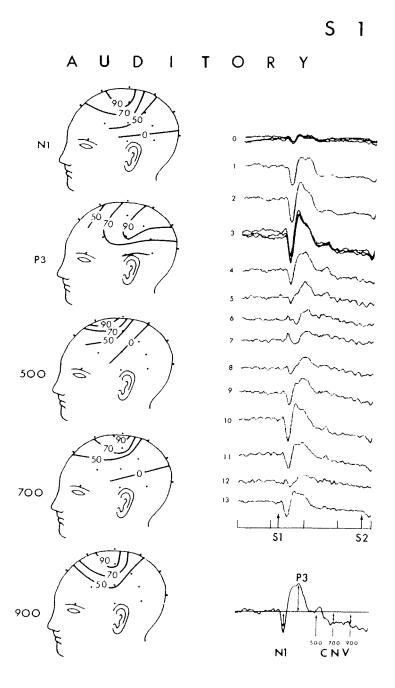
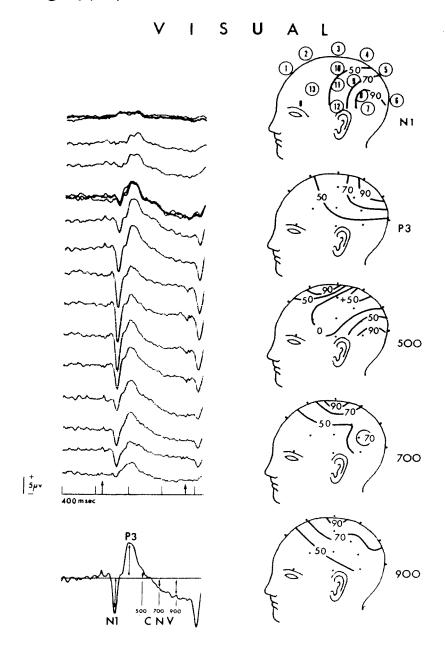


FIG. 8.3 Event-related potential average over eight subjects to all S1 stimuli in the auditory and visual conditions. Supraorbital (0) and vertex (3) waveforms superimposed

CNV



for three runs. See text for explanation of the isopotential maps. Reproduced from Simson et al. (1977).



A U D - V 1 S

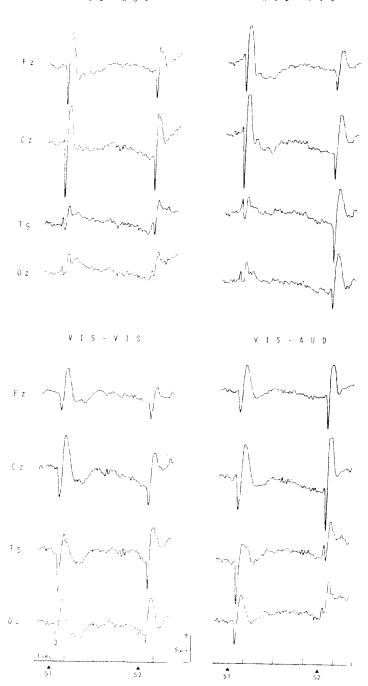


FIG. 8.4 Grand mean waveforms from eight subjects for four conditions. See text for an explanation of the experimental conditions. Reproduced from Ritter et al. (in press).

data displayed in the upper panels, the scalp distribution of the early slow negativity is essentially unaffected by the sensory modality of S2. Finally, a late slow negativity begins about 1 sec prior to S2, increases until S2 occurs, and is largest in amplitude at the vertex.

The left two panels of Fig. 8.4 replicate the results depicted in the isopotential maps of Fig. 8.3 with respect to the early and late portions of the slow negativity when S1 and S2 are of the same modality. When S1 is auditory, there is a single frontocentral focus of the early slow negativity, but when S1 is visual, there is a frontocentral and a posterior focus. In Fig. 8.3 the scalp distributions of the slow negativities for the two sensory modalities had pretty much merged by 900 msec after S1, whereas in Fig. 8.4 this was not the case. The reason for the merging in Fig. 8.3 by 900 msec was probably because of overlap with the late negativity, which in Fig. 8.4 is delayed until 2 sec after S1. In both Fig. 8.3 and 8.4 the negativity prior to S2 has mainly a single, central focus, consistent with its being a readiness potential.

When the left and right panels of Fig. 8.4 are compared, it is clear that the modality-specific distribution of the early negativity is related to the modality of S1 and not S2. Thus the early negativity is not an event-preceding negativity (in the original sense of the CNV reflecting preparation for perception of or response to S2) but rather is a response to S1.

The late negativity has been sometimes labeled the terminal CNV, as it is measured in the last 100 to 200 msec immediately before S2. It has struck me that the use of that word terminal here may be appropriate. Perhaps the CNV is a terminal case. Several investigators (Gaillard, 1978) have suggested that the "classical" CNV is a combination of a slow negative wave that occurs as part of the ERP elicited by S1 and the readiness potential that occurs immediately prior to S2. The CNV recorded when the interval between S1 and S2 is 1 sec is a combination of these two potentials. There is, according to this view, no CNV. It is merely a combination of two other phenomena. I do not believe, however, that the issue is closed. Marta Kutas will review data that suggest that there are yet other negative waves associated with preparation that cannot be accounted for by the two negativities that I have just described.

POSNER: Are you suggesting that the early slow negative wave is exogenous?

RITTER: That is an excellent question. Our data cannot answer that question. I guess at this point I am undecided. John Rohrbaugh and colleagues (Rohrbaugh, Syndulko, & Lindsley, 1978) have reported a slow negative wave, in the general latency range of the early negativity we have been discussing, in response to unpaired stimuli in a "passive" condition. It is not clear, however, that the slow negative wave reported by Rohrbaugh et al. is the same as the early negativity obtained for paired stimuli.

190 REPORT OF PANEL III

POSNER: Was that to an auditory warning signal?

RITTER: There was no warning signal. They just presented tones about once every 6 sec.

POSNER: It was an auditory transient event. For how long was the wave sustained?

KUTAS: The first of two waves they describe peaked 500 to 600 msec after the stimulus. Rohrbaugh (Rohrbaugh et al., 1978) reports that the negativity in a totally passive situation peaks around 550 msec.

RITTER: I see. And when does the second component begin?

KUTAS: The onset of the second component is difficult to determine as the two components overlap; it seems to start around 500 to 700 msec post-S1. Rohrbaugh has found that the entire negativity lasts for a second.

RITTER: Or more. The second negativity persisted beyond 1500 msec.

DONCHIN: There is no such thing as a totally passive situation.

RITTER: The subjects were asked to "listen attentively" to the tones, so they were not totally passive.

ALLISON: I'm still confused by the answers to Posner's question. There is a difference between these two situations. You don't obtain a slow negative wave if no information is carried by the stimulus and the subject doesn't have to perform any task. If the component is exogenous, why don't you see a slow negative wave in passive conditions?

RITTER: If the negativity peaking at 550 msec reported by Rohrbaugh is the same as the early slow negativity I have been discussing, then you do.

DONCHIN: Well, I am not ready to accept Rohrbaugh's claim that he can record this slow wave in a passive, "no-task" situation. I take issue with the no-task concept. Their study is very similar to the oddball experiments, and we know a slow wave is elicited in these conditions (Squires, N.K., Donchin, Squires, K.C., & Grossberg, 1977).

RITTER: But they used a passive condition and neither a P300 nor a slow wave were observed.

DONCHIN: There is no such thing as a "passive" condition! All the phrase means is that the experimenter had no information about the subject's reaction to stimuli.

PICTON: Walter, why do you think there are two foci in the early slow negativity when S1 is visual in Fig. 8.3 and 8.4?

RITTER: We think the scalp distributions of the modality-specific early negativities are consistent with the notion that they are generated in their respective primary and secondary cortical areas (Simson et al., 1977, pp. 869-871). As with the P2 component of auditory and visual stimuli, the early slow negative wave has a single fronto-central focus for auditory stimuli and two foci, one in the parieto-occipital region and one in the central region, for visual stimuli. There is an interesting implication of this interpretation, because of the long peak latency (600-800 msec) of these slow negativities. Note in Fig. 8.1 that a small P300 was elicited by S1 (and was mapped in Fig. 8.3). As is well-known, P300 is considered to be modality-nonspecific. What this suggests is that a stimulus can elicit the exogenous components up to P2, which are modality-specific, followed by P3, and that the latter is followed by further activity in primary- and secondary-specific cortex. It is analogous to the overlapping, parallel activity that occurs in occipital and inferotemporal cortex to visual stimulation.

8.2 KUTAS: SUBCOMPONENTS OF THE CONTINGENT NEGATIVE VARIATION

KUTAS: Oscar-Berman inquired whether one can obtain a CNV without a motor response. I believe the answer is yes. For example, on occasion, a CNV comparable to that recorded during a reaction-time task can be obtained when the subjects' task is merely to count silently all or some of the imperative stimuli. The CNV also can be recorded when a person is asked to guess the nature of the imperative stimulus (S2) before the SI-S2 pair is presented (Donchin, Gerbrandt, Leifer, & Tucker, 1972). These findings have in the past been used to support the statement that the CNV is not contingent on a motor response. However, over the last 5 years it has been argued that because short interstimulus intervals (e.g., 1 sec) were used, the results and interpretations of these earlier studies were misleading (Gaillard, 1977; Kok, 1978; Loveless & Sanford, 1974; Rohrbaugh, Syndulko, & Lindsley, 1976; and Weerts & Lang, 1973). Proponents of this view claim that with the employment of longer interstimulus intervals (4-8 sec) it becomes clear that the CNV is comprised of two overlapping components. In the strongest version of this

two-component theory (discussed by Ritter in his presentation), an identity is assumed between the late component of the CNV and the readiness potential (RP). The implication is that there is no such entity as the "classic CNV" but merely a waveform caused by the superimposition of the warning-stimulus evoked potential and an RP (Kok, 1978; Rohrbaugh et al., 1976). By inference, then, the late CNV is in fact contingent on a motor response.

Before presenting data that are not consistent with this two component theory, I want to examine the logic of the argument for employing a long foreperiod. The argument assumes that the processes associated with short warning periods are identical, or at least similar, to the processes associated with long foreperiods. But this is a questionable assumption. There is no question that a warning stimulus facilitates the speed of reaction. Furthermore, there is an abundance of data demonstrating that the amount of facilitation is influenced by the interval between the warning and the imperative stimulus. One of the earliest problems faced by CNV investigators was that the maximum RT facilitation provided by the warning stimulus occurred earlier than I see (around 400 msec); yet the CNV did not even begin until around that time. Most of those studies used 1000- to 1500-msec foreperiods, as that interval seemed necessary for the CNV to reach its maximum.

It may be true that when the warning and imperative stimuli are separated by 4 to 8 sec, the CNV appears to decompose into two separate components and does not appear to be sustained throughout the interval. However, this may also be true for the underlying psychological process(es). Thus, the CNV may not be evident because the preparation is not maintained during the foreperiod and not because there is no such entity as the CNV. The behavioral consequences of the contingency between the warning and imperative stimuli cannot be denied. Whether this contingency is also manifest in the components of the CNV is one of the questions we're trying to resolve.

Now, I shall show a series of CNVs from different experiments that I feel will underscore the inadequacies of this two-component theory. As I mentioned previously, a motor response is not always necessary to generate a CNV. I have already mentioned a CNV that can be elicited during a counting task. That CNV was recorded over a I-sec interval. However, in the examples shown in Fig. 3.7 (Chapter 3, this book), CNVs were recorded over much longer intervals. The first waveform is from a study by David Woods (Woods, Hillyard, Courchesne, & Galambos, 1980), in which subjects had to report verbally or by pushing a button how many tones (one, two, or three) were presented during an interval slightly longer than 3 sec. A response was required, but this response came quite a bit after the trial. The R in the figure represents the cue after which a response could be given. Notice the waveform in the far left corner. No tones were presented in the interval and yet a CNV was maintained for over 3 sec. This CNV had a frontocentral distribution

throughout. It is not easily explained by the superimposition of the O wave (the early negative shift) and an RP.

RITTER: I find these rather convincing data, although Rohrbaugh contends that a later slow negativity, which follows the O wave but is also associated with S1, can persist for 3 and even 4 sec.

McCARTHY: Marta, what electrode position is that coming from?

KUTAS: From Cz. The second example appears in Fig. 8.5. This waveform represents an 8-sec interval during which a person silently read a seven-word sentence presented one word at a time. No motor response was required. As is usually the case, all movements were discouraged although of course there were some eye movements. Despite the absence of a consistent motor response, a fairly large CNV is generated and maintained throughout the 8-sec interval. I find these data difficult to explain in terms of the two-component theory.

ALLISON: Marta, would you explain why you think these data are hard to explain by the two-component theory? You can think of this as a series of separate stimuli to which a cognitive response is to be made and a series of seven or eight 1-sec CNVs.

RITTER: It might be claimed that one of the reasons there is a longer CNV is because you're getting early slow negative waves to each of the stimuli.

KUTAS: It's quite possible that the 8-sec CNV is comprised of a series of 1-sec CNVs. I should clarify my position. I am not arguing that all versions of the two-component theory are insufficient to account for the CNV. I am questioning the proposal that all short foreperiod CNVs are produced by the superimposition of a negative wave reflecting the processing of the warning stimulus and a readiness potential. When a motor response is required, there is no question that the late part of the CNV is partially comprised of a readiness potential. However, when a movement is not required, then some other component must be invoked to account for the CNV or negativity sustained for longer than 1-sec intervals.

The data in Fig. 8.6 were again obtained during a 1-sec foreperiod. The important comparisons for our purposes are those between the waveshapes and distributions of the CNVs in the WARNED and CHOICE WARNED conditions. The three waveforms in each case represent the potentials recorded at the frontal, central, and parietal locations on the hemisphere contralateral to the responding hand. In each of the warned conditions the subjects' task was

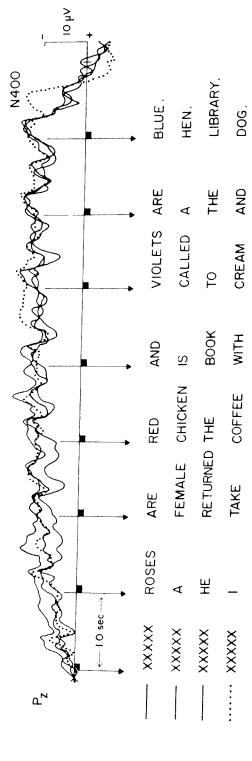


FIG. 8.5 ERPs recorded throughout the presentation of complete seven-word sentences, with the words flashed at one per second. Each tracing is the Samples of the 160 different sentences that were presented to this subject are shown below the waveforms. D.C. recordings from the Pz electrode. (Data from averaged ERP across 40 sentences in which the last word was either appropriate for the context (solid lines) or semantically inappropriate (dotted line). Kutas & Hillyard, 1980.)

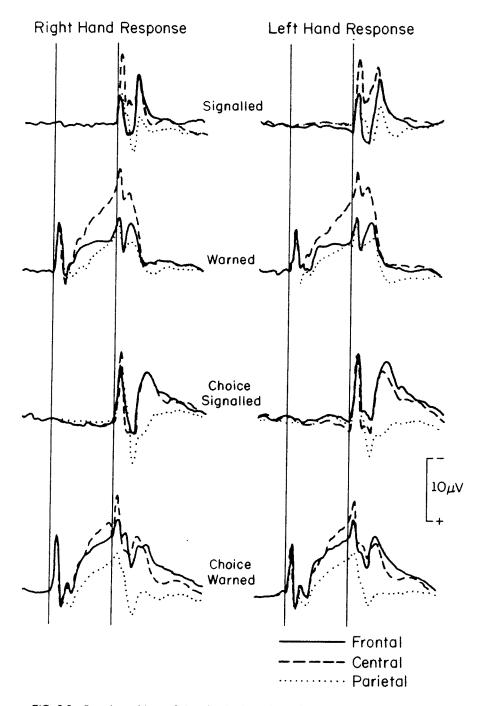
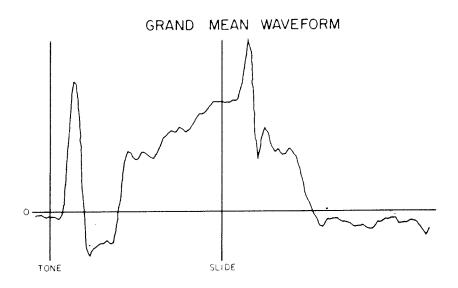


FIG. 8.6 Superimpositions of the stimulus-locked grand mean ERPs from the contralateral frontal, central, and parietal locations for right- and left-hand responses in four different experimental conditions. The vertical line separates presqueeze from postsqueeze activity. Calibrations: 250 msec, $10\mu V$.

to squeeze a dynamometer as quickly as possible after the occurrence of the imperative stimulus, which was, in all cases, preceded by a warning stimulus. The two conditions differed in that the same hand was used for responding in the WARNED conditions whereas the right or the left hand as cued by the frequency of the imperative stimulus was used in the CHOICE WARNED conditions.

First, note that there is a sharp rise in the negativity immediately preceding the imperative stimulus in the central leads. At least part if not all of this increase is probably a reflection of the superimposition of the RP associated with the movement. However, the most interesting and perplexing aspect of these data is evident in the waveforms recorded at the frontal locations. The frontal waveforms from these two CNV-eliciting paradigms are remarkably dissimilar; there is appreciably more negativity associated with the CHOICE than the simple WARNED conditions. The warning stimulus for both conditions was physically the same and provided the same information. Likewise, the physical parameters of the response in both conditions were quite similar. The reaction times were, of course, different. I find it difficult to argue that the additional negativity in the CHOICE WARNED condition is either a reflection of warning stimulus processing or an RP. If it is an RP, why does it influence the frontal and not the central location waveforms? Furthermore, given that the RTs in the CHOICE WARNED condition were significantly slower than in the WARNED condition, the prediction of waveshape predicated on the superimposition of the RP would have been opposite to the data actually obtained. I believe that these data, even with a 1-sec ISI, indicate that there must be still another negative component to be accounted for.

Figure 8.7 is from McCarthy and Donchin (1978). Again the CNV was recorded over a 1-sec interval. The warning stimulus was a tone. The imperative stimulus was a slide of three line drawings. The subjects were asked to make either a structural or a functional match between items on the slide. The details of the study are unimportant for present purposes. The waveform on the top is the grand average of all the evoked responses that were recorded; that is, the ERPs collapsed over conditions, electrodes, and subjects. The PCA of these data yielded the component loadings presented in the bottom half of the figure. Notice that there are two components during the foreperiod. However, the second component does not seem to be related to an RP. It is not influenced by response variables. The RTs in this experiment were quite slow, occurring 1 to 1.5 sec after the imperative stimulus. Furthermore, there is a post-S2 component that is related to the response. The early component loading probably is related to information provided by the warning stimulus. However, the question remains as to what the second component loading in the S1-S2 interval reflects. It is not the readiness potential and it is not the negative afterwave to the warning stimulus. I don't know what ERP component or psychological process it manifests, but these data indicate to me that some other component must exist.



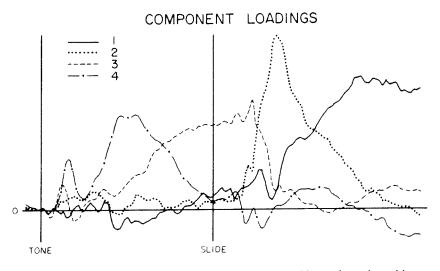


FIG. 8.7 The grand mean waveform (averaged across subjects, electrode positions, and experimental conditions) is shown at the top. Below are displayed the component loadings for the first four components derived from the principal components analysis (using the covariance matrix) of the waveform data.

ZAIDEL: Were any components associated with the functional versus structural matches?

McCARTHY: No.

POSNER: Marta, would you know how the factor loadings would change in that kind of paradigm if you switched from a visual warning signal? Would you get rid of, or reduce, the factor loading that seems to be closely related to the stimulus?

KUTAS: No, I think it would probably still be there.

DONCHIN: That factor was related to whether the stimulus did or did not provide information.

POSNER: Oh, I'm sorry. I didn't realize—it was not just a warning signal.

DONCHIN: There were two conditions. One in which S1 did and one in which S1 did not provide information. The variance accounting for that component was related to this variable.

KUTAS: It is important to remember that a tone or a stimulus rarely occurs in isolation, even in a so-called passive task. The subject may always be anticipating a future event, regardless of experimenter instructions.

POSNER: That's certainly true. There is intersensory facilitation that seems to be very closely related to these effects. For example, if you present an auditory event that's not a warning signal but just an event, even if it doesn't carry any information with respect to the occurrence of other events, it will improve reaction time to a visual event that occurs in close proximity to it (Nickerson, 1973). It has been suggested that the auditory signal produces an automatic alerting effect that improves processing of stimuli that follow it. This effect might be sustained if the stimulus is a warning for some new event. Thus, this would predict a component associated with the alerting produced by the auditory event and another component associated with a voluntary sustaining alertness. Visual events don't seem to produce this automatic facilitatory effect. Hence, you might expect that the visual signal would produce only a sustained component, not an automatic one. The data you present seem consistent with this prediction. The evoked potential ought to be related to the kinds of results that have been obtained behaviorally (Posner, 1978, Chap. 5).

PICTON: Marta, there appears to be a frontal component in the example you've shown. Is that component different from the other components that are related to the processing of S1 or the preparation for S2?

KUTAS: I don't know. It may be related to nonmotor preparation for the imperative stimulus. I assume that a variety of cognitive processes are activated during the foreperiod interval, one of which might be influenced by the S1-S2 contingency and some of which might be reflected in components of the foreperiod negativity. We need to determine the functional role of this nonwarning and nonmotor potential or at the least to define the psychological factors with which it covaries. However, the position taken in the controversy about the structure of the CNV may influence the design of experiments that address the "CNV phenomenon." For example, those who claim that the CNV consists of the superimposition of an "O wave" and the RP deny the presence of an additional negative component. In this view there is not much point in searching for the psychological process underlying the CNV.

PICTON: There is a frontal CNV when the subject is uncertain about which hand will have to make the response. During your sentences there is also a long CNV. Does this also have a frontal distribution?

KUTAS: I don't know. Its distribution varies considerably across subjects.

PICTON: Perhaps there is a third component of the CNV that is frontal and related to uncertainty.

DONCHIN: Well, it seems to me that the idea that there are two components has not been too helpful. There is too much emphasis on the idea that long intervals somehow tease apart the CNV. But the statement that you need a 3-sec interval to bring out multiple components is just not true. As McCarthy and Donchin (1976) have shown, the two components can be observed with 1-sec intervals if the S1 is informative. But that does not mean that there is no CNV.

RITTER: Figure 8.3 also shows 1 sec can suffice to reveal two components.

KUTAS: I don't agree with Donchin. We have come closer to explaining two aspects of the CNV.

DONCHIN: I don't see what has been explained. Rohrbaugh et al. (1976) suggested that the CNV is constructed of an early negativity (which is supposedly an orienting reflex) and a late negativity (which is a readiness potential). But, this is just not supported by the literature. The late negativity is *not* a readiness potential as Kutas has shown.

KUTAS: No. I have not just shown that. In fact, I have shown that in some situations the late negativity might well be a readiness potential.

DONCHIN: Yes, it sometimes is and sometimes is not. The important point is that the data demonstrate clearly that it is possible to get a CNV without requiring any motor response. This has been reported by Grey Walter (1965) and by Low, Borda, Frost, and Kellaway (1966) and by Donchin et al. (1972). In short, there are very strong data showing that one can obtain a CNV without a motor response. The "only-readiness-potential" advocates ignore these data and simply fail to cite them. But that doesn't make the data go away. I don't think there is any strong evidence to suggest that the late CNV is entirely a readiness potential. As for the early CNV, it appears whenever the S1 is informative. That an informative stimulus elicits a slow wave is quite well-known.

RITTER: But of course the circumstances where the CNV has been reported to occur without a motor response have generally employed a one second ISI, and the early slow negativity that I was describing can last up to 1500 msec.

KUTAS: That's why I didn't use those data. Rather, I presented waveforms from experiments in which the foreperiod intervals were longer than 1 1/2 sec.

RITTER: That's not entirely true. Only in the data from David Woods was the interval between stimuli longer than 1 1/2 sec. It has been argued that the "CNV" observed when there was no motor response for short intervals was the early slow negativity.

DONCHIN: But that early negativity appears if, and only if, the S1 is informative. In the Donchin et al. study (1972), both an informative and an uninformative S1 were used. This didn't make any difference. We still recorded CNV in the absence of a motor response. If the subject had to perform some task, such as modifying a running product at S2, we always found a CNV. If I'm right and the early negativity appears only if the S1 is informative, then you cannot claim that early negativity accounts for all the CNVs we had without a motor response.

RITTER: But in our studies an early negativity was recorded even though the S1 was only a warning stimulus and did not provide any information specific to S2.

McCARTHY: The information in S1 seems to enhance the positive aspect of the early component. I think there is probably one there frontally regardless, but Marta was showing data from centrals with very large CNVs from Woods et al. (1980) that was from the central and my data also were from Cz. There is no motor response and there is no slow potential as you described at Cz that could account for that.

RITTER: Let me emphasize, my mind is still not made up on the issue. When you don't have a motor response, you still can have the slow negativity that persists for quite a long time and could be mistaken for the classical CNV.

KUTAS: That persistent slow negativity related to the processing of the warning stimulus has been reported to be largest at frontal electrodes. All the waveforms exhibiting features that cannot be explained by the two-component theory that I presented were recorded from the vertex.

RITTER: The early negative waves in Fig. 8.4 have their maximum at the vertex, not at the frontal lead, for both auditory and visual stimuli.

DONCHIN: Let me raise another issue. A panel on the CNV was included in this program not to determine if there is one or two components to the CNV. What is more puzzling is this: the CNV was discovered in 1964. It is a very robust component of the ERP. It is one of the more robust phenomena in the ERP field. It is very easy to record CNVs. They are large and apparently interesting. It appeared to be of great utility. Yet, I submit not a single useful insight about physiology or behavior can be credited to CNV studies done in the past 15 years. I want to know why. What is it about the CNV that makes it so refractive to interpretation? It's easy to talk about "preparation." Grey Walter said the CNV reflects priming for the motor response. Preparation has been studied, behaviorally, in enormous detail. We know a lot about choice reaction times and the response to preparatory stimuli; yet no one seems to find out anything useful from the CNV. Perhaps I am wrong. I will be delighted. But, if I am right, then we should try to understand why this has been the case.

RITTER: One of the reasons for the little progress is that the motor responses used in almost all experiments have been meaningless, isolated movements. Yet the motor system is quite capable of more complex, meaningful activities. Perhaps if more complicated motor performances were required of subjects, more could be learned about the ERP components associated with preparation for movement. In fact, this issue is developed in Scott Kelso's presentation.

[Footnote: The following presents Dr. Kelso's revision of the remarks he made at the conference. The floor discussion of his views has, therefore, been omitted from the transcript.]

8.3 KELSO: CONSIDERATIONS FROM A THEORY OF MOVEMENT

KELSO: Let me first express a concern about the approaches that I have heard thus far to problems of identifying neurophysiological counterparts to behavior. It is one that is not by any means unique to event-related potential work, but

rather may be addressed to much of psychology and neurophysiology (see, for example, Gyr, Willey, & Henry, 1979). I refer to the classical Cartesian distinction between sensory and motor function. While such a dichotomy may have served a useful purpose at one time, it is quite clear that modern neurophysiology can no longer support such a view. Sperry (1952) alerted us to this fact many years ago, and it has recently been reiterated by Diamond (1979) as well as in an excellent monograph of Evarts, Bizzi, Burke, DeLong, and Thach (1971). To distinguish between afferent systems on the one hand and efferent systems on the other makes little sense, and it would be a mistake for this relatively new field to adopt such a style of inquiry.

Indeed the whole area of "preparation" rejects a view (common to cybernetic and information-processing approaches) that input and output stages are fundamentally separable. What I wish to do here is discuss ways of thinking about preparation (specifically for activity) in reference to newly developing insights on coordination and motor control. I then wish to point to paradigms that may be useful in identifying more clearly the neural counterparts of movement preparation. As Walter Ritter has already remarked, much of the work on readiness potentials has involved relatively "aimless" tasks. Thus we know little about what aspects of behavior (in terms of the motor tasks employed) relate to the "preparatory waves" that we observe when we record from the brain.

The typical information-processing models about which we have heard much thus far—and which appear to provide the theoretical backdrop for much of the event-related potential work—run into some problems when we raise the issue of preparation. Like its counterpart, attention, preparation is not easily tied to any particular structural stage but rather may be more appropriately viewed as a functional process that manifests itself throughout the system. In this perspective preparation is that process that modifies the functional state of the system in advance arising as an output from some earlier processing stage. Preparation is often tied to the response side of the system and presumably bears a close tie, the related notion of preprogramming. I wish to diverge from this view for principally two reasons: First, the foregoing view perpetuates the sensorimotor distinction that as I have emphasized here and elsewhere is no longer a viable one; second, this view of preparation ignores certain fundamental problems of movement organization that must be considered if we are to understand what preparation really involves.

Recently Requin (1980) has made a strong claim that we can usefully proceed in studying preparation with stage models of information processing and neurophysiological models of the CNS that are isomorphically felated. Requin views preparation not only as an intrinsic facilitory aspect of the "building" of motor programs but also as playing a modulatory role in the execution process. In an isomorphic model, however, the structures and pathways involved in programming are distinct from those involved in execution (Requin, 1980). This is an example of the sensorimotor, input-output dichotomy in a more refined guise. Instead of considering simply a response stage as a single

entity (which is the case in many information-processing models), the suggestion is to break it up to include response determination (i.e., which stimulus goes with which response), response programming (selection and preparation of the appropriate response), and response execution. Although partialling out the motor system enables experimenters to use chronometric methods to distinguish hypothetical stages experimentally, it does not provide much insight into the organization of movement. At best such experiments have a questionable motivation because there is no neurophysiological support for a view that separates programming and execution. When an animal makes an active movement, for example, afferent information transmitted in ascending spinal tracts is modulated at the level of the second-order neuron (Ghez & Lenzi, 1971; Coulter, 1974). There is therefore centrifugal control of incoming information prior to and during the execution of an activity that renders the programming-execution distinction virtually untenable. Furthermore, there is no clear relationship between neural activity in precentral cortex and movement parameters such as extent or velocity. To view preparation as having selective effects at various serially ordered stages is a conceptual luxury, for such stages overlap considerably, as indeed they must if they are to be consonant with a neurophysiology indicating interaction at all levels of the neuraxis (Evarts et al., 1971).

How then—given a dissatisfaction with serial-order models—should we conceptualize preparation and what should be our direction for an adequate analysis? I believe a more realistic view of movement preparation will come only when we appreciate some of the problems facing a theory of movement coordination and control. Let me briefly discuss motor control theories as they are currently delineated in most corners of neurophysiology and psychology. I should point out that it is not at all clear what the role of preparation may be in these theories. In contrast a viable alternative that I shall suggest includes preparation (feedforward) as an intrinsic aspect of its style of organization.

The currently dominant theories of motor control are essentially offshoots of the past. Peripheralist theory is best expressed in closed-loop, cybernetic models where sensory feedback from the periphery is compared against an internally stored referent value (or setpoint) so that errors in production may be detected and corrected (Adams, 1977; Schmidt, 1975). Centralist theory is exemplified in the motor program viewpoint where the details of the movement are structured prior to initiation. Thus the various dimensions or components of the movement (e.g., amplitude, direction [see later discussion]) are selected in advance and then translated into some muscle-usable code. Although preparation may be seen as a process involved in constructing the motor program, little is known about how this process works. Motor programs are assumed as a priori facts; few have questioned their status as controllers.

In my opinion neither of these models (or their hybrid versions) provides a principled basis for understanding the control and coordination of movement. The arguments for this position have been laid out in detail elsewhere (Fowler,

1977; Kelso, Holt, Kugler, & Turvey, 1980; Kugler, Kelso, & Turvey, 1980 Turvey, 1977) and can only be briefly drawn here. First, the theories prev ously referred to ignore the problem of what Bernstein (1967) called function: nonunivocality or context-conditioned variability (Turvey, Shaw, & Mace 1978); second, they ignore the fundamental problem of perception-productio systems, namely the regulation of a potentially large number of degrees of freedom. Functional nonunivocality refers to the fact that centrally generate signals are not mapped invariantly to movement outcomes. Movements cannot be direct reflections of neural events because muscular and nonmuscular (reactive forces have to be taken into account. In fact, a notable characteristic of skiller individuals is that of providing only those changes in force during a particula movement that are not given reactively. But the effect of movement context i manifested at a neurophysiological level as well. Monosynaptic control of al phamotoneurons is the exception rather than the rule in the neural regulation of movement. Instead, whether a motoneuron fires or not is ultimately con tingent on the influences of suprasegmental, intersegmental, and intrasegmen tal interneurons whose status varies from one instant to the next (Evarts et al. 1971). The point is that the effects of descending commands are continually modulated by virtue of the continuously active state of the spinal machinery Thus we can't prepare a program and assume that it will be faithfully executed by the peripheral musculature. That would be to ignore the contextual background against which cortical influences are realized. Indeed, because there can be no isomorphic relationship between muscle commands and the effects observed in the periphery, it seems more appropriate to consider supraspina influences as organizational rather than executive (Fowler, 1977). This view has significant implications for the concept of preparation and how we might approach it. Although it might be argued that a closed-loop model could solve the problem of context by making available detailed information about the current states of muscles and joints, closed-loop and motor programming models both fail to account for the degrees of freedom problem.

A step toward resolving this dilemma—following the insights of the Soviet school and their supporters (Bernstein, 1967; Gelfand, Gurfinkel, Fomin, & Tsetlin, 1971; Greene, 1972; Turvey, 1977)—is to claim that the skeletomuscular variables are partitioned into collectives where the variables within a collective change related and autonomously. Control and coordination are defined over autonomous muscle collectives rather than potentially freely varying individual muscles. We have referred to these synergistic groups as coordinative structures (Fowler, 1977; Kelso, Southard, & Goodman, 1979; Turvey et al., 1978) defined as functional groupings of muscles often spanning several joints that are constrained to act as a single unit. Evidence for a coordinative structure style of organization comes from research on activities as varied as locomotion, mastication, postural control, and respiration, and extends to volitional two-handed mastication, postural control, and respiration, and extends to volitional two-

movements, handwriting, and speech (Fowler, 1977; Kelso et al., 1980; Kugler et al., 1980).

According to this perspective, coordinative structures are created when the interneuronal pools in the various low-level structures (e.g., brainstem, spinal cord) are selectively facilitated and inhibited (Greene, 1972; Gurfinkel, Kotz, Krinskiy, Pal'tsev, Feldman, Tsetlin, & Shik, 1971). As a consequence of these tunings or biasings—which I wish to refer to as preparation—an aggregate of neuromuscular variables is constrained to act as a functional unit. Wellknown examples of this style of control come from work on postural reflexes in the cat (Roberts, 1967). On seeing a mouse, neck flexion reactions as well as the tilt of the head will tune lower spinal centers such that a simple signal for "jump" will be sufficient to initiate the act in the correct direction. As Greene (1972) points out, these feedforward, preparatory adjustments must be set as the act begins; for without them, accurate performance would be impossible. The onset of any active movement then, as Bernstein (1967) theorized, is preceded by a preliminary tuning of sensorimotor elements in accordance with the intended act. Planning and preparing a movement might be best considered as a progressive linking of variables specific to the upcoming action.

I have reviewed a good deal of the evidence for preparatory adjustments elsewhere (i.e., efference as a feedforward mode of organization rather than as a central set of commands to muscles) both in relation to normal animal and human movement (Kelso, 1979) and in pathological conditions such as apraxia (Kelso & Tuller, 1981). A principal source of experimental support for this view comes from findings that show progressive changes in spinal and brainstem reflex organization before and during voluntary movements (Coquery, 1978; McClean, 1978). The complex of preparatory adjustments can be broken down into three phases (Kots, 1977). The first, pretuning, occurs prior to the signal to move and extends throughout the latency period of the movement. It involves a "background" increase in the reflex excitability of all motoneuron pools (as measured by H-reflex techniques, Desmedt, 1973) and is the same regardless of the function of the muscles in the upcoming movement (see Fig. 8.8). Pretuning appears to be associated with a state of expectancy rather than a muscle-specific readiness for movement; it is absent during the latent period of elicited reflex or involuntary movements.

Changes in the spinal apparatus specific to the future movement are described by the processes of *tuning* and *triggering*. Approximately 50 to 60 msec prior to the onset of EMG activity in the agonist of the impending movement, there is a smooth and progressive increase in the reflex excitability of the motoneuronal pool of the agonist ("tuning"). During the last 25 to 30 msec of the latency period, the "fast" motoneurons of the agonist show a sharp increase in reflex excitability—as a result of pyramidal "triggering"—and this is accompanied by depression of the inhibitory interneuronal system acting on the motoneuronal pool of the future agonist. In effect, production of the upcom-

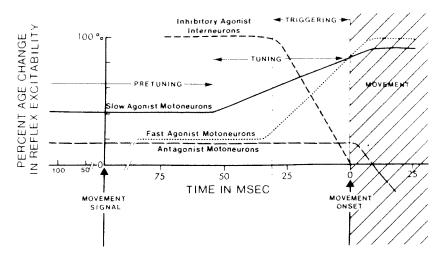


FIG. 8.8 Schematic showing changes in reflex excitability of agonist and antagonist motoneuronal pools during the preparation of voluntary movement. Adapted from Kots (1977).

ing movement is facilitated, whereas movements in the direction opposite to the intended movement are inhibited. Thus, when the functional state of the motor system has been modified, the performer is constrained to produce one of a limited class of acts, reducing the number of control decisions necessary to perform an extended sequence of movements. Preparation then involves the progressive linking of variables specific to the upcoming movement; it is an adaptive functional organization of the motor system that facilitates a specific class of motor activity. The main point is that this view of preparation does not assign priority to any one stage or level of the system but rather is a process that is manifest throughout the system.

Although tuning and triggering may be best reflected by changes in spinal organization, pretuning may be explored (and enlightened upon) via ERP techniques. What types of behavioral paradigms might be most significant as aids to advancing our knowledge of preparatory events in the brain? From our previous discussion (see Donchin and Ritter comments), there seems to be a general dissatisfaction with the behaviors examined thus far: Waving the hand for several hours has not afforded much insight into brain-behavior relationships. In this case the event may be so boring and aimless as to preclude the possibility of finding significant neural correlates. Let me suggest some alternative approaches that are not so complicated that they negate the tight experimental control necessary in brain potential work. Consider the finding that the time to initiate a movement increases as the number of elements in the response increases (Henry & Rogers, 1960). No one, to my knowledge, has pursued this result (which has been replicated on numerous occasions; see Kerr, 1978 for

review) with a view to systematically identifying possible neurophysiological counterparts of the preparation involved. More recently, Sternberg, Monsell, Knoll, & Wright (1978) have shown, in a task that required subjects to recite a list of words following a reaction signal, that initiation time increases as a linear function of the number of elements (specifically stressed syllables). Incidentally, this datum speaks against a view that assigns response preparation to a single stage. If the subject were allowed to plan the movement sequence well in advance of the reaction signal, then the latency to initiate production after completion of a programming stage should not change as the number of elements in the planned response changes. The fact that it does suggests that preparatory biasing adjustments are a function of the entire act and not simply the initial segment. But even more interesting for present purposes is the question of identifying neural events that might be related to the preparation of extended movement sequences. Recently, Grunewald, Grunewald-Zuberbier, Homberg, and Netz (1979) have demonstrated a widespread bilateral potential occurring in both parietal and precentral cortical regions whose negativity is influenced by the accuracy demands of the task. These experiments are among the first to explore brain correlates of goal-directed movements, even though the latter were of the single, discrete type. The Sternberg et al. (1978) paradigm provides a potentially enlightening method for establishing relationships between preparatory brain events and movements of a much more complex kind within an easily controlled experimental setting.

Are event related potentials correlated to specific movement parameters or is preparation at supraspinal levels a more generalized phenomenon? The analysis of pretuning presented earlier suggests the latter. Very recently however, Rosenbaum (1980) has argued that the various parameters of movement tend to be prepared in advance in a serial, invariant order. Consider a situation in which there is uncertainty about which of the two arms is to produce a forward or a backward movement of a short or a long extent. Suppose now that we precue the subject by telling him that the upcoming movement is to be made by the left arm in a forward direction, thus leaving only extent of movement uncertain. Does the subject use this prior, precue information to prepare only those parameters that are known (arm and direction), leaving only extent to be prepared at signal onset, or does the subject use the prior information to simply reduce the number of response alternatives from eight to two? Rosenbaum (1980) found the choice reaction time was shortest when only extent was left to be selected, longer when a directional decision was required, and longer still when arm remained to be selected. Furthermore, when two of three parameters (arm, direction, or extent) had to be selected, reaction times were further elevated and followed a pattern consonant with singly precued conditions. On the basis of this result, Rosenbaum concluded that the parameters were ordered such that first arm, then direction, and finally extent were selected in the movement initiation process.

Our own experiments (Goodman & Kelso, 1980) have failed to support Rosenbaum's selective preparation model, at least when precues and stimuli are mapped compatibly with responses. Using procedures designed to maximize differential parameter selection, we found, like Rosenbaum, that reaction time did decrease systematically as a function of the *number* of precued parameters, but there were no systematic effects of precuing a particular parameter.

Our experimental setup is shown in Figure 8.9. The subject (N=10) in this study) sat with his fingers resting on the home keys of a precuing display that was mounted in an identical configuration to the response board illustrated in Fig. 8.9. To precue a subject on a single parameter, four light-emitting diodes (LEDs) were turned on. For example, to precue left arm, the four lights on the left (1, 3, 5, and 7) appeared. Similarly, to precue a long extent, the outermost lights were activated (1, 2, 7, and 8). A trial sequence consisted of a precue lasting 3 sec followed after a variable foreperiod by the stimulus to move. Subjects were instructed as to the meaning of the precues and to respond as quickly as possible without making errors. Practice was given to familiarize subjects with the response key configuration that was not open to view.

The results of one of our experiments are shown in Fig. 8.10. Each data point under the eight precue conditions consists of 384 trials averaged over

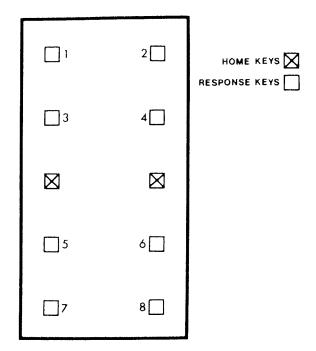


FIG. 8.9 Response configuration for the Goodman and Kelso study. An identical configuration of LEDs was used for precue and initiation signals.

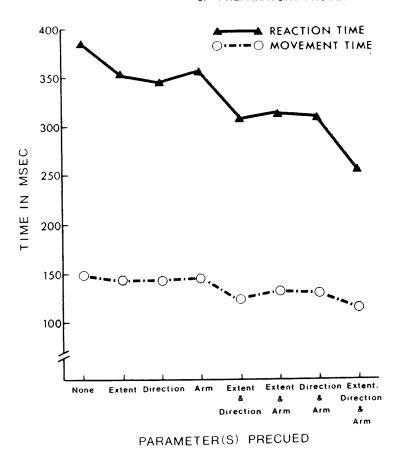


FIG. 8.10 Mean reaction time and movement time (in milliseconds) as a function of various precue conditions in Goodman and Kelso study.

subjects. Initiation times revealed the following pattern: Completely precued initiation times (i.e., a simple reaction time situation) were less than two parameters precued which in turn were less than singly precued conditions. Significantly, however, the latency function within a given precue condition is essentially flat; there are no differential effects of specific parameters. This finding, as well as those of additional experiments (Goodman & Kelso, 1980) suggests that subjects use prior information to reduce the number of possible alternatives but not to prepare response components partially. Indeed there does not appear to be any prioritized ordering at least among the parameters that we have manipulated.

Obviously it would be very elegant indeed to examine event-related brain potentials in this type of paradigm; the fact that subjects effectively use prior information to speed response initiation suggests strongly that there should be

brain correlates of this process and the issue of parameter-specific preparation could be readily examined. Some preliminary evidence (see Kutas' comment, p. 214) favors specificity at least for the limb to be used. When this is known in advance, there is a clearly defined readiness potential that is largest over the hemisphere contralateral to the limb about to be moved. Similarly, Grune wald et al. (1979) have demonstrated a negativity prior to and during goaldirected movements that is restricted to precentral cortex and is larger or the side of the brain contralateral to the moving hand in right-hand subjects. The implication of Kutas' finding is that preparation is at least limb-specific in that there is no negativity when the subject knows neither the time at which to initiate a movement or which limb to move. In contrast, Grunewald et al. (1979) point out that the lateralized component they have identified is not a preparatory phenomenon but rather corresponds to the execution of the movement itself. Clearly there is a good deal of work to be done to establish whether these potentials are parameter-specific or not. Our behavioral results (Goodman & Kelso, 1980) and theoretical orientation suggest that preparation at cortical levels does not involve specifying particular parameters in a particular order. That is not to say that brain potential may not reflect the degree to which the individual is prepared for the occurrence of an event, as Kutas' data seem to show. Indeed I shall argue in the following that we may well expect to see neural counterparts of this process. Unlike Rosenbaum, however, and for reasons delineated earlier, I do not envisage a motor program whose role it is to order response components and prescribe values for them. However, the paradigm introduced by Rosenbaum is a clever one and ERP researchers could usefully employ it to provide some insight into the issue of parameter-specific preparation.

The final issue that I want to address here concerns a behavioral phenomenon that I believe to be related intimately to preparation and that we have termed the preselection effect (Kelso, 1975, 1977a, 1977b; Kelso & Stelmach, 1976; Kelso & Wallace, 1978). I refer to the finding that when a subject makes a self-defined movement of the limb to a certain position (with vision excluded), the subject can reproduce the movement much more accurately than under constrained, exploratory conditions where the movement is defined by an experimenter-defined stop. Elsewhere we have reviewed evidence from over 25 studies illustrating the generality of this effect (Kelso & Wallace, 1978, for a review). Importantly, preselected performance is not dependent on the presence of proprioceptive information from joint and cutaneous sources, whereas constrained and passively generated movements are (Kelso, 1977a; Roy & Williams, 1979). These data on functionally deafferented human subjects appear to concur with the rather global view espoused by investigators in speech control, namely that the greater the ability of the central nervous system to "predictively determine" a motor response, the less the need for peripheral information from sensory receptors (MacNeilage & MacNeilage, 1973).

Are there identifiable neural counterparts to movement preparation in preselected movements? We have some behavioral data that suggest there might well be. Some investigators have suggested that the superiority of preselected movements over those of an exploratory kind might be due to differential attention demands of the two types of movements. The notion is that more so-called "central capacity" is allocated during a preselected than a nonpreselected movement. However, the studies that have been performed thus far (Roy, 1976; Roy & Diewert, 1975) using the probe reaction-time technique to assess attention demands have produced no differences between preselected and constrained trials. The problem with these experiments is that they examined probe performance during the movement itself and not in the period of preparation for the movement. We performed some experiments that measured subjects' reaction time to an auditory tone prior to movement initiation (Kelso & Pruitt, unpublished). Subjects (N = 18) performed 36 preselected and 36 constrained trials, half of which were probed at four different temporal locations during the preparatory period. On probed trials when the subjects heard a tone, they released a microswitch with the nonpreferred hand. After a 3-sec preparatory period, subjects made a preselected movement of their own choice or a constrained movement to an experimenter-defined stop with their preferred hand. Reproduction of the movements followed 3 sec later when subjects were returned to the starting position. These movements were performed in blocks of 12 trials; constrained movements were yoked to preselected trials to facilitate a valid comparison of reproduction errors for different movement extents. In addition, subjects performed 72 nonmovement probe trials that served as baseline controls.

Figure 8.11 shows the reaction time data as a function or probe position (i.e., at 750, 1500, 2250, and 3000 msec). It is quite clear that movement per se is more attention demanding than when no primary task is involved. Moreover, although the latency functions for preselected and exploratory movements are similar, the preselected function is considerably—and significantly—elevated overall. I should mention that there was no effect on the primary movement of the probe task. Preselected errors were significantly smaller than constrained both for absolute and variable error (p < .01), and groups did not interact with presence or absence of the probe task.

These results suggest quite strongly that one of the differences between preselected and contrained movements lies in the degree to which the former requires preparation. (I should point out that these effects are not unique to limb movements. Bizzi and Dichgans [see Bizzi, 1974 for review] in their work on eye-head coordination show clear differences between the saccadic velocity and agonist—antagonist control of the neck depending on whether the monkey looks for an expected target versus a target that suddenly appears unexpectedly. The "set" that seems to be manifested in probe RT differences in our studies is a fundamental aspect of the pattern of coordination observed.)

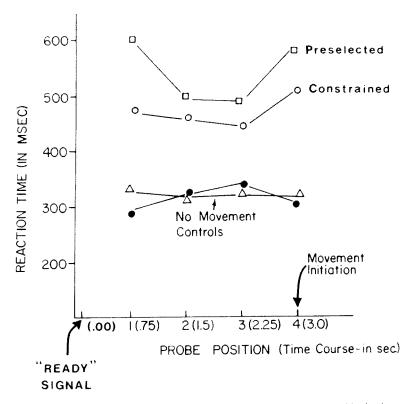


FIG. 8.11 Probe reaction time (in milliseconds) at each of four temporal loci prior to the initiation of preselected and constrained movements.

I am proposing that here we have a significant behavioral effect that appears to reflect varying amounts of movement preparation and that we should be able to identify the same neural processes except to differential degrees. In preselected movements, for example, we might expect to see a well-defined readiness potential, particularly over association areas of cortex. Others have argued that this slowly increasing negativity arising 300-2000 msec before EMG activity represents neural discharges related to preparatory motor set (Vaughan et al., 1968) or motor cortex facilitation (Shibasaki & Kato, 1975). In the foregoing brain-potential studies, however, the tasks employed rather simple stereotyped responses (e.g., thumb flexions, tongue movements) unlike the purposeful and goal-directed movements requiring a high degree of accuracy in the preselection paradigm.

Elsewhere I have argued, after Teuber (1974) and Bernstein (1967), that the preselection effect may be due to a central, feedforward tuning of sensorimotor systems preparing them for the perceptual consequences of the act (Kelso,

1977b). Thus in preselected movements the subject has prior information regarding the terminal position of the limb; constrained, exploratory movements do not have any advance information but must await an externally defined signal to determine the position of the limb. Just as Grunewald et al. (1979) have found "goal-directed movement potential" amplitude differences between tasks requiring low- and high-accuracy demands, so we too might expect to see larger amplitudes of this widespread component in preselected than constrained movements. In sum, my proposal here is one that is consonant with Donchin's (1976) stated "need to examine move complex and skilled tasks... so that skilled sequences [may] be compared in terms of electrocortical events synchronous with or related to them [p. 237]." In this case I am presenting the psychophysiologist with a problem that has a good deal of empirical background and asking him to identify possible neural counterparts.

A final cautionary word about the ubiquity of preparation. It now seems to be well-established that events in the brain related to preparation are not at all confined to cortical areas. Neafsey, Hull, and Buchwald (1978a, 1978b), for example, among others have shown the occurrence of single-unit activity in basal ganglia and thalamus long before that of the lateral region of the feline pericruciate motor cortex. There is some reason to believe that this early activity represents "response set" or the priming of neural mechanisms concerned with integrated movements of the body and limbs. I have presented evidence earlier that this type of tuning also extends to spinal levels.

The point, as embellished by Jung (1974), is that we should not expect to see any simple array of cortical correlates of preparation; rather, preparation is manifested in subcortical, reticular and spinal systems as well. All movements, as Sherrington noted long ago, must have preparatory support mechanisms that identify the postural preconditions for goal-directed activities. Recently Lee (1980) has demonstrated—in a simple reaction-time/movement-time task involving arm raising—the presence of a highly ordered sequence of EMG activity in the axial musculature well before activation of the muscles involved in moving the limb itself (Belen'kii, Gurfinkel, & Pal'tsev, 1967). This result is exactly what we would expect on the realization that supportive mechanisms must be activated to prepare the trunk for subsequent actions of limbs.

To reiterate, we should not expect "simple" cortical correlates of preparation as if all that preparation involves is the construction of motor programs at cortical levels. Rather an elaborate preparation is necessary to provide a context of constraint for supraspinal signals, otherwise aimed movements of the distal linkages would be impossible. It seems to me that it would be very difficult indeed to arrive at the perspective on preparation just outlined from currently extant information-processing models. Although cortical correlates are the obvious bailiwick of the cognitive psychophysiologist, they alone are not going to provide much insight into the nature of preparatory processes. Neural events

with rather longer time scales appear to be involved in the "psychic" preparation of voluntary action. Cortical activities—we might venture to guess—are closer to the endpoint of preparation than the beginning.

KUTAS: Two important factors in the preparation for a hand movement might be noted: (1) when the movement is to be made; and (2) which hand is going to be making that movement. What you see in Fig. 8.12 are ERPs recorded during several different conditions in which these two factors were varied. At the top are movement-related potentials obtained in association with self-paced ("voluntary") movements. Under those circumstances a person could choose the hand and the timing of the movement. The associated brain potential is the classic RP or Bereitschaftspotential, largest over the contralateral central hemisphere for right- and left-hand movements.

The ERPs in the second row were obtained during a condition in which the subject had to make a response as quickly as possible to the occurrence of a tone whose exact timing was unknown. The interstimulus interval varied randomly from 6 to 15 sec. Thus the subject did not know when he was going to be making that response; however, he did know which hand he was going to respond with, as that was held constant within an experimental run. Under such conditions, the movement-related potentials over the central areas do not show a slow ramp-shaped negativity but rather only a burst of negativity within the 200 msec immediately preceding movement onset, that is, as if the subject, even though he knew the responding hand, could not really prepare because he did not know when the response would be required.

The ERPs in the third row were elicited in a condition in which each trial consisted of a simple warning tone followed 1 sec later by a second tone to which the subject was asked to respond as quickly as possible. Again, in any given experimental run, the same hand was used. Thus, the subject not only knew which hand would be responding but also could estimate fairly accurately when the movement would be required. The associated ERPs are characterized by a large, centrally dominant, asymmetric, premovement negativity.

The ERPs in the final two rows were elicited by movements made in conditions similar to the second (SIG) and third (WARN) ones; however, in the latter two conditions the imperative stimulus provided the subject with information as to the responding hand on a trial-by-trial basis. When the subject knew neither the hand nor the time of the response, the premovement negativity is limited to the 200 msec immediately preceding movement onset. On the other hand, when the subject knew only when he was going to make the response, but not with which hand until the imperative stimulus occurred (as in the WARN condition), there is a large event-preceding negativity but its asymmetry is not consistently related to the responding hand.

KELSO: You're preparing both in that case.

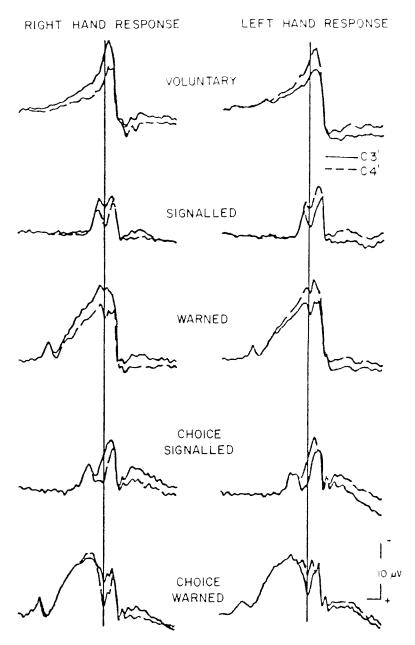


FIG. 8.12 A comparison of the response-locked grand average ERPs recorded at electrodes placed at left central (C3', solid line) and right central (C4', dashed line) loci for right- and left-hand squeezes in five experimental conditions. The vertical line separates presqueeze from postsqueeze activity. Calibrations: 250 msec, $10\mu V$.

KUTAS: Maybe, or alternatively preparing only one or the other hand or different trials based on the preceding sequence of responses, etc. Thus different parameters of the movement-preceding negativity seem to be index ing the timing and the hand selection aspects of a movement. The presence o absence and onset of the negativity seem to reflect the anticipation or prepara tion for a movement, and the asymmetry in this component seems to manifes the hand selection process.

ZAIDEL: I'm not sure that I am convinced that the subjects are in fact no expecting intermediate feedback. All you have shown is that when you don't have feedback, you don't need it and you would behave as if it was not there.

KELSO: I accept that wholeheartedly. Nevertheless, these data are supplemented by probe RT effects on preplanned movements. But I'm not saying that feedback is not important here. I'm saying that indeed one can do without it.

TREISMAN: Dr. Kelso said that probes can be interpreted as a demand on general resources, on "conscious attention." Why could it not be a more specific competition between programming and initiating the response to the probe and preparing the preselected movement? One has to prepare one movement and at the same time to make another.

KELSO: Well, then you might expect that there may be some interfering effect of the probe on the movement.

TREISMAN: Well, it would depend on which of the two was more important to the subject. It would be possible to vary that experimentally. Did you look at that?

KELSO: Yes, but there was no interference. That is one of the important features of the probe technique.

TREISMAN: You mean they were giving priority to the preselected movement?

KELSO: Yes. May I ask what the P300 does? Does it change as a function of practice? Have you really looked at that?

DONCHIN: Within the experiments we normally run, using one or two sessions, the subjects have a lot of practice. Subjects receive many hundreds, in fact, thousands, of stimuli and there is no marked reduction in P300 ampli-

tude. We tried to run subjects in an oddball paradigm for 3 months. The subjects and the experimenters did not hold up very well and we could not use the data.

FORD: Tom Roth ran subjects for 3 days and found that the reaction times changed and P300 almost disappeared.

DONCHIN: The P300 seemed to disappear with practice in our long-term study but the data were so poor, and the experiment was so poorly done, that I can't trust it.

SHIFFRIN: Needless to say, I'd like to warn anybody who does this to pay attention to what kind of training sets you're using—whether you are using variable mapping or consistent mapping and so forth.

DONCHIN: Well, we just recruited six people and told them to come in to the lab daily for 3 months. We ran the routine beep/boop study. I wouldn't be surprised if P300 disappears in a beep/boop oddball but will not be reduced when the subject needs to categorize names as male or female, or when they are monitoring complex displays. Very few things are more boring, I think, than an oddball paradigm with tones.

SCHVANEVELDT: Judy, what task was this where you ran subjects for 3 days?

FORD: It was a beep/boop oddball experiment where 80% of the tones were high pitched, 10% were medium pitched, and another 10% were low pitched.

SCHVANEVELDT: The P300s to the rare events disappeared?

FORD: Yes, but the reaction times became slightly shorter with practice.

DONCHIN: One of the longest-duration experiments in our lab was run by Johnson (Johnson & Donchin, 1982). There were many, many conditions and, I think, six sessions per subject with maybe 2000 stimuli. P300 was elicited in all the conditions. The subjects had to detect whether or not the probability in a Bernoulli series changed, so it was a little bit more interesting to the subject.

KUTAS: I've required as many as 800 to 1000 movements from a person in a 3-hr session without an appreciable decline in the amplitude of the associated premovement potentials (RPs).

KELSO: To go back to the issue of whether you might "cue" yourself, as it were, to move a particular extent. This could be more "cognitive" than motor, so you might find the so-called selection process linked to a P300 event rather than a motor event. For example, when I talked about the Rosenbaum paradigm, the notion was that when you prepare movement dimensions you're doing some sort of cognitive operation. Now I'm precued on the limb I have to move and how far to move it. So when you set up this paradigm, do you expect to see some cognitive evoked potentials as well as evidence of general motor preparation?

KUTAS: Yes. There are undoubtedly cognitive as well as motor-related components or potentials elicited prior to preparation for a movement or response. The RP recorded during simple, voluntary movements has a large ipsilateral component that may well manifest cognitive rather than motor processes. It is conceptually and technically difficult to tease apart the various overlapping components whether they represent different aspects of motor or motor and cognitive acts. At present, I view the RP as functionally quite similar to other event-preceding negativities. It seems to differ primarily in its scalp distribution. Much of the emphasis on its motor-relatedness may have to do with the paradigm in which it has generally been recorded.

DONCHIN: I would define operationally as "motor related" that component of the negativity that lateralizes with the responding hand and reverses when you reverse hands. And all other negativity is not necessarily motor.

McCARTHY: Well, you know you can get postural adjustments and synergistic movements on the other side, so that's kind of dangerous to do. Isn't it dangerous to decide that the only thing that is motor is the lateralized portion?

DONCHIN: I did not say necessarily that potentials that do not lateralize are not motor. All I am saying is that I accept as *definitely* motor what is lateralized; the rest is open.

KUTAS: It's been said that my subjects were making simple, relatively inane movements. It's necessary to investigate more complex movements; those may be associated with still other endogenous potentials.

DONCHIN: I am not sure I agree. Squeezing a dynamometer and producing a carefully defined response pattern in an isometric squeeze is not "inanely lifting your hand." It requires a lot of skill for the subject to perform those movements.

KUTAS: True, but we have barely tapped the store of even the most mundane human movements. The few statements about movement-related potential shapes and distributions that we can make, apply with very few exceptions, only to the finger, hand, and arm movements that have been investigated. At this point we cannot generalize to the movement(s) involved in slipping an arm through a shirt sleeve. The area is wide-open for investigation.

DONCHIN: The Grunewalds in Freiburg (1979) have been looking at "goal-directed movements." The subject is required to move a pointer to a target. It turns out that a large, lateralized potential appears as long as the subject is moving the pointer. This lateralized potential disappears if the movement is not goal directed or if the movement is passive.

ZAIDEL: What does "lateralized" mean? Where is the difference?

DONCHIN: Oh, it's always larger contralateral to the responding hand, that's what I mean by lateralized.