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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

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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 related. Requin views preparation not only as an intrinsic facilitatory 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 previously referred to ignore the problem of what Bernstein (1967) called functional nonunivocality or context-conditioned variability (Turvey, Shaw, & Mace, 1978); second, they ignore the fundamental problem of perception-production systems, namely the regulation of a potentially large number of degrees of freedom. Functional nonunivocality refers to the fact that centrally generated 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 skilled individuals is that of providing only those changes in force during a particular movement that are not given reactively. But the effect of movement context is manifested at a neurophysiological level as well. Monosynaptic control of alphamotoneurons is the exception rather than the rule in the neural regulation of movement. Instead, whether a motoneuron fires or not is ultimately contingent on the influences of suprasegmental, intersegmental, and intrasegmental 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 supraspinal 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. Well-known 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-

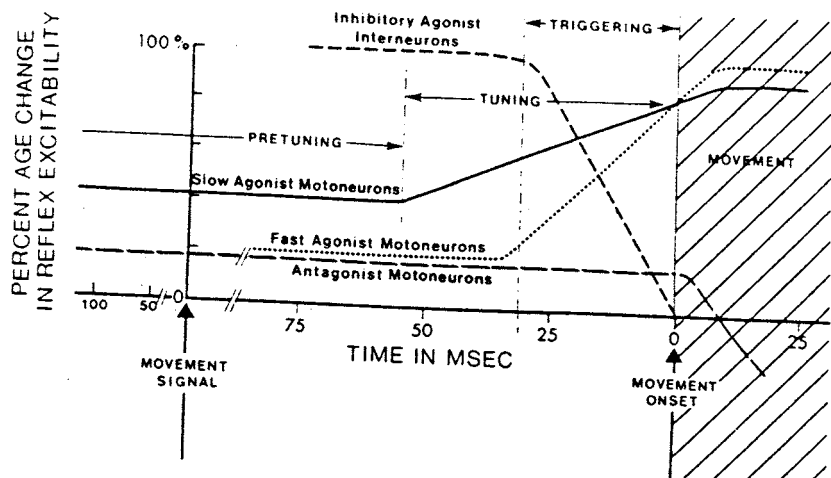


FIG. 8.8 Schematic showing changes in reflex excitability of agonist and antagonist motoneuronal pools during the preparation of voluntary movement. Adapted from Kots (1977).

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

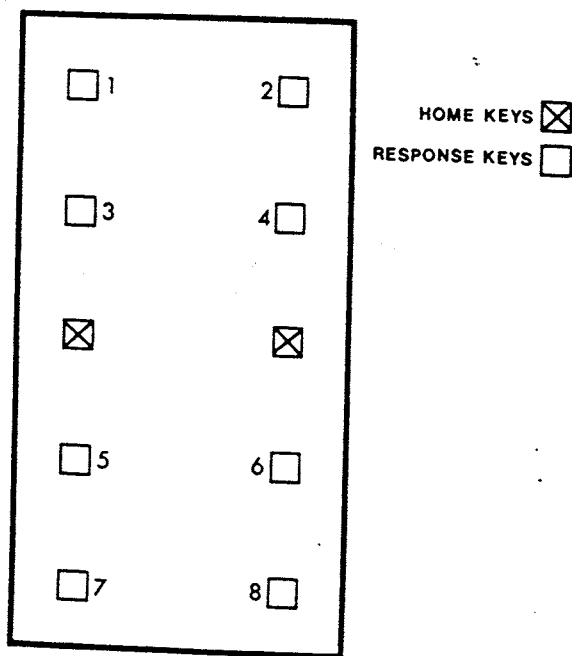


FIG. 8.9 Response configuration for the Goodman and Kelso study. An identical configuration of LEDs was used for precue and initiation signals.

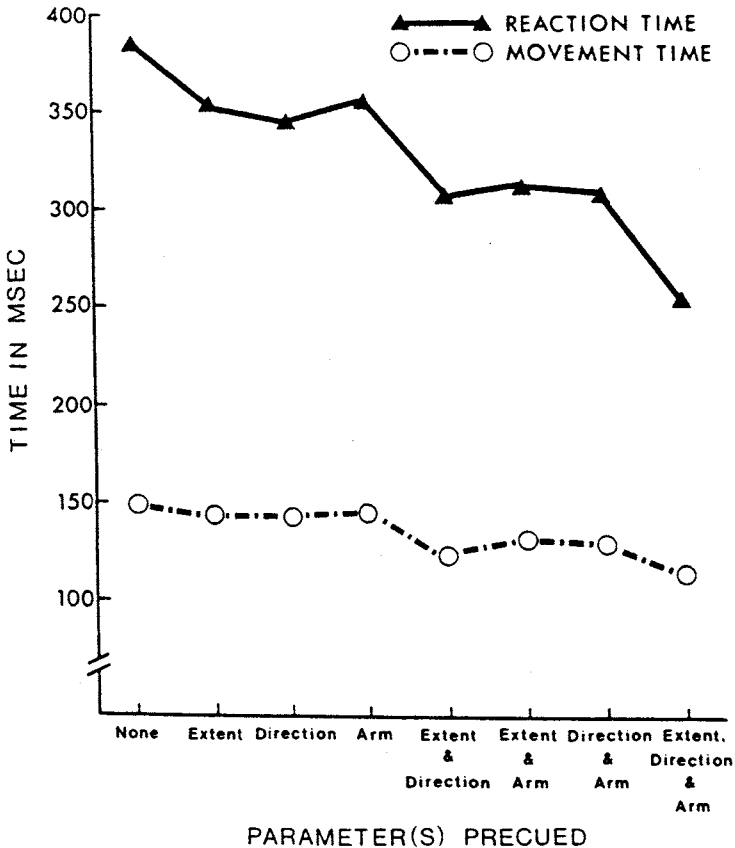


FIG. 8.10 Mean reaction time and movement time (in milliseconds) as a function of various precue conditions in Goodman and Kelso study.

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, Grunewald et al. (1979) have demonstrated a negativity prior to and during goal-directed movements that is restricted to precentral cortex and is larger on 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 of 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 constrained 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.)

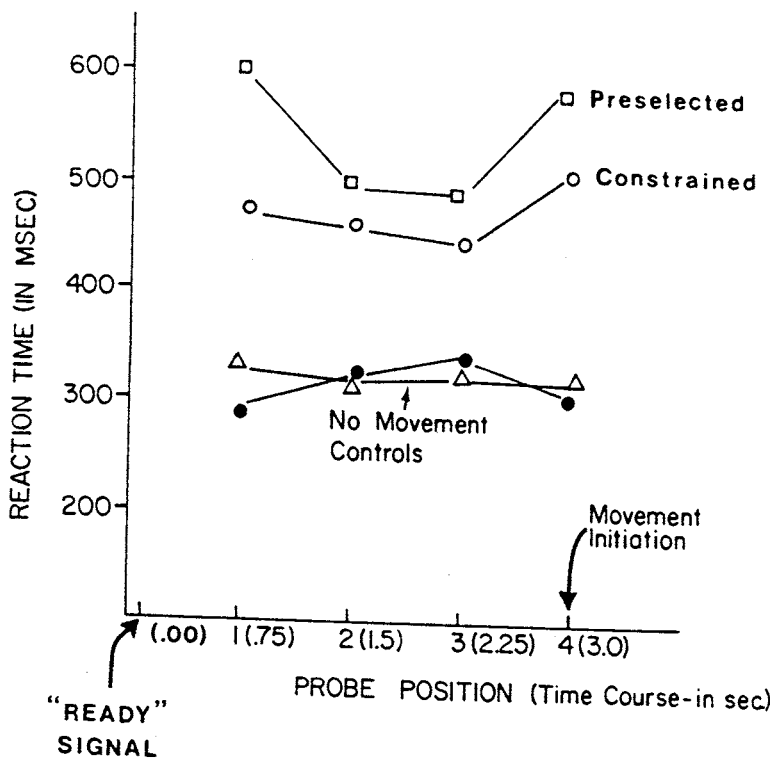


FIG. 8.11 Probe reaction time (in milliseconds) at each of four temporal loci prior to the initiation of preselected and constrained movements.

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 psychophysicist 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 psychophysicist, 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.

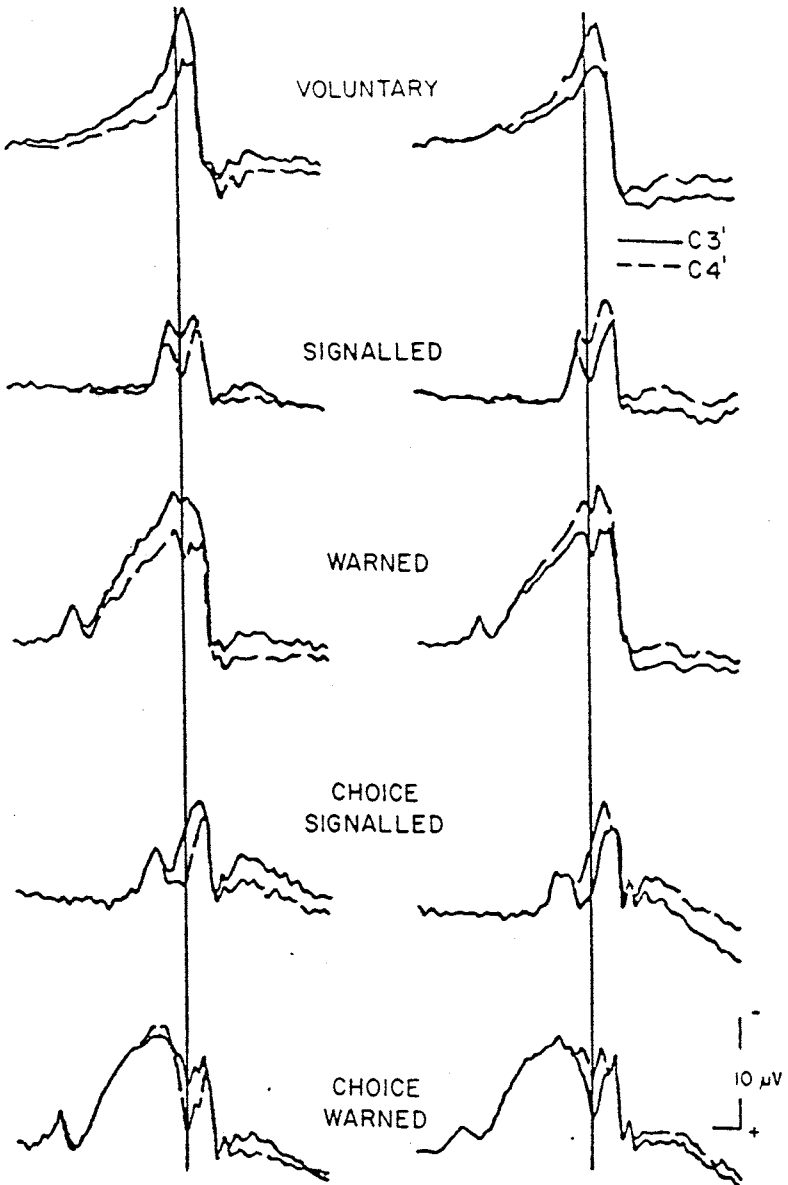


FIG. 8.12 A comparison of the response-locked grand average ERPs recorded at electrodes placed at left central (C3', solid line) and right central (C4', dashed line) loci for right- and left-hand squeezes in five experimental conditions. The vertical line separates presqueeze from postsqueeze activity.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

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

ZAIDEL: I'm not sure that I am convinced that the subjects are in fact not 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 "inane 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.