

# *SPR Presidential Address, 1988*

## Modern Mind-Brain Reading: Psychophysiology, Physiology, and Cognition

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### ABSTRACT

This paper reviews the actual and potential benefits of a marriage between cognitive psychology and psychophysiology. Psychophysiological measures, particularly those of the event-related brain potential, can be used as markers for psychological events and physiological events. Thus, they can serve as "windows" on the mind and as "windows" on the brain. These ideas are illustrated in the context of a series of studies utilizing the lateralized readiness potential, a measure of electrical brain activity that is related to preparation for movement. This measure has been used to illuminate presetting processes that prepare the motor system for action, to demonstrate the presence of the transmission of partial information in the cognitive system, and to identify processes responsible for the inhibition of responses. The lateralized readiness potential appears to reflect activity in motor areas of cortex. Thus, this measure, along with other psychophysiological measures, can be used to understand how the functions of the mind are implemented in the brain.

**DESCRIPTORS:** Cognition, Mental chronometry, Preparation, Partial information transmission, Response inhibition, Cognitive psychophysiology, Cognitive neuroscience, Event-related brain potentials, Lateralized readiness potential, Motor cortex.

Advances in science can often be attributed to the "marriages" between two apparently unrelated disciplines. These marriages frequently lead to paradigm changes in which the concepts, methods, and procedures of one discipline are applied to answer the questions of another discipline. Examples of previously successful marriages include those between chemistry and biology, and between physics and astronomy. Within psychology, considerable

progress has been made following the marriages between cognitive psychology and linguistics and between engineering and experimental psychology. It will be the thrust of the arguments to be presented in this paper that the recent marriage between psychophysiology and cognitive psychology shows the promise of being as beneficial as the marriages mentioned above (see Meyer, Osman, Irwin, & Yantis, 1988).

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Like most good marriages, the marriage between psychophysiology and cognitive psychology may have benefits to both participants. On the one hand, the psychophysiological approach can be used to address questions that arise in the study of human cognition. On the other hand, the conceptual framework and the paradigms of cognitive psychology may aid in understanding how the brain works. This two-way interaction is made possible by the fact that psychophysiological measures, particularly those of the event-related brain potential<sup>1</sup>, have a dual status. They can serve as markers for psychological processes—as “windows” on cognition—and they can also serve as markers of physiological processes—as “windows” on the brain.

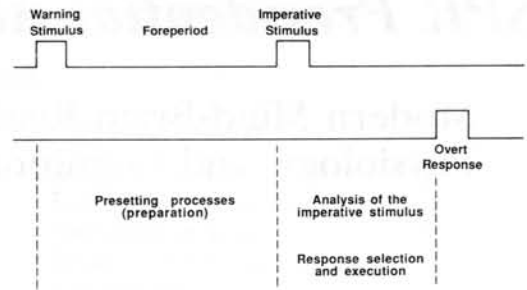
### The Study of Cognition: The Chronometric Approach

One major contemporary approach to the study of cognition involves what Posner (1978) has called *mental chronometry*—the study of the time-course of information processing. The assumption of this approach is that the cognitive system is comprised of a sequence of time-consuming mental processes whose activities are manifested through certain overt behavioral measures, including reaction time, response accuracy, and speed-accuracy trade-offs (see Meyer, Osman, Irwin, & Yantis, 1988). For most chronometricians, there are processes associated with stimulus recognition and evaluation, and with response organization and execution. There are also meta-processes, such as attention and preparation, which preset the system to behave in certain ways. The challenge for the cognitive scientist is to discover what these processes are, to identify their transformations, to specify their temporal properties, and to describe their patterns of communication (see Meyer, Osman, Irwin, & Yantis, 1988).

The chronometrician presents a series of discrete events or imperative stimuli to human subjects. The events may be either auditory or visual (or occasionally somatosensory) and can range from simple tones or visual symbols to words and pictures. The subjects are required to execute an overt behavioral response (usually a button-press) as quickly as possible following the imperative stimuli.

In some cases, a warning stimulus is presented in advance of the imperative stimulus. At a minimum, this stimulus warns the subject that an imperative stimulus is about to occur. The warning

### THE CHRONOMETRIC PARADIGM



**Figure 1.** The events of the chronometric paradigm. Of particular interest are the covert processes that occur during the foreperiod (presetting processes) and between the imperative stimulus and the subject's overt response (analysis of the imperative stimulus and response selection and execution).

stimulus may also provide information about the kind of imperative stimulus to be expected or about the nature of the response that will be required.

Within the sequence of events in the chronometric paradigm, there are time zones of special interest (see Figure 1). The first time zone is the foreperiod or warning interval. During this interval, presetting or preparatory processes are assumed to occur. These processes preset elements of the system such that the speed or accuracy of the subsequent overt response to the imperative stimulus is changed. Presetting processes may operate on almost any element of the system, including those concerned with stimulus evaluation and response activation (see Meyer, Yantis, Osman, & Smith, 1985; Miller, 1982; Posner & Snyder, 1975; Requin, 1985).

The second time zone of interest occurs between the presentation of the imperative stimulus and the execution of the overt response. Again, during this time zone, a variety of processes are assumed to be engaged, especially those involving the analysis of the imperative stimulus and the selection and execution of an appropriate response (see, for example, McClelland, 1979; Sanders, 1980; Sternberg, 1969). These processes also affect the accuracy and latency of the overt response.

By varying the parameters and the timing of the stimuli, and the experimental instructions, and by observing the subject's overt behavior, the chronometrician hopes to learn about the nature of the covert processes that occur during the foreperiod and between the imperative stimulus and the overt response. Note that this strategy is intrinsically problematic because the chronometrician is interested in the *covert* processes that occur when there is actually no *overt* behavior.

<sup>1</sup>The emphasis in this paper is on measures of the event-related brain potential. However, other psychophysiological approaches, involving noninvasive measures of human physiological function, may also have a role to play in the study of human cognition.

### Inferential Procedures

For this reason, the chronometrician must establish an inferential procedure that will allow the behavior of these covert processes to be inferred from the measures of overt behavior.

Some of these inferential procedures have been based on the Subtraction Method (Donders, 1868/1969) and on the Additive Factors Method of Sternberg (1969). More recently, complex mathematical models have been used to express assumptions about the behavior of the underlying processes (see, for example, Logan & Cowan, 1984; Luce, 1986; Meyer, Irwin, Osman, & Kounios, 1988; Townsend & Ashby, 1983). Then, the models are used to make numerical predictions about overt behavior. Observations of the actual overt behavior are compared to the predictions and the assumptions of the models are either strengthened or weakened.

An alternative strategy has involved the use of probe stimuli, presented during the foreperiod or after the imperative stimulus (see Posner & Boies, 1971; Posner, 1978; Schouten & Bekker, 1967). The subject's responses to these probes are used to infer the state of various processes at the time the probe is presented.

Although these methods, either alone or in combination (see Meyer, Irwin, Osman, & Kounios, 1988), have succeeded in providing important insights into the processes that underlie overt performance, they have all suffered from challenges to the assumptions that underlie their application. For example, the Subtraction Method rests on the assumption of *pure insertion*—namely that different stages may be inserted or deleted from the processing system by changing the subject's task. If, in fact, a change in the task results not only in the removal or addition of a stage but also in a change in a way the other stages behave, then the logic of the subtraction method falls apart.

The more sophisticated Additive Factors Method (Sternberg, 1969; see also Sanders, 1980) does not rely on the assumption of pure insertion. However, the method does assume that a particular experimental manipulation will affect only the duration of different stages. If, for example, the quality of the output of a stage is influenced by some experimental manipulation, then the inferential basis of the method falls apart. For a more detailed discussion of these issues, see Luce (1986, pp. 472–491), Pachella (1974), Pieters (1983), and Townsend and Ashby (1983).

The assumptions that underlie mathematical models can be evaluated, at least indirectly, by determining the match between the predicted and observed data. However, problems can arise when dif-

ferent models based on different assumptions provide equally good predictions. (See Townsend, 1974, for a discussion of this problem in the context of the serial/parallel distinction.) Application of the probe technique presupposes that the task that is ongoing when the stimulus probe is presented is unaffected by the presentation, or even the possible presentation, of the probe.

These inferential procedures are all designed to deal with the fundamental problem alluded to above—namely, that the chronometrician must rely on measures of overt behavior to understand what are, by definition, covert processes. Although the procedures have provided important insights into the workings of the human information processing system, limitations to their applicability are evident in the challenges reviewed above.

### An Analogy

By way of illustration, it may be helpful to consider the following analogy. Figure 2 depicts a demonstration of the measurement of average human reaction time taken from a book by E.W. Scripture, published in 1907<sup>2</sup>. A group of individuals is arranged in a circle. Each individual is told "when-ever you feel a sudden pressure on your head, you must immediately press the head of the person in front." The experimenter (with the watch) initiates the signal and measures the time required for the signal to progress around the circle. This time represents the sum of the individual reaction times. Thus, to obtain a measure of average individual reaction time, this time is then divided by the number of participants. Although this procedure can yield a measure of the average reaction time of the members in the group, it cannot provide direct information about the reaction times of individual

<sup>2</sup>I am grateful to Professor Bob Hendersen at the University of Illinois for drawing my attention to this example.



Figure 2. The measurement of average human reaction time. From Scripture (1907, p. 26).

members. Furthermore, the measure of average reaction time is multiply determined—depending both on the reaction times of the individual members of the group and on the way in which the members communicate. Thus, some kind of procedure, of the kind described in the previous section, is needed if one is to infer anything about the individuals in the group from the average individual reaction time.

Let us assume for a moment that this group of individuals is a model of the human cognitive system. Our interest, then, is in describing the individuals, their functions, and how they communicate with each other. In this example, we have a Bishop, a Queen, and a Prime Minister, among others, all of whom have particular roles. Furthermore, we can imagine that there would be particular channels of communication among them. For example, Queen Victoria might be thought of as a control process who communicates continuously, but only with Disraeli, her executive. One can take the analogy as far as one wants. The point is that cognitive psychologists are concerned with understanding this kind of complex system—and, for the chronometrician, the only observation available is the response of the system to variation in the input. In terms of our analogy, it is like trying to figure out the details of the group when all one knows is what went into the group, what came out, and when it came out.

This problem has been articulated by Luce (1986) in his recent book entitled "Response Times." In referring to the traditional chronometric strategy, Luce says the following:

Let me admit at the outset that there are reasons to be skeptical of the enterprise. . . . as psychologists, we can hope at best to learn something about overall organization and very little if anything about the details. That presumably will develop only as we look, in some fashion or another, inside the "black box." This means using physiological observations. . . . (Luce, 1986, p. 1).

In this quotation, Luce anticipates the possible benefits of the psychophysiological approach. Because the cognitive system is implemented in the brain and because cognitive processes must be realized by physiological processes, it makes sense to examine these physiological processes.

### The Two Faces of Psychophysiology

As I mentioned above, when we apply the psychophysiological approach to the study of cognition, there are two distinct courses of action. First, we can take the position of the chronometrician. Our aim, then, is to discover the cognitive processes, to identify their transactions, to specify their

temporal properties, and to describe their patterns of communication. In this case, the psychophysiological measures we derive can be viewed as markers for psychological processes—that is, as windows on cognition—and by using them we hope to achieve understanding at the *psychological* level. In terms of the group analogy, psychophysiological measures may enable us to infer what process is occurring (that is, who is speaking), when the process occurs (that is, when a person speaks), and perhaps, the degree of processing involved (that is, how much the person is speaking).

The second course of action is to try to understand how the cognitive system is implemented in the neural hardware. The activity we record at the scalp is certainly generated in the brain—although it is debatable whether what we observe is merely a by-product of neural activity or whether it is directly related to a neurally meaningful signal. In either case, our measures have the status of markers of *physiological* processes. Psychophysiological measures, then, might enable us to infer which part of the brain is active at a particular moment in time, and what physiological process is occurring there.

It is important that these two uses of psychophysiological measures are kept distinct because they entail quite different courses of action in establishing the validity of the measures. In the case of psychological validation, we need to study the effects of various manipulations on the behavior of the measures—that is, we need to study the antecedents of change in the measure. We also need to investigate the relationship between the measures and some aspect of the subject's overt behavior (such as its accuracy or speed)—that is, we must evaluate the consequences of variability in the measures. Again, in terms of the group analogy, we need to find out what conditions lead the bishop to speak and what are the consequences to the output of the system when the bishop speaks. On the basis of this information we can establish what function is served by the bishop speaking. The traditional chronometric approach can provide a valuable framework within which such validation work can be conducted. In the case of physiological validation, we need to investigate the neural substrate of the measure and specify those physiological processes that occur when we observe changes in our measure. Where does the bishop reside, and what is going on there when the bishop speaks? (For a detailed discussion of the issue of validation in psychophysiology, see Coles, Gratton, & Fabiani, in press; Coles, Gratton, & Gehring, 1987; Donchin & Coles, 1988a, 1988b.)

The relative emphasis on these two faces of psychophysiology varies with the domain of inquiry.

For example, in the areas of stress and behavioral medicine, great attention is paid to the physiological meaning of the measures. In other domains, however, including the areas of orienting and habituation, the tendency has been to emphasize the psychological meaning of the measures. As we shall see, cognitive psychophysiology is concerned with both aspects of psychophysiology. In the next section of this paper, I will concentrate on the idea that psychophysiological measures can be used as markers for psychological processes. Later, I will review the implications of the physiological status of our measures.

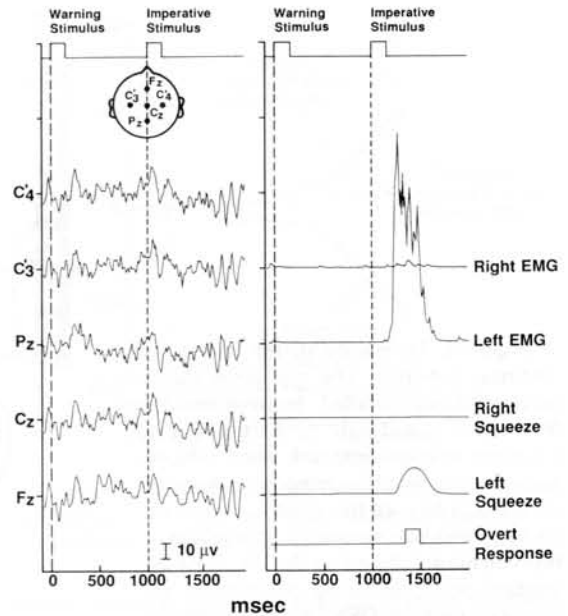
#### Application of Psychophysiology to the Study of Cognition: The Lateralized Readiness Potential

How do we bring the psychophysiological approach to bear on the study of cognition? If we are to contribute to a solution of some of the problems encountered by the chronometric approach, we should begin by adopting the chronometric paradigm. At least initially, we should also adopt the same theoretical framework used by the chronometric approach. Thus, we should replicate existing chronometric experiments, but we should include psychophysiological measures. To this end, we should present warning and imperative stimuli to our subjects, and measure their overt responses. However, we will also derive measures of psychophysiological functions (see Figure 3).

In our work, we have chosen to focus on measures of brain activity, as well as on measures of electromyographic activity from muscles associated with overt responses. We have also required subjects to indicate their responses by squeezing dynamometers rather than by pressing buttons (the characteristic response requirement of traditional mental chronometry). The squeeze response requirement enables us to examine in detail the dynamics of overt response execution.

The decision to choose measures of central nervous system activity is based on a consideration of their temporal properties. In contrast to autonomic measures, central nervous system measures provide the kind of temporal resolution we would expect of markers of those psychological processes engaged in the chronometric paradigm. Of the variety of brain potential measures available, we have recently focused on the lateralized readiness potential—a measure that is intimately related to the preparation for, and execution of, motor actions.

This potential was first observed by Kornhuber, Deecke, and their colleagues in their analysis of voluntary movements (Kornhuber & Deecke, 1965). Prior to hand movements, a negative potential occurs at the scalp, and this potential is maximal at



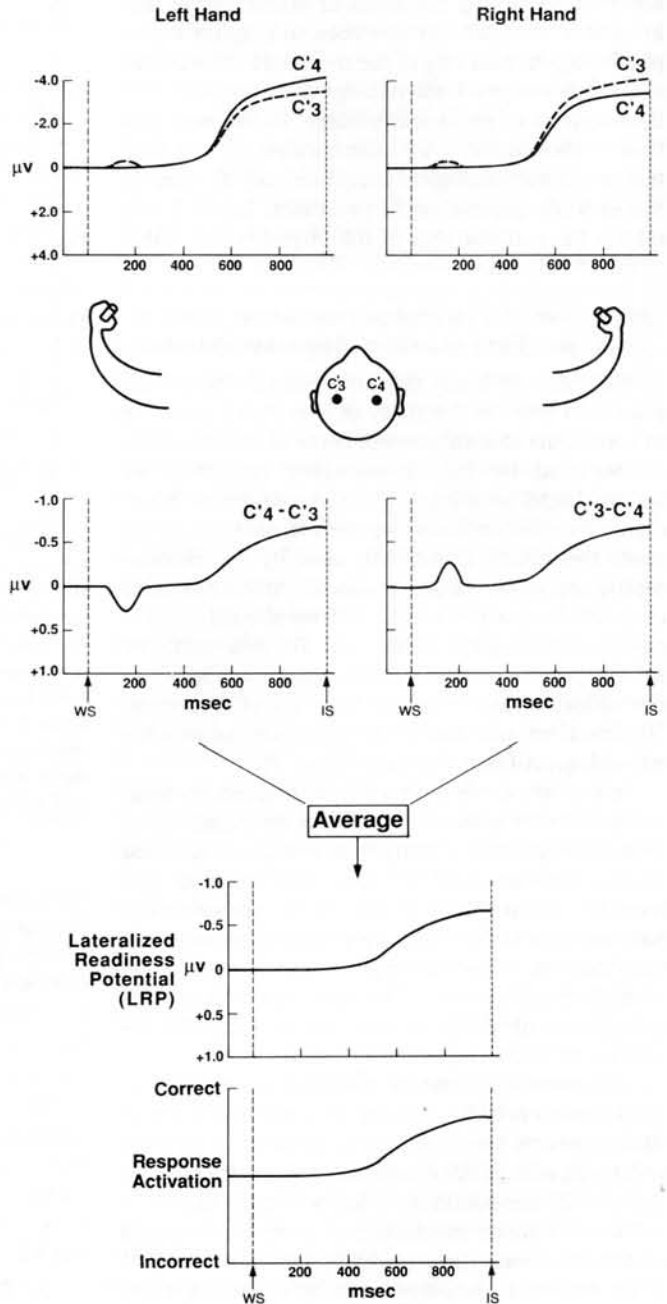
**Figure 3.** Cognitive psychophysiology and the chronometric paradigm. We present warning and imperative stimuli and record overt behavioral responses. However, we also measure electrical brain activity (in this case from five scalp locations, Fz, Cz, Pz, C<sub>3</sub>, and C<sub>4</sub>) and electromyographic activity (EMG) from muscles involved in the overt behavioral response, and we require our subjects to squeeze zero-displacement dynamometers to indicate their responses. The overt response is defined in terms of the force-output of the dynamometers, with a criterion generally set at 25% of maximum force.

central sites, contralateral to the responding hand (Vaughan, Costa, & Ritter, 1968).

The potential (see upper panel of Figure 4) is also observed in the foreperiod of warned reaction time tasks when subjects know in advance which hand to use in response to the imperative stimulus (e.g., Gaillard, 1978; Kutas & Donchin, 1980; Rohrbaugh, Syndulko, & Lindsley, 1976). Thus, when subjects prepare to move their left hands, the negativity is larger over the right side of the scalp (designated C<sub>4</sub>). When subjects prepare for movements with their right hands, the potential is larger over the left side of the scalp (designated C<sub>3</sub>). Given what we know about the neural organization of the motor system, the contralateral nature of these potentials suggests that they are related to motor action (Vaughan et al., 1968).

The steps used to derive the lateralized readiness potential are shown in Figure 4. First, to illustrate the lateralized nature of this activity, we subtract potentials recorded over the left and right sides of the scalp. This subtraction is performed separately

## The Lateralized Readiness Potential



**Figure 4.** Derivation of the lateralized readiness potential. The top panel shows idealized scalp-recorded brain potentials from left ( $C'_3$ ) and right ( $C'_4$ ) scalp sites in a warned reaction time task when subjects know in advance of the imperative stimulus the hand to be used to execute a correct response. Potentials associated with left-hand movements are shown on the left; those associated with right-hand movements are shown on the right. (WS = warning stimulus, IS = imperative stimulus.) As subjects prepare to execute a movement, a negativity develops that is maximum at scalp sites contralateral to the responding hand. The asymmetry in these potentials is illustrated by subtracting the potential recorded at the scalp site ipsilateral to the movement from that recorded contralateral to the movement (second panel). Then, the difference potentials for left- and right-hand movements are averaged to yield the lateralized readiness potential (third panel). Note that this procedure eliminates the negative deflection following the warning stimulus that occurs consistently at  $C'_3$  irrespective of the side of movement. We propose that the lateralized readiness potential reflects response activation (lower panel). When these procedures are performed with reference to the correct response hand on each of a group of trials, deviations of the trace in the upward (negative) direction reflect preferential activation of the correct response, whereas downward deflections indicate preferential activation of the incorrect response. The formula for deriving the lateralized readiness potential (LRP) is as follows:

$$\text{LRP} = [\text{Mean}(C'_4 - C'_3)_{\text{left-hand movement}} + \text{Mean}(C'_3 - C'_4)_{\text{right-hand movement}}] / 2.$$

for left- and right-hand movements. In each case, the potential ipsilateral to the responding hand is subtracted from the potential contralateral to the responding hand. Then, the values for left- and right-hand movements are averaged to yield a measure of the average lateralized activity as subjects pre-

pare to move. This average measure is the lateralized readiness potential. A critical aspect of this procedure is that lateralized activity unrelated to the movement will average to zero. In Figure 4, the negative deflection following the warning stimulus, which is present at  $C'_3$  and absent at  $C'_4$  regardless

of the side of movement, is missing in the derived lateralized readiness potential waveform. Thus, the lateralized readiness potential will deviate from zero only if there is activity associated with the side of movement. Asymmetrical activity that is the same for both left- and right-hand movements will be eliminated by the averaging.<sup>3</sup>

In all the experiments to be discussed in this paper, this subtraction is performed with reference to the hand that should be used to execute a correct response on a particular trial. Deviation of the trace from the zero line in the upward direction will indicate that the subject has activated the correct response, deviation in the downward direction reflects preferential activation of the incorrect response (lower panel of Figure 4).

### Validating the Measure

If we are to use this measure as a marker for response activation processes, we must conduct experiments to demonstrate its validity. As was noted earlier, these experiments should identify those variables whose manipulation influences the measure—that is, we should identify the antecedents.

Such an experiment was conducted by Gratton, Bosco, et al. (1989). The experiment involved a choice reaction time task in which the subject had to respond with one hand if the imperative stimulus was the letter *S* and with the other hand if the letter *H* was presented. The warning stimulus was also the letter *H* or the letter *S*; however, when a letter appeared as a warning stimulus, it was flanked by a dot. The position of the dot indicated the probability that the same letter would follow as the imperative stimulus. In fact, the dot could appear in three different positions, each dot-position occurring on 33% of the trials. One dot position indicated that the same letter would follow as the imperative stimulus with a probability of .8. Another dot position indicated the different letter would follow as the imperative stimulus with a probability of .8. For these two dot positions, the warning stimulus could be valid (if the predicted imperative stimulus occurred), or invalid (if the unpredicted imperative stimulus occurred). For another dot position, the probability that the same or the different letter would follow as imperative stimulus was .5. This constituted a neutral cue condition.

The data from this experiment are shown in Figure 5. When the cue was valid, the lateralized read-

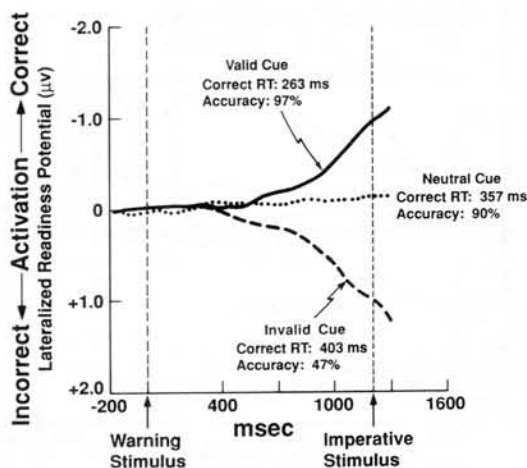
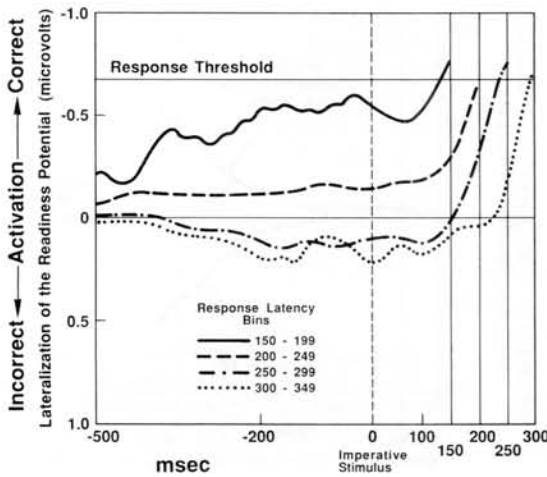


Figure 5. The effects of cue validity on the lateralized readiness potential and overt response measures are shown. From Gratton, Bosco, et al. (1989).

iness potential indicated that the correct response was primed during the foreperiod. When the cue was invalid, the subjects primed the incorrect response. In other words, the subjects primed the response associated with the letter predicted by the warning cue. Note that, on the average, there was no evidence of priming in the neutral cue condition. As one would expect, there was a considerable benefit to correct reaction time and accuracy when the cue was valid. Conversely, there was a considerable cost when the cue was invalid (see Figure 5). This pattern of overt behavioral data has been attributed by some chronometricians to response preparation or bias processes (see Meyer et al., 1985; Miller, 1982). It appears, therefore, that the lateralized readiness potential makes evident these presetting processes as they occur. (See also Gehring, Gratton, Coles, & Donchin, 1989, who conducted a similar experiment in which cue validity was varied between rather than within trial blocks, and replicated the results obtained by Gratton, Bosco, et al., 1989.)

This experiment reveals something about the antecedents of the lateralized readiness potential. Stimuli that provide information about the hand to be used in response to a future event are followed by the development of lateralized readiness potentials (see also Kutas & Donchin, 1980). In turn, it appears that the development of these potentials has consequences for the subject's overt behavior. Other evidence concerning consequences is provided by data from an experiment by Gratton, Coles, Sirevaag, Eriksen, and Donchin (1988). In this experiment, we analyzed the lateralized readiness potential at the time of response initiation, which was defined as the latency of the onset of EMG activity, rather than the latency of the overt response. We

<sup>3</sup>For further information about this measure, see Gratton, Coles, Sirevaag, Eriksen, and Donchin (1988). Note that the measure is identical to that proposed by de Jong, Wierda, Mulder, and Mulder (1988), who refer to it as "Corrected Motor Asymmetry" or CMA.



**Figure 6.** The lateralized readiness potential at the time of the electromyographic response for trials with different response latencies. See text for details. From Gratton, Coles, Sirevaag, Eriksen, and Donchin (1988). Copyright 1988, American Psychological Association. Reprinted with permission.

sorted trials into different response latency bins, with each bin corresponding to a particular range of response latencies. We then derived lateralized readiness potential waveforms for the trials associated with each response latency. As shown in Figure 6, this yielded a waveform for each response latency bin. For each of these waveforms, the vertical line in the figure marks the average time of response initiation for that group of trials. Regardless of the actual response latency, it appears that the magnitude of the lateralized readiness potential is approximately the same at the time of response initiation. Thus, it appears that when the lateralized readiness potential achieves a relatively fixed threshold value, overt responses are initiated. The horizontal line, labelled *Response Threshold* in Figure 6, represents this value, averaged over subjects and trials.

These two experiments are part of the body of evidence obtained by us and by many other investigators (e.g., Rockstroh, Elbert, Lutzenberger, & Birbaumer, 1982; Jaeger, Elbert, Lutzenberger, & Birbaumer, 1987), which supports the idea that our measure can serve as a window on covert response-related processes. In particular, when subjects are required to respond with either the left or the right hand, a significant deviation from zero in the lateralized readiness potential indicates that one of the two responses has been preferentially primed. Furthermore, preferential priming must have occurred at or before the time at which this deviation is significant. In subsequent examples, I will illustrate how the measure can be used to shed light on the

behavior of these processes in situations in which the questions addressed were motivated by specific theoretical issues.

### *Using the Measure*

The questions with which we have been concerned fall into three general categories: (a) First, we have been interested in the presetting processes that prepare the motor system for action. Can we identify these preparatory processes during the foreperiod and what are their consequences? (b) Second, we have been concerned with the way in which information about the imperative stimulus is transmitted to the motor system so that an overt motor response is executed. Is information transmitted continuously or discretely? (c) Third, we have been concerned with the possibility that there is a point-of-no-return in response processing. Is there a point beyond which response processes cannot be interrupted and the response is executed? If so, what is the mechanism responsible?

In all our experiments in this series, we have adopted the standard chronometric paradigm. Following presentation of an imperative stimulus, subjects must choose whether to respond with their left or right hands. Given that subjects are choosing between left- and right-hand responses, we can use measures of the lateralized readiness potential to indicate whether there is a bias toward one or the other of the two responses.

*Presetting Processes.* To examine the phenomenon of presetting, we have focused on the foreperiod. In the Gratton, Bosco, et al. (1989) experiment described above, we demonstrated that lateralization develops in the foreperiod, when the subject receives a warning cue that heralds the probable arrival of a particular imperative stimulus. It is not surprising that a brain potential measure that is intimately related to the activity of the motor system (see below) increases as the time for a particular movement approaches—even when the information provided by the warning stimulus is not completely reliable. Rather, it is more interesting to determine what happens when the warning stimulus provides no information about a forthcoming imperative stimulus—that is, to examine the neutral cue condition in detail. On the average, there is no preferential priming of one response over the other in this condition (see the neutral cue condition in Figure 5). However, on the basis of work in human expectancies (e.g. Yellott, 1971), we might predict that subjects will make guesses about the response to be made on some trials—especially in the face of our exhortations that they respond as quickly as possible without making too many errors. That is, even when both responses are equiprobable, and



when a neutral warning cue is presented, we might expect to see the development of response biases during the foreperiod on at least some trials.

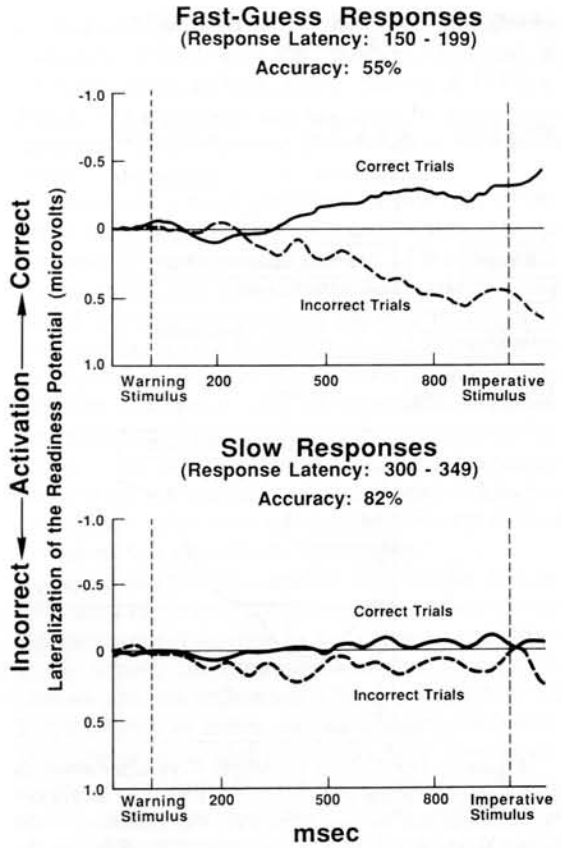
This possibility was evaluated in the experiment by Gratton et al. (1988). The overt behavioral data from this experiment suggest that subjects were indeed adopting a guessing strategy from time to time. (As above, electromyographic activity from the muscles used to execute left- and right-hand responses served to define both the latency and accuracy of the overt response.) On some trials, their overt responses were very fast, and the accuracy of these fast responses was no greater than chance. To determine whether these fast guesses were associated with advanced preparation during the foreperiod, we identified these fast response trials and sorted them into two categories—those for which the subject happened to guess the correct response and those when an incorrect response was made. Then, we derived measures of the lateralized readiness potential for these trials.

The data are shown in the upper panel of Figure 7. For these fast guess trials, average reaction time was about 175 ms and the accuracy of these trials was only 55%. These trials were associated with considerable lateralization in the foreperiod. Furthermore, when the subject happened to guess correctly in response to the imperative stimulus, the lateralization observed during the foreperiod was in the direction of the correct response—when the subject guessed incorrectly, the lateralization was in the direction of the incorrect response. As the lower panel shows, no development of the lateralized readiness potential was evident for slower responses.

These data indicate that, on occasion, subjects may develop biases and prepare a particular response during the foreperiod. The accuracy of these fast guesses depends on whether the subjects happened to have prepared the correct response.

In this example and the Gratton, Bosco, et al. (1989) experiment (see also Gehring et al., 1989), I have considered evidence for the covert presetting mechanisms that operate during the foreperiod. These presetting mechanisms appear to involve response preparation such that under some conditions subjects will select and activate particular responses during the foreperiod. Thus, some of the costs and benefits that occur when subjects guess can be attributed to an early activation of the motor system which takes place during the foreperiod.

More generally, these two experiments indicate that we are able to detect a covert bias to act in a particular way several hundred milliseconds before the action occurs. Moreover, as we shall see in the

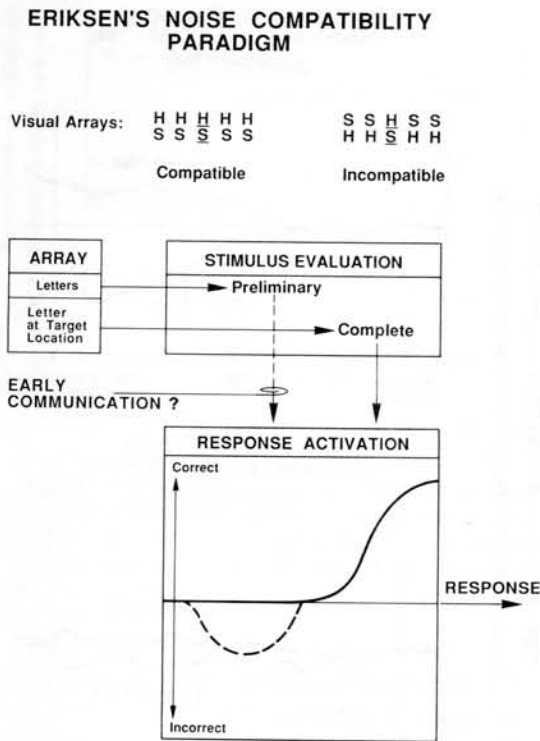


**Figure 7.** Lateralized readiness potential data for fast guess trials in which the subjects happened to guess correctly or incorrectly (upper panel). Data for slower response trials are also shown (lower panel). From Gratton, Coles, Sirevaag, Eriksen, and Donchin (1988). Copyright 1988, American Psychological Association. Reprinted with permission.

next example, we can also monitor action decisions that occur following an imperative stimulus.

*Early Communication.* As with the foreperiod effects reviewed above, our interest here is in monitoring covert processes during a time zone in which there is no overt behavior. However, we now focus on the period following the imperative stimulus and examine the behavior of the lateralized readiness potential as the subject is processing stimulus information.

The issue here concerns the degree to which partial information about a stimulus is used to prime responses before that information is fully processed. For contemporary research on human information processing, this issue falls under the general heading of the question of discrete versus continuous communication (see Eriksen & Schultz, 1979; Meyer et al., 1985; McClelland, 1979; Miller, 1988; Sanders, in press). Does the stimulus evalu-



**Figure 8.** The Eriksen paradigm. Five-letter stimulus arrays can be compatible or incompatible. The arrays can be characterized by two attributes: the identities of the letters in the array, and the identity of the letter at the central target location. If there is early communication between stimulus evaluation and response activation systems, then there should be a dip in the activation function (see lower panel, dashed line) on incompatible trials.

ation system communicate with the response system before it has finished its processing? In other words, is there early communication between the systems?

In this research, we have used the noise compatibility paradigm (see Figure 8) first employed by the Eriksens in their studies of response competition (Eriksen & Eriksen, 1974). In the Eriksens' noise compatibility paradigm, the subject is required to respond to the central target letter in a five-letter visual array. This is the letter that is underlined in the four arrays shown in the figure. In our case, subjects must respond with one hand if the central letter is an *S* and with the other if it is an *H*. On compatible noise trials, the target letter is flanked by replications of the same letter. On incompatible noise trials, the target letter is surrounded by letters calling for the other response.

On the basis of previous research, we have reason to believe that subjects can identify the letters in the array before they know about the relative location of the letters (see, for example, Treisman & Gelade, 1980). Thus, they know what the letters

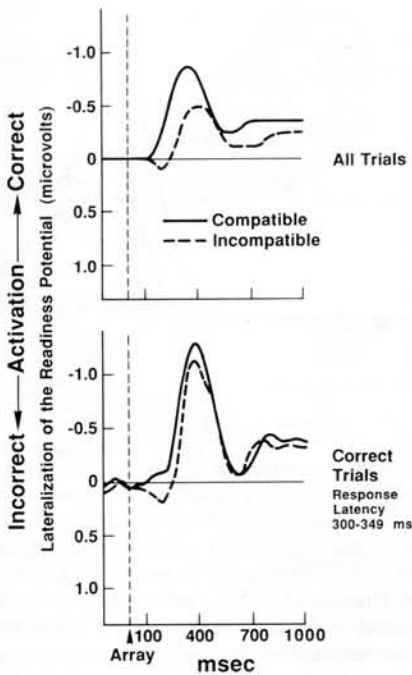
are before they know where they are. We can therefore consider that the visual arrays contain two attributes: first, the identities of the letters, and second, the identity of the letter in the central location (see Figure 8). Thus, for incompatible arrays, the results of early or preliminary evaluation would suggest that the dominant letter in the array is the letter associated with the incorrect response. For example, when the target letter *H* is surrounded by *S*s, the first impression is of the letter *S*. Complete evaluation of incompatible arrays would lead to the correct identification of the letter *H* as the central target letter. This letter is, of course, the letter associated with the correct response. For compatible arrays, information from both preliminary and complete evaluation should converge in leading to the activation of the correct response.

Now we want to know when the information about the stimulus is passed on to the response system. Crucial data are provided by the incompatible trials. If early communication occurs on these trials, and the results of preliminary stimulus evaluation are passed to the response system, then we should see a tendency for initial activation of the incorrect response on incompatible trials. This tendency may be overridden later by the results of complete evaluation which should lead to the activation and subsequent execution of the correct response. These ideas are illustrated in the lower panel of Figure 8.

Given the relationship between the lateralized readiness potential and response activation, our measure should help illuminate this question. If early communication occurs, and there is an early tendency for incorrect response activation, we should see a dip (positive shift) in the lateralized readiness potential on incompatible trials. If there is no early communication, then only the correct response should be activated.

The upper panel in Figure 9 shows the lateralized readiness potential data for compatible and incompatible trials. All trials were included in these averages regardless of the speed or accuracy of the overt response. Note that there is, indeed, a dip in the lateralization function on incompatible trials. No dip is evident for compatible trials.

Although suggestive, these data do not necessarily support the idea of early communication. The waveforms are based on average data and they may not present an accurate picture of what actually happens on individual trials. Indeed, the logic underlying the derivation of the lateralized readiness potential requires that the waveforms be averaged across left- and right-hand responses. To try to address this problem, we selected a subset of trials that were clearly not fast guess trials (because of their relatively long response latency), for which the



**Figure 9.** Lateralized readiness potential data for compatible and incompatible trials. For the data shown in the upper panel, all trials regardless of response accuracy or latency were included in the averages. Data shown in the lower panel are based on correct responses with a latency of 300–349 ms. For correct responses, either there was no EMG activity from muscles associated with the incorrect response or EMG activity associated with the correct response occurred first. Data from Gratton, Coles, Sirevaag, Eriksen, and Donchin (1988). Copyright 1988, American Psychological Association. Reprinted with permission.

overt reaction time was relatively constant, and for which the correct overt response was evident first. Thus, any dip in the lateralized potential for these trials cannot be attributed to the inclusion of trials on which the incorrect overt response occurred. The lower panel of Figure 9 shows the data for this subset of trials. Note that the dip is clearly evident on incompatible trials.

On the basis of this and other evidence (Coles, Gratton, & Donchin, 1988; Smid, Mulder, & Mulder, in press), it seems that some form of early communication does indeed occur. As stimulus evaluation progresses, the results of the process are communicated to the response system. Because we must average our waveforms to extract the lateralized readiness potential, the smooth waveforms we obtain do not prove that communication is continuous. However, our data do indicate that communication takes place in at least two phases and not in an all-or-none fashion. Furthermore, the data challenge the simple notion, prevalent in traditional mental chronometry, that only one response is ac-

tivated on any particular trial. As we have shown elsewhere (Coles, Gratton, Bashore, Eriksen, & Donchin, 1985; Eriksen, Coles, Morris, & O'Hara, 1985), two responses can not only be simultaneously activated, they can also compete with each other.

The study I have described in this part of the paper indicates that responses can be activated on the basis of a preliminary analysis of the stimulus. In this sense, our data inform the question of the nature of communication in the information processing system. We have also seen that tendencies to respond incorrectly on the basis of preliminary stimulus evaluation can be overridden by later tendencies to respond correctly (lower panel of Figure 9). This suggests that at least partial development of the lateralized readiness potential does not constitute a point of no return. The next experiment evaluates this issue more thoroughly.

*Response Inhibition and the Point of No Return.* The point of no return has been the subject of considerable recent interest in the chronometric literature. Among the proponents of this concept are Osman and his colleagues (Osman, Kornblum, & Meyer, 1986, in press; see also Logan & Cowan, 1984), who argue that there may be a time in the course of information processing after which processing cannot be interrupted and the complete overt response becomes inevitable. We have recently used both psychophysiological measures and the traditional measures of mental chronometry to analyze the process by which responses are inhibited and to locate the point of no return (De Jong, Coles, Logan, & Gratton, in press).

In this research, the subject was required to perform a choice reaction time task with a neutral warning cue. The imperative stimulus indicated whether a left- or a right-hand squeeze of a dynamometer was required. To register a response, subjects had to squeeze at a certain force level. On some trials, a stop-signal was presented after the imperative stimulus. The subject was told to try to inhibit the overt response on these stop-signal trials. This paradigm yielded four different kinds of trials. There were normal trials on which no stop-signal occurred, and the subject proceeded to respond to the imperative stimulus in the usual way. Then, there were three kinds of trials on which the stop-signal occurred: (a) uninhibited trials on which the subject could not stop; (b) partially inhibited trials when the subject started to respond but did not squeeze the dynamometer to the criterion level of force; we were able to detect these trials by recording electromyographic activity from the muscles associated with the two responses and by examining the force output of the dynamometers; and finally, (c) inhibited trials on which the subject successfully stopped;

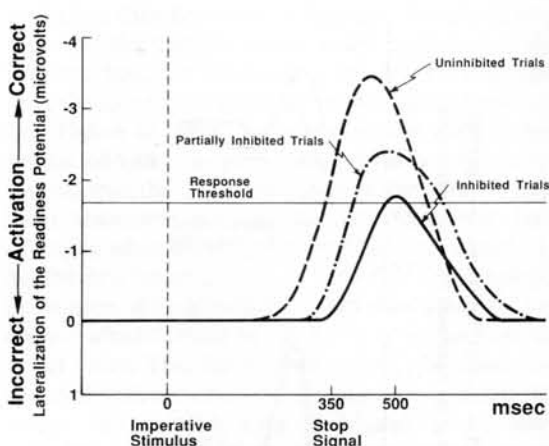
on these trials, there was no evidence of any overt behavioral response or any muscle activity.

Figure 10 shows lateralized readiness potential data for the three kinds of trials on which the stop signal was presented. First, it should be noted that the very existence of partially inhibited trials (on which a below-criterion squeeze response occurred) suggests that the point of no return must be located subsequent to response initiation. Second, we looked at normal trials on which no stop signal was presented and the subject proceeded to make an overt response in the usual way. From these trials, it was possible to determine the average threshold level of the lateralized readiness potential at which overt responses are normally released. This response threshold level is represented in the figure by the horizontal line. Surprisingly, the lateralized potential crossed this average threshold value or, at least, was not significantly below this level, when the response was successfully inhibited. That is, on some trials when the overt response was completely inhibited, the lateralized readiness potential exceeded the level normally associated with the release of the overt response.

These data suggest then that at least some successfully interrupted responses were inhibited by a mechanism that operates at a peripheral level in the system.<sup>4</sup> This peripheral level must be located more downstream in the system than the level at which the lateralized readiness potential is generated. Because, as we shall see, the lateralized readiness potential appears to reflect the activity of motor cortex, this inhibitory mechanism is likely to operate peripherally somewhere subsequent to the central motor command.

This experiment illustrates very clearly the power of the psychophysiological approach. When subjects successfully inhibit their responses, there is, by definition, no overt response for the chronometrician to measure. The measure of the lateralized readiness potential, on the other hand, can provide insights into the covert processes that occur on these successfully inhibited trials. Furthermore, the existence of partially inhibited trials suggests that the point of no return must be located after response initiation.

<sup>4</sup>It appears that this peripheral inhibitory mechanism, operating perhaps at the level of the brainstem, is relatively nonspecific, resulting in the inhibition of a wide range of responses. Thus, it would be unsuitable in situations in which one response has to be inhibited, but an alternative response has to be made. In this case, a more specific, central inhibitory mechanism would be used. See De Jong, Coles, Logan, and Gratton (in press) for a discussion of these issues.



**Figure 10.** Lateralized readiness potential data from the stop-signal paradigm. Averages are shown separately for inhibited trials, partially inhibited trials (on which sub-threshold squeeze and EMG activity occurred), and uninhibited trials. The response threshold, indicated by the horizontal line at  $-1.7 \mu\text{V}$ , was derived by computing the average level of the lateralized readiness potential at the time of the response on "normal" trials on which no stop-signal occurred. The waveforms for these no-signal trials were identical to those for the uninhibited trials. See text for further details. Data from De Jong, Coles, Logan, and Gratton (in press).

### Psychophysiology and Physiological Processes

In the three examples described above, I emphasized how measures of the event-related brain potential can be used to understand human cognitive function. In some sense, we have indeed been able to read our subjects' minds. The lateralized readiness potential has provided important information about fast guesses, about early communication, and about response inhibition. In these experiments, we have treated the measure as a marker for psychological processes (like covert response preparation). Because the measures are clearly manifestations of the electrical activity of the brain, they can also be thought of as signs of physiological processes. The critical questions are, of course, which physiological systems are engaged when we observe a lateralized readiness potential and what are the processes that occur in these systems?

### Physiological Significance

*Topographic Distribution.* Clues to physiological significance can be derived by looking at the topographic distribution of the potentials across the scalp. Figure 11 shows data from the fast guess experiment described above (Gratton et al., 1988). It represents the transformed voltage distribution of the scalp-recorded potential at the moment of the imperative stimulus. The subject is about to make



**Figure 11.** Topographic scalp distribution of the event-related brain potential at the onset of the imperative stimulus when the subject is about to make a fast guess with his right hand. Input values for this map were obtained by applying the Vector filter procedure (see Gratton, Coles, & Donchin, 1989) to data from five scalp electrodes. The filter removes the influence of non-lateralized components. Data from Gratton, Coles, Sirevaag, Eriksen, and Donchin (1988).

a fast guess with his right hand. The figure indicates that there is considerable negativity over left central areas of the scalp. Given that the motor system is organized contralaterally in motor cortex, these data suggest that, perhaps, the potentials recorded on the scalp are indeed coming from the motor cortex.

Similar findings have been reported by many other investigators. In addition, Vaughan and his colleagues (e.g. Vaughan et al., 1968) found that the locus of maximum amplitude varied along the lateral plane as a function of the type of movement. This movement-dependent distribution corresponded very closely to the known somatotopic distribution of the areas of motor cortex responsible for control of different types of movement.

These kinds of distributional data provide clues to the source of the lateralized readiness potential. However, it is important to remember that they are only clues. This is because the spatial distribution of potentials on the scalp does not necessarily reflect the spatial distribution of the underlying source. The brain and scalp act as a volume conductor, and this means that the source of an ERP component may be quite distant from the point of maximal activity on the scalp.

A striking example of what one might call the *topographic fallacy* is given by the case of foot-

movements. Brunia (1980) has shown that such movements are preceded by ipsilaterally maximum potentials. How can this be—when we know that the motor system is arranged contralaterally? As Brunia points out (see also Boschert & Deecke, 1986), this anomalous result can be explained on the basis of what we already know about brain structures associated with foot movements. In particular, the equivalent dipole associated with these movements, although located contralaterally, is oriented in such a way as to produce ipsilaterally maximum scalp potentials. Note that in this case we can understand the scalp distribution because we know the location of the underlying source. When we know nothing about the underlying source, it cannot be inferred solely on the basis of scalp distribution.<sup>5</sup>

Thus, in spite of the obvious aesthetic appeal of these topographic maps, they cannot be used to locate the sources of electrical brain potentials. We need additional information. In the case of movement-related potentials, it turns out that there is a considerable literature that converges in implicating precentral motor cortex as the structure that is active when we observe the lateralized readiness potential on the scalp.

*Intracranial Recording.* One source of information comes from intracranial recording in animals. Thus, Arezzo and Vaughan (1975) recorded from transcortical electrodes in the motor cortex of monkeys, while the monkeys prepared to execute hand movements. Arezzo and Vaughan divide the movement-preceding activity into three components, N1, P1 (which is observed only occasionally), and N2 (or N2a—see Arezzo & Vaughan, 1980). The N1 component appears to correspond to the lateralized readiness potential we observe during the foreperiods of warned reaction time tasks (see Figure 5), whereas the N2 component corresponds to the increase in negativity immediately preceding

<sup>5</sup>It is important to distinguish between the use of distributional information to infer the source of a component of the event-related brain potential and using the same information as a defining characteristic of a particular component. For many researchers in this area, components are judged to be different if they arise from different sources (see Gratton, Coles, & Donchin, 1989). Since activity in different brain regions is likely to give rise to different scalp distributions, the appearance of distinguishable scalp distributions suggests the presence of different sources and, therefore, different components. In addition, as several investigators have argued (Vaughan, 1974), distributional information can be used to distinguish among various putative sources. The comments here are therefore relevant only to those cases in which distributional information is the sole basis for inferring sources.

the movement (see Figure 6). Arezzo and Vaughan found that the distribution of the N2 component was quite localized with its maximum in the hand area of precentral motor cortex (for hand movements). Furthermore, although they did not map the N1 component in detail, Arezzo and Vaughan (1975) state that its distribution was "roughly comparable to that of the N2." In addition, there was a polarity inversion in the antecedent motor potential (presumably including both N1 and N2) across layers 4 and 5—implicating this area as the source of the potential (see Wood & Allison, 1981).

There is a marked correspondence between unit activity in precentral motor cortex and the macropotential data recorded at the scalp or intracortically. Thus, Schmidt, Jost, and Davis (1974) found that, as the N1 develops, there is an increase in the activity of some of the same neurons that fire when the movement actually occurs. Furthermore, Arezzo and Vaughan (1980) found a correspondence between increases in multiple unit activity in deep cortical layers (4 and 5) and the movement-preceding macropotentials.

Converging data have been obtained by Requin and his colleagues (e.g. Requin, 1985; Requin, Lecas, & Bonnet, 1984; Requin, Riehle, & Seal, 1988). They have recorded single unit activity in layers 4 and 5 of motor cortex while monkeys performed a variety of complex motor tasks. These layers are rich in pyramidal neurons. On the border between Areas 4 and 6, there is a type of neuron that appears to have a role in both presetting and executive motor processes. It fired both in the foreperiod and after the imperative stimulus when the motor response was being executed.

The upper panel in Figure 12 shows the relationship between the firing patterns of these neurons and reaction time. The neurons fired more during the foreperiod when a fast response was made than prior to slow responses. In the lower part of the slide, we see comparable data obtained in our lab for scalp-recorded macropotentials in human subjects. Although these kinds of correlated observations do not prove a causal relationship between neuronal and scalp-recorded activity, they are suggestive. There is a remarkable convergence between the single unit activity described by Requin (1985) and the surface recorded macropotentials we have observed.

*Synthesis.* Taken together, these data implicate precentral motor cortex (Area 4) and perhaps premotor cortex (Area 6) as the source of the lateralized readiness potential (see also Brunia, 1988). Furthermore, it appears likely that it is specifically the activity of pyramidal neurons in layers 4 and 5 (see also Arezzo & Vaughan, 1980). Pyramidal neurons

are generally oriented such that activity in their apical dendrites forms an open field recordable at the scalp (see Allison, Wood, & McCarthy, 1986).

### Implications

What are the implications of knowing the source of the lateralized readiness potential? First, we know that the motor cortex is involved in the preparation and execution of movement, so we can use this information to strengthen our claim that the lateralized readiness potential is involved with these same processes. Second, observations of the lateralized readiness potential can be used to infer the behavior of these neurons in particular cortical areas. In this sense, the psychophysiological measure provides a window on the brain, and we can use this and other measures to begin to realize the goals of cognitive neuroscience and understand how the human cognitive system is implemented by activity in different brain structures and the interconnections among these structures.

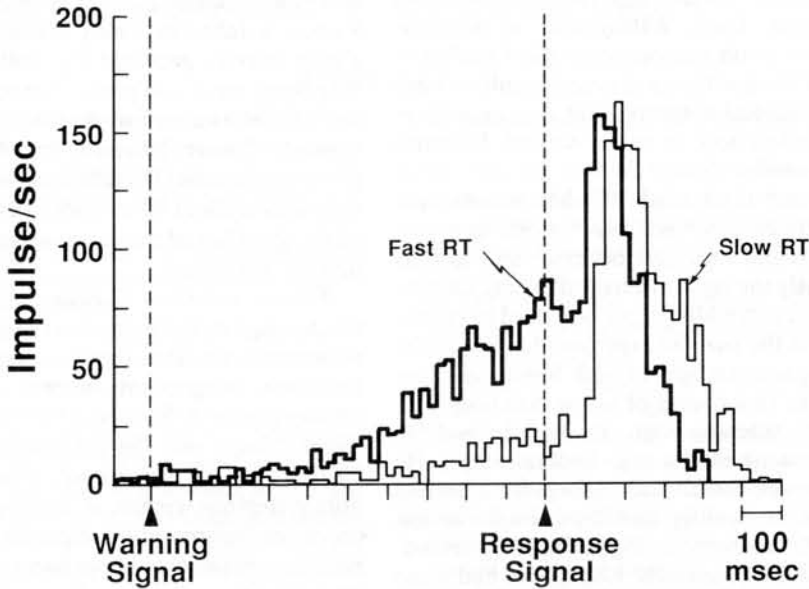
Models of this kind have already been proposed by both Requin and Brunia. The Requin model (Requin et al., 1984, pp. 261 & 279) specifies the neural structures involved in preparatory processes. Direct links between structure and function are proposed that suggest where preparation may be implemented in the brain. The Brunia model (Brunia, Haagh, & Scheirs, 1985, p. 71) identifies the sensory and motor structures and the connecting pathways involved in the performance of a warned reaction time task.

These kinds of neurophysiological models provide us with the link between cognitive processes, such as preparation, and the underlying neural systems in which such processes may be implemented. However, the models are but a first step toward a complete understanding of the method of implementation of cognitive processes in the nervous system. Several developments must occur before we have the kind of theory to which cognitive neuroscience aspires. We need to develop a comprehensive framework that will accommodate all relevant elements (see Posner, Pea, & Volpe, 1982, for a discussion of these issues). These elements include the neuron, aggregates of neurons that form neural structures, the interconnections among these structures, and, of course, the emergent properties of the system that should correspond in some fashion to those cognitive structures and processes proposed by the cognitive scientist.

What might be the form of such a framework? The past few years have seen the rapid development of connectionist models. These models are based on elementary units whose properties are similar to neurons. Furthermore, the models have emergent properties that can accommodate some of the rich-

Firing rate of single unit in monkey motor cortex

(From Requin, 1985)



Lateralized readiness potentials from scalp electrodes located over human motor cortex

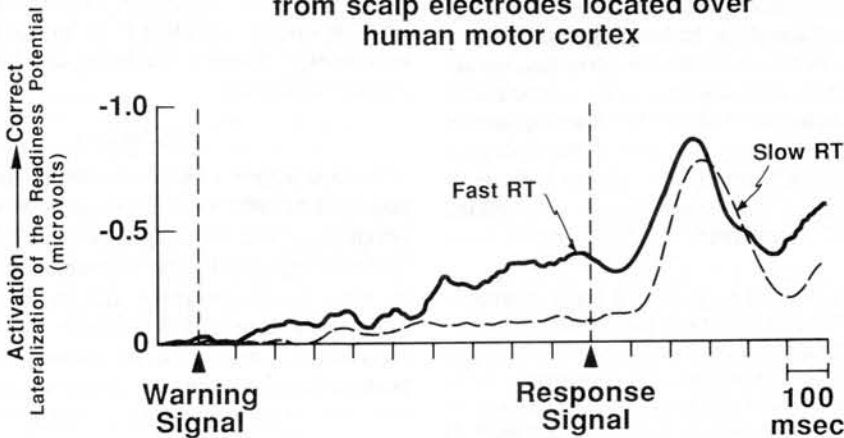


Figure 12. Upper panel: firing rate of cell in monkey motor cortex on trials with fast and slow reaction times. Data from Requin (1985). Copyright 1985, The Stichting International Association for the Study of Attention and Performance. Reprinted with permission of the author and publisher. Lower panel: lateralized readiness potential data from scalp electrodes located above motor cortex. Data from Gratton, Coles, Sirevaag, Eriksen, and Donchin (1988); see also Coles and Gratton (1986). Copyright 1986, Martinus Nijhof Publishers. Reprinted with permission of the publisher.

ness of cognitive phenomena (see, for example, McClelland & Rumelhart, 1986; Rumelhart & McClelland, 1986). As these models take more account of the knowledge-base of neuroscience, they will provide a more satisfactory account of the mind-

brain relationship. Related models, such as those of Grossberg and his colleagues (Grossberg, 1982), are also viable candidates.

In parallel with the development of a conceptual framework, we will need more data to constrain and

inform our models. Such data will come from several sources.

Insofar as it is available, we will rely on invasive research on human subjects (e.g. Halgren et al., 1980; Wood, Allison, Goff, Williamson, & Spencer, 1980)—as well as on neuropsychological studies of the effects of various forms of neural insult on both psychophysiological measures and cognitive function (e.g. see Johnson, in press; Knight, Hillyard, Woods, & Neville, 1980).

We will also need more of what Mountcastle (1976) has called *combined experiments* in which "one controls and measures behavior and records simultaneously the signs of cerebral events thought relevant" (p. 1). In addition, we will need to pursue the strategy of the *parallel experiment* in which the same paradigm is applied to both human and animal subjects. This course of action has been pursued with considerable vigor by Requin and his colleagues, among others (e.g. Requin, 1985). He has relied on well-established findings from human experimental psychology and then sought to understand their neurophysiological basis by recording brain activity in animals. Requin has had some stunning successes in elucidating the neurophysiological mechanisms that underlie preparatory processes and this approach should continue to yield important data.

The psychophysiological research strategy will also provide critical data. In keeping with Mountcastle's notion of the combined experiment, we are able to gain information about neural processes from human subjects as they behave. In choosing appropriate measures, it is critical that the physiological basis of the measure be understood, as is increasingly the case for at least some of the event-related brain potential measures.<sup>6</sup> However, other mea-

asures can undoubtedly yield important data. As developments in superconductivity proceed, measures of magnetic brain activity will become more and more tractable (see, for example, Beatty, Barth, Richer, & Johnson, 1986). Measures of brain metabolic activity provided by positron-emission tomography must also play a role because of the precise spatial localization that they provide (see, for example, Posner, Petersen, Fox, & Raichle, 1988). However, because the temporal resolution of these measures is about 40 seconds, they may not be suited for the study of the processes involved in chronometric paradigms.

Finally, measures of autonomic activity should not be neglected. In previous research, I was able to demonstrate that these measures also provide important insights into human information processing (Coles & Strayer, 1985; see also Jennings, 1986a, 1986b, and van der Molen, Somsen, & Orlebeke, 1985). Furthermore, insofar as the autonomic nervous system is involved in energetical processes, incorporation of information about autonomic processes should put some of the "heat" back into cognition that was lost with the demise of arousal theory (Hockey, Coles, & Gaillard, 1986; Hockey, Gaillard, & Coles, 1986). This course of action may require elaboration of the conceptual framework that I alluded to earlier. However, such an elaboration is critical if we are to build a rapprochement between the brain and body facets of psychophysiology.

### Conclusions

In this paper, I have considered the actual and potential benefits of a marriage between cognitive psychology and psychophysiology. I have argued that psychophysiological measures can be used both as windows on the mind and as windows on the brain. I have provided evidence that the psychophysiological approach has already provided important insights into the nature of cognitive processes—that is, we have been able to read our subjects' minds using measures of the event-related brain potential. We have not, of course, used the measures to read the contents of the mind. Rather, the measures have enabled us to draw conclusions about how the mind works. Although the examples I have used are drawn from research in our laboratory, examples are evident in the research of many other investigators (e.g. Hillyard & Hansen, 1986; Kutas & Van Petten, 1988; Näätänen, 1982; Ritter, Vaughan, & Simson, 1983).

Several techniques are available for exploring the relationship between brain potential measures and brain function. As this relationship becomes clear-

<sup>6</sup>In her discussion of event-related brain potentials, Churchland (1986) identifies three problems with the use of measures of these potentials in understanding the mind-brain. These are individuation of a component in the waveform, individuation of a component in terms of its electrogenesis, and individuation of the component in terms of the higher-level functional process it is presumed to manifest. On the basis of evidence presented in this paper, the lateralized readiness potential can be individuated at all three levels: at the waveform level, in terms of its distribution and sensitivity to the side of the body to be moved; at the source level, in terms of activity in precentral cortex; and at the functional level, in terms of response preparation. In addition, it should be noted that the requirement for individuation at the level of electrogenesis is necessary only if one is concerned with making physiological inferences on the basis of measures of the event-related potential. As was argued in the first part of this paper, use of these measures to make psychological inferences does not require knowledge of their sources.



er, the inferences we can draw concerning those brain processes engaged in cognitive tasks will become more precise. In turn, this will enable us, as psychophysiologicalists, to be a major contributor to

cognitive neuroscience. Because of its place between psychology and physiology, psychophysiology will have a critical role to play in the development of this discipline.

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