

For Distinguished Early Career Contribution to Psychophysiology: Award Address, 1985

A Triarchic Model of P300 Amplitude

RAY JOHNSON, JR.

National Institutes of Health, National Institute of Neurological and Communicative Disorders and Stroke, Medical Neurology Branch, Bethesda, Maryland

ABSTRACT

A model of P300 amplitude is proposed that reduces the many hypothetical constructs invoked to explain variations in P300 amplitude to three dimensions: 1) Subjective Probability, 2) Stimulus Meaning, and 3) Information Transmission. Evidence is presented to support the assertion that variables on the subjective probability and stimulus meaning dimensions have independent and additive contributions to overall P300 amplitude. The amplitude contributions of both of these dimensions, however, are modulated by a multiplicative relation with the proportion of transmitted stimulus information. Within each dimension, the fundamental experimental variables and their interrelations are specified. An example is presented to show how, by using an additive factors method, the respective amplitude effects of the probability and stimulus meaning dimensions can be separated. Supporting data are presented to show that the proposed model provides a reasonable and testable framework in which to conceptualize P300 results.

DESCRIPTORS: Event-related potentials, P300.

The prospect of having an electrophysiological index of cognitive operations has led many researchers to explore the nature of the P300 component of the event-related brain potential (ERP). Since its discovery by Sutton and his colleagues (Sutton, Braren, Zubin, & John, 1965; Sutton, Tueting, Zubin, & John, 1967), studies have demonstrated that P300 amplitude and latency can be used as indices of the nature and timing of a subject's cognitive response to a stimulus.¹ As a result of

studying the P300 in a wide variety of behavioral paradigms, a large number of hypothetical constructs have been suggested to account for the observed variations in P300 amplitude (e.g., attentiveness, orienting, decision making, uncertainty reduction, intentional engagement, processing demand, salience, task relevance, equivocation, and value). Although there are many similarities among the proposed constructs, little effort has been made to sort out the nature and interactions of the basic factors that are reflected in P300 amplitude. The desirability of developing such a taxonomy is threefold: First, a viable schema would be heuristically useful and provide conceptual guidance for making accurate a priori predictions about the results of proposed experiments; second, it would systematize the existing data base and thereby aid the development of theories about the functional significance of P300; and third, it would provide a theoretical framework for interpreting amplitude variations such as those in P300 studies of patient groups.

Any theoretical account must begin with the recognition that many of the constructs used to explain P300 amplitude are related to the delivery and subsequent processing of relevant information. For ex-

¹Although there now appears to be a variety of late positive waves that are elicited under different circumstances, the model proposed here applies only to the best understood of these positivities, the P300 or P3b.

This paper is based on an address given upon receipt of the Early Career Contribution Award, Society for Psychophysiological Research, Houston, Texas, October, 1985, and represents an elaboration of ideas first presented as part of a doctoral dissertation in 1979. I am grateful for the numerous helpful comments given by John Rohrbaugh, Connie Duncan, Dan Ruchkin, Sam Sutton, Walter Ritter, and Dave Friedman.

Address requests for reprints to: Ray Johnson, Jr., National Institutes of Health, NINCDS, MNB, Building 10, Room 4N246, Bethesda, Maryland 20892.

ample, the subjective probability construct refers to the well-documented inverse relation between P300 amplitude and the probability of an event's occurrence. Nevertheless, a major problem has been how to account for the observation that P300 amplitude varies as a function of the subject's task even when event probability is held constant.

To address this problem, two general accounts of the factors that modulate P300 amplitude have been advanced. In one, Donchin (1979) proposed that P300 amplitude is a function of both the observer's subjective probability for the occurrence of an event and its relevance to the assigned task. In this context, the term "task relevance" has been used to explain all changes in P300 amplitude that cannot be attributed directly to variables affecting subjective probability. Other investigators have suggested that, in addition to these two factors, P300 amplitude also appears to depend on the specific nature of the subject's task (Courchesne, 1978; Picton, Campbell, Baribeau-Braun, & Proulx, 1978; Tueting & Sutton, 1976). Even among these researchers, however, there is no consensus on the nature of this third factor.

In this paper, I will propose a testable model that reduces the many variables known to affect the amplitude of P300 to three categories or dimensions. I will begin with an overview of the model and then describe the rationale for this classification scheme by reviewing the data from key studies that reveal the nature and interactions of these three dimensions.²

A MODEL OF P300 AMPLITUDE

The nature of the cognitive processes underlying P300 amplitude can be clarified by considering the different kinds of information conveyed by any discrete event of the type that elicits a P300. It is reasonable to propose that every event that influences P300 triggers processing of two independent aspects of an event: 1) its probability, and 2) its meaning. Consider first the probabilistic aspect of information. Probability information cannot be conveyed by an isolated stimulus; the relative frequency of a stimulus can be determined only in relation to the stimuli that preceded it. In addition, the sequential structure of the stimulus series serves to confirm or disconfirm trial-to-trial expectancies. Together, relative frequency and sequential structure provide the basis for formulating subjective probabilities. Consider next the aspects of information related to the significance or meaning of an event that must be taken into account whenever a stimulus is associ-

ated with a task. Information about meaning is contained within a stimulus although the specifics of its meaning depend on the nature of the situation or task. Thus, the meaning conveyed by a particular stimulus can vary widely across situations even though stimulus probabilities and even the stimulus itself remain constant. This distinction between externally determined information and internally determined information provides the basis for the separation of the subjective probability and stimulus meaning dimensions, respectively.

While P300 amplitude appears to depend on the two general factors of subjective probability and meaning, the extent to which these two factors operate depends entirely on the extent to which the information content of a stimulus is extracted. It is therefore necessary to accommodate a third general factor that describes the effectiveness with which the stimulus information is transmitted to the observer. This factor becomes important when, for example, stimuli are difficult to discriminate and information about their exact identities may not be processed by the observer. Such situations are problematic since the appropriate formulation of subjective probabilities and the complete processing of stimulus meaning depend entirely on the observer's accuracy and certainty in perceiving the event. Hence, any uncertainty about the precise nature of the stimulus must necessarily affect the extraction of both probability information and meaning from the stimulus.

It is the thesis of this paper that all of the experimental variables that influence P300 amplitude can be described by three categories or dimensions: 1) *Subjective Probability*, 2) *Stimulus Meaning*, and 3) *Information Transmission*. The nature of these dimensions has been recognized previously in a general way by others (Courchesne, 1978; Picton et al., 1978; Ruchkin & Sutton, 1978; Tueting & Sutton, 1976). In the present paper, however, I will blend and recast these other formulations in two ways. First, by showing that, through careful definition, the effects of these three dimensions can be quantified more rigorously than has been the case in the past, and second, by showing how the effects of these dimensions interact to determine the overall amplitude of P300. It is my contention that the subjective probability and stimulus meaning dimensions have independent and additive effects on P300 amplitude and that the amplitude contributions of these two dimensions are dependent on the proportion of transmitted stimulus information. The relations between these three dimensions may therefore be denoted as:

$$P300 \text{ Amplitude} = f[T \times (1/P + M)]$$

²For a more thorough review of P300 studies and their relation to the model, see Johnson (in press).

where T represents the proportion of transmitted information, P represents subjective probability, and M represents stimulus meaning. The experimental variables associated with each dimension will be described in detail. In each case, these variables have either been demonstrated, or logically appear, to have effects on P300 amplitude that are independent of those due to other variables on the same dimension. As explained below, the terms in this equation may be expanded to include the variables specified for each dimension (e.g., a modified version of the expectancy model proposed by K. Squires, Wickens, Squires, & Donchin, 1976, may be substituted for the $1/P$ term).

Two of these three terms are quite similar to those in formal information theory (Shannon & Weaver, 1963). Subjective probability, for example, differs from logical probability only in that it takes the element of human judgment into account. Similarly, as used here, the information transmission dimension incorporates all of the tenets of the formal concept of equivocation as well as acknowledging the fact that humans do not attend to all stimuli in their environment (see Sheridan & Ferrell, 1974). The stimulus meaning dimension, in contrast, has no analog in information theory because this theory defines information exclusively in terms of uncertainty reduction. Unlike machines, however, humans extract meaning from events (see Johnston, 1979, for a discussion on this point).

The mathematical expressions used in this formulation require comment. The additive relation between the subjective probability and stimulus meaning dimensions signifies that the effects of these two dimensions are independent of one another: variations due to manipulations of either dimension will not affect the magnitude of the contribution to P300 amplitude made by the other dimension (i.e., in an ANOVA, the main effects of probability and meaning would be significant but their interaction would not be significant). In contrast, the multiplicative relation between information transmission and the other two dimensions indicates that the amplitude contributions made by subjective probability and stimulus meaning variables are *both* simultaneously increased or decreased in equal *proportions* as a direct function of changes in information transmission.

Subjective Probability and P300 Amplitude

Without question, the subjective probability dimension is the best established aspect of the proposed model: P300 amplitude is directly related to the amount of uncertainty reduced by a stimulus. The experimental variables that have been found to influence the magnitude of this dimension's con-

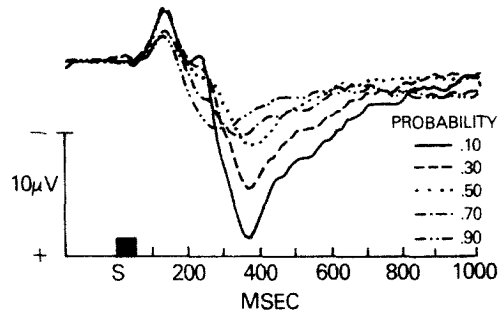


Figure 1. Grand-mean waveforms ($N=7$) from P_z for auditory stimuli in an oddball paradigm under RT instructions at five levels of a priori probability. In this and subsequent figures, negative voltages are plotted as upward deflections. Stimulus presentation is indicated by the filled rectangle on the time scale.

tribution to the overall amplitude of P300 affect either: 1) a priori probability, or 2) sequential expectancies.

P300 Amplitude and A Priori Probability

The data in Figure 1 show the widely reported inverse relation between stimulus probability and P300 amplitude.³ This inverse relation has been observed in every type of task from simple counting (e.g., Duncan-Johnson & Donchin, 1977; Friedman, Simson, Ritter, & Rapin, 1975; Johnson & Donchin, 1980, 1982; Kutas, McCarthy, & Donchin, 1977; Picton & Hillyard, 1974) and reaction time paradigms (Duncan-Johnson & Donchin, 1982; Johnson & Kopell, 1980; Kutas et al., 1977), to prediction (Friedman, Hakerem, Sutton, & Fleiss, 1973; Tueting, Sutton, & Zubin, 1970) and feedback tasks (Campbell, Courchesne, Picton, & K. Squires, 1979). Furthermore, this relation has been found

³All of the data from the oddball task presented in Figures 1, 2, 5, and 9 were collected using the same stimulus conditions and instructions. These data represent grand means from 7 subjects (3 males; average age = 41 yrs). The auditory stimuli were 50dB SL 1000 Hz and 1500 Hz tones presented binaurally through headphones over a background of white noise. The visual stimuli consisted of the letters "X" and "O" presented on a CRT. All stimuli were presented in a Bernoulli series for 50 ms with an interstimulus interval of 1705 ms. The EEG and eye movements (EOG) were sampled every 5 ms for a 1150-ms epoch beginning 150 ms prior to stimulus onset. Trials contaminated by EOG artifacts were excluded from the averages. During the Counting condition, the subjects were told to count the low-pitched tones and the "O"s. During the Reaction Time condition, the subjects were instructed to press a different button for each stimulus as quickly as possible.

for virtually every kind of stimulus, including the omission of an expected stimulus (Ruchkin, Sutton, & Tueting, 1975). Moreover, when large numbers of different stimuli are presented to the subject, P300 amplitude is related to the probability of the stimulus categories rather than to the probabilities of the individual stimuli (Courchesne, Hillyard, & Courchesne, 1977; Johnson & Donchin, 1980; Johnson, Pfefferbaum, & Kopell, 1985; Kutas et al., 1977).

P300 Amplitude and Sequential Expectancies

In addition to assessing relative frequency, humans also develop expectancies based on perceived sequential dependencies among stimuli in a series. Consequently, the identical stimulus at a given level of global probability will elicit P300s of different amplitudes on different occasions depending upon the specific sequence of preceding stimuli. K. Squires et al. (1976) were the first to quantify the association between changes in P300 amplitude and the sequential structure of the series. They showed that repeated stimuli (i.e., AA) elicited smaller P300s than non-repeated stimuli (i.e., BA). Overall, they interpreted these findings as indicating that subjects expect events to repeat and are therefore surprised when their expectations are violated. This sequential expectancy effect has been replicated in virtually every paradigm used to elicit a P300 (Duncan-Johnson & Donchin, 1977; Horst, Johnson, & Donchin, 1980; Johnson, 1984; Johnson & Donchin, 1980, 1982; Johnson & Kopell, 1980; Munson, Ruchkin, Ritter, Sutton, & N. Squires, 1984; K. Squires, Petuchowski, Wickens, & Donchin, 1977; Tueting et al., 1970).

The magnitude of the variations in P300 amplitude due to sequential expectancies is remarkably constant in all of these studies. Thus, when the P300s elicited by the extreme repetition and non-repetition sequences are compared (i.e., AAAAA vs. BBBBA), the amplitude difference between them is consistently found to be between 3 and 5 μ V despite large variations in overall P300 amplitude (i.e., from 1 to 30 μ V) in different paradigms. This consistency strongly suggests that the generation of sequential expectancies is independent of, and additive to, all other variables that determine the amplitude of P300. This observation is hardly surprising since sorting stimuli according to the preceding sequence of events is equivalent to controlling the precise context of the event's occurrence. Since the stimulus sequences are identical in different tasks, these effects on P300 amplitude would be expected to be constant.

Summary of the Subjective Probability Dimension

The subjective probability dimension describes the observation that P300 amplitude is directly related to the unexpectedness of an event. Moreover, the variations in P300 amplitude as a function of the preceding sequence of events attest to the great sensitivity of this measure to even graded changes in expectancies. As demonstrated by K. Squires et al. (1976), the $1/P$ term in the model can be replaced by the independent sums of the following variables: global probability, the preceding sequence of stimuli, an alternation sequence factor, and a factor for the ratio of repetitions to non-repetitions at each level of global probability.

Stimulus Meaning and P300 Amplitude

The second dimension of the proposed model is that of stimulus meaning. Variables on this dimension account for the processing of stimulus information not related to probability. The effects of this dimension have been widely noted within the context of observations that the magnitude of the P300 elicited by a particular stimulus at a given level of probability varies as a function of the subject's task. Since probability is unrelated to the meaning or significance of an event, the variables on this dimension must necessarily be independent of those on the subjective probability dimension. The portion of P300 amplitude sensitive to changes in meaning is a function of three independently manipulable variables: 1) task complexity, 2) stimulus complexity, and 3) stimulus value.

Although the term "stimulus meaning" is a convenient label for the dimension that subsumes these three variables, it is, admittedly, a compromise for want of a better term. The lack of a more suitable term reflects our current lack of knowledge about how subjects react to this aspect of stimuli, and this lack of knowledge affects attempts to quantify precisely the variables on this dimension. Whereas some variables on this dimension, such as stimulus complexity and stimulus value, may be readily quantified, the methods for measuring task complexity are less precise. The three variables on this dimension do appear to be related to the concept of task demand: increased complexity requires more extensive processing of a stimulus in order to extract its full content. This observation seems to be the basis for many of the hypothetical constructs proposed to account for the non-probabilistic changes in P300 amplitude: for example, stimulus meaning (Johnson, 1979; Picton et al., 1978; Sutton & Ruchkin, 1984), task difficulty (Courchesne, 1978), task demand (Rosler, 1983; Tueting & Sut-

ton, 1976), intentional engagement (Campbell et al., 1979), and resource allocation (Kramer, Wickens, & Donchin, 1983) are all related concepts that refer to the fact that stimuli are processed to a greater or lesser extent depending on the complexity of the situation in which they are presented.

At the present time, however, only a limited set of methodologies exists for quantifying the relative information processing demands of different tasks. Other than reaction time techniques, the existing methods, for the most part, establish the processing demands of a particular task by measuring the extent of performance decrements that result when another, primary, task is performed concurrently (cf. Sheridan & Ferrell, 1974). A drawback of this dual-task procedure is its sensitivity to extraneous factors such as changes in the subject's level of arousal or motivation. An alternative approach is to use paradigms borrowed from experimental psychology: there are many such paradigms in which a variety of variables have been studied systematically, thereby providing a framework in which to place individual results.

P300 Amplitude and Task Complexity

A major difficulty in illustrating the relation between P300 amplitude and task complexity is the scarcity of data from experiments in which one group of subjects performed more than one task using the same stimulus conditions. Nevertheless, the results from a large number of different studies generally replicate one another quite well whenever similar paradigms are used. Together, they provide a reasonable data base from which to conclude that P300 amplitude increases directly with the degree of task complexity.

The effect of task complexity on P300 amplitude is shown in Figure 2. These data were collected from the same subjects during the performance of three different tasks using the same stimuli ($p = .50$). The ERPs elicited in an oddball paradigm run under two different task conditions (i.e., Counting and Reaction Time) are superimposed on the ERP from a task in which the same stimuli delivered feedback. These data reveal that P300 amplitude increased from Counting to Reaction Time, with a still larger P300 in the feedback paradigm.⁴ While the relative task demands of these three paradigms have not

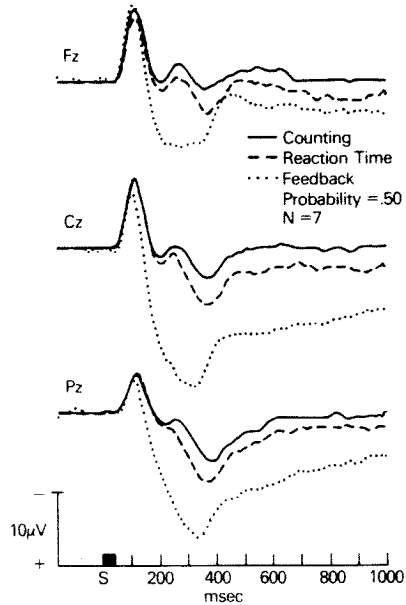


Figure 2. Grand-mean waveforms ($N = 7$) from F_z , C_z , and P_z from three different tasks. The ERPs elicited in an oddball paradigm run under two different task conditions, Counting (solid line) and Reaction Time (dashed line), are superimposed on the ERP elicited when the same stimulus signified correct performance in a feedback paradigm (dotted line). The waveforms were all elicited by a 1000 Hz, 50dB SL tone ($p = .50$).

been assessed, it is plausible to suggest that the processing demands associated with these tasks would follow the same order as shown by P300 amplitude.

Variations in P300 amplitude as a function of the subject's task have been documented extensively. Chesney and Donchin (1979), for example, reported that much larger P300s were elicited when the stimuli in a random series had to be predicted than when the same stimuli were counted. Similarly, stimuli conveying feedback in a time estimation task (Johnson & Donchin, 1978) or a paired-associate learning task (Horst et al., 1980) elicited larger P300s than when the same stimuli were counted. In addition, Donchin, Kubovy, Kutas, Johnson, and Herning (1973) reported that smaller P300s were elicited when subjects had to predict stimulus outcomes than when they made a RT response to the same stimuli. Finally, Eason, Harter, and White (1969) and Wilkinson and Morlock (1967) demonstrated that stimuli in RT tasks elicited larger P300s than stimuli in counting tasks. In combination, these results suggest that a hierarchy of tasks can be created for predicting P300 amplitude: Reaction Time > Prediction > Counting.

Another method for assessing the effects of task complexity on P300 amplitude is to create para-

⁴Another noteworthy result illustrated by this figure is that changes in the subject's task may be accompanied by changes in the scalp distribution of P300. In this case, although P300 amplitude is maximal at P_z in the oddball task, the largest P300s are found at C_z when the same stimuli deliver feedback.

digs in which the processing demands of different events in a series are varied. This was the strategy behind an unpublished experiment of mine in which subjects performed a prediction task. The letters "A" and "B" were presented randomly with equal probabilities and structure was imposed on the series by informing the subject that every third occurrence of the letter "A" (i.e., the "Signal A") would always be followed by an extra "A" (i.e., the "Signalled A"). The subjects were instructed to count both the "A" and the "B" stimuli and to reset their respective counts after the third occurrence of each letter. On each trial, along with their prediction, subjects gave their counts so that their knowledge about their exact position in the series could be verified. The event structure in this task is shown in Figure 3.

The imposition of this structure on the event series permitted experimental control over the effects of task complexity on P300 amplitude. For example, the first and second "A" stimuli and all "B" stimuli delivered feedback concerning the predicted trial outcome and were counted. The Signal stimulus was the most complex because, in addition to providing feedback and being counted, it also

indicated the identity of the following event. The Signalled "A" stimulus, in contrast, was the least complex since it neither delivered feedback nor was counted. It is possible to conceptualize task complexity in this paradigm in terms of the number of "messages" conveyed by each stimulus. It is clear, however, that different amounts of resources would be required to process each of the different "messages" and that a "quantum" theory of messages will have to be developed to determine the elemental size of a "message" unit.

The waveforms for the three kinds of "A" stimuli in this task are displayed in Figure 4. These averages show that the Signal "A" elicited a larger P300 than either the first or the second "A" stimulus which, in turn, elicited a larger P300 than the Signalled "A." As expected, no difference in P300 amplitude was found between any of the "B" stimuli or between the first and second "A"s and "B"s. The results for the counted "A"s and "B"s cannot be explained in terms of probability since each of these events occurred equally often. Probability was a factor for the Signalled "A"; since it had a probability of 1.0, it did not deliver any feedback. These results were therefore consistent with the hypoth-

Task 1: EVERY THIRD "A" SIGNALS ANOTHER "A"

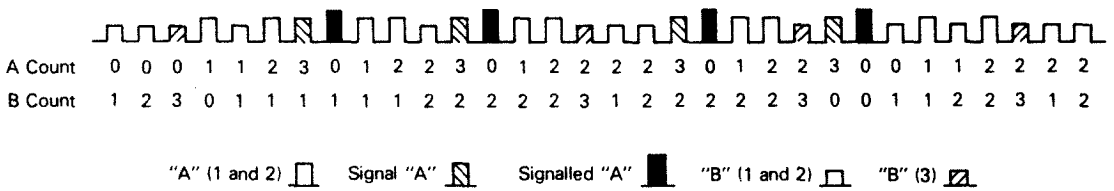


Figure 3. Diagram of a task in which structure was imposed on the events in a random series. The five different types of stimuli are indicated along with the subject's counts for the different categories of events.

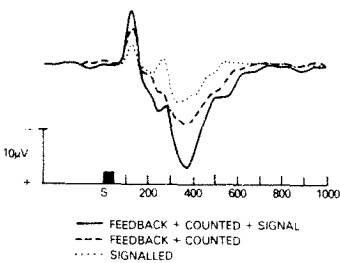


Figure 4. Averages from a subject showing the P300s elicited at Cz by the three different types of "A" stimuli. The waveforms elicited by the Signal stimulus (solid line), the first and second "A" (dashed line), and Signalled stimulus (dotted line) are superimposed to show the relation between task complexity and P300 amplitude.

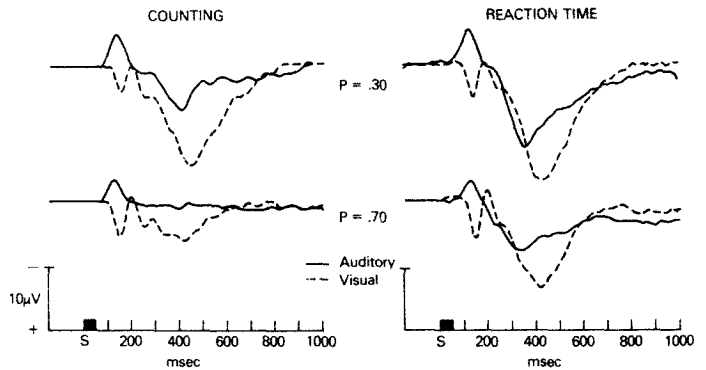


Figure 5. Grand-mean waveforms (N=7) from Pz elicited in an oddball paradigm under Counting and Reaction Time conditions at two levels of a priori probability and two sensory modalities. The averages for the auditory stimuli (solid line) are superimposed on those for the visual stimuli (dashed line).

esis that the P300 amplitude is a monotonically increasing function of task complexity. Similar results have been reported in other experiments in which task complexity was varied on a trial-to-trial basis (e.g., Johnson & Donchin, 1982; Rosler, 1983; Stuss & Picton, 1978; Stuss, Toga, Hutchison, & Picton, 1980).

In summary, the data from experiments that have systematically manipulated the degree of task complexity either within or across tasks provide convincing evidence that P300 amplitude is directly related to the extent to which a stimulus must be processed. Moreover, the results show that P300 amplitude is quite sensitive to even temporary fluctuations in task complexity.

P300 Amplitude and Stimulus Complexity

Stimulus complexity, or perceptual demand, is the second variable on the stimulus meaning dimension. It is obvious that some stimuli have more relevant features than others and thus require more processing for identification and categorization. These differences may be quantified by using information theory or traditional measures of difficulty such as RT.

Figure 5 presents ERP waveforms that were elicited by auditory and visual stimuli in an oddball paradigm under two different task conditions. At both probability levels, the patterned visual stimuli (i.e., "X"s and "O"s) elicited larger P300s than auditory stimuli (i.e., 1000 Hz and 1500 Hz tones). Moreover, in both modalities, larger P300s were elicited during the RT condition than during the Counting condition. Since the visual stimuli were associated with later P300 latencies and longer RTs (RTs were 438 ms and 366 ms for the visual and auditory stimuli, respectively), it is reasonable to expect that P300s of equal amplitude would have been elicited had the stimuli from both modalities been equated for difficulty (e.g., by using simpler stimuli such as blank flashes). The data addressing this point are, however, mixed with one study supporting this position (N. Squires, Donchin, Squires, & Grossberg, 1977) and one contradicting it (Synder, Hillyard, & Galambos, 1980).

Data from experiments in which perceptual difficulty is varied within a single modality are easier to obtain. Verbaten (1983) used patterned visual stimuli at two levels of complexity and found that larger P300s were elicited by the stimulus with the more intricate pattern. In contrast, there is only indirect evidence that linguistic stimuli elicit larger P300s than blank flashes because the data were not collected in the same subjects. For example, Kutas et al. (1977) had subjects count the occurrences of male names in a set of stimuli containing a mixture

of 20 different male and female names. These, and other experimenters (e.g., Johnson & Kopell, 1980; Johnson et al., 1985), have found that word stimuli elicit substantially larger P300s with longer RTs than those reported previously for more simple visual stimuli (e.g., N. Squires et al., 1977). This amplitude increase may be interpreted as reflecting the increased processing that must be performed before linguistic stimuli can be properly categorized. Kutas et al. (1977) also demonstrated that the effects of stimulus complexity add to the effects of task complexity since they found that P300 amplitude was at least 25% greater when a speedy response was required compared to when the same stimuli were counted.

In summary, although the data are not extensive, they are consistent with the interpretation that P300 amplitude is directly related to stimulus complexity, independent of the level of task complexity.

P300 Amplitude and Stimulus Value

The third category of variables on the stimulus meaning dimension is stimulus value or significance. Since the significance (e.g., monetary rewards) of events can be varied in all task and stimulus situations, it seems clear that these variables are independent of either task complexity or stimulus complexity. When monetary payoffs have been manipulated, larger P300s were elicited by high-value stimuli than by low-value stimuli (Begleiter, Porjesz, Chou, & Aunon, 1983; Johnston, 1979; Steinhauer, 1981; Tueting & Sutton, 1976; Wilkinson & Morlock, 1967). Moreover, Steinhauer (1981) reported a high positive correlation between the amount of money associated with a particular stimulus outcome and P300 amplitude.

Presumably there are many instances in which the significance of events is determined by experience. Thus we have all learned that some sounds, such as a car horn, are high-value stimuli. Similar examples exist for the other sensory modalities (e.g., flashing lights, intense heat, noxious smells). Since intensity is a stimulus attribute that is frequently used to gain attention, this association may explain why P300 amplitude has been observed to increase as a direct function of loudness (Johnson & Donchin, 1978). This relation was confirmed by Roth, Blowers, Doyle, and Kopell (1982) who showed that very loud (115dB) stimuli elicited large P300s even when subjects were instructed to ignore the stimuli.

Summary of the Stimulus Meaning Dimension

This dimension of the model describes the findings that P300 amplitude is sensitive to experimental variables that are independent of those affecting the formulation of subjective probability.

Although sometimes difficult to quantify precisely, the stimulus meaning dimension is comprised of three variables: task complexity, stimulus complexity, and stimulus value. While there are few data to confirm the nature of the interrelations among these variables, they do not appear, at least on logical grounds, to overlap, and thus each appears to have an independent and additive contribution to P300 amplitude. Moreover, P300 amplitude has been demonstrated to be sensitive enough to index trial-to-trial graded changes in variables on this dimension. Finally, since peak amplitude is inversely related to the amount of latency variability, increases in task complexity and stimulus complexity could lead to the mistaken conclusion that P300 amplitude decreases in these situations. Therefore, great care must be taken in determining both the amplitude and latency of the P300 in any experiment in which a large amount of latency variability is expected, or when mean RT exceeds 500 ms.

Information Transmission and P300 Amplitude

The third dimension of the proposed model is that of information transmission. The term information transmission, as used here, is defined as the *proportion* (i.e., it will have a value between 0 and 1) of stimulus information received by a person relative to the total amount of information originally contained in the stimulus. Because the loss of stimulus information can affect every paradigm used to elicit a P300, variables on this dimension are especially significant since they modulate the amplitude contributions of the other two dimensions. The two categories of experimental variables on this dimension are: 1) those creating equivocation, and 2) those affecting the allocation of attention.

Because this dimension covers situations in which information is lost, an important consequence of manipulating these variables is that the subject's level of task performance must be altered measurably. Thus, changes in P300 amplitude that are accompanied by changes in the subject's level of performance are, by definition, due to changes in the amount of transmitted information. This relation provides the basis for quantifying the effects of variables on this dimension.

P300 Amplitude and Equivocation

Ruchkin and Sutton (1978) originally proposed that P300 amplitude is modulated by the subject's degree of equivocation. Equivocation, a term from classical information theory (Shannon & Weaver, 1963), describes the amount of information loss that occurs during the presentation of a stimulus as a result of the subject's a posteriori uncertainty about

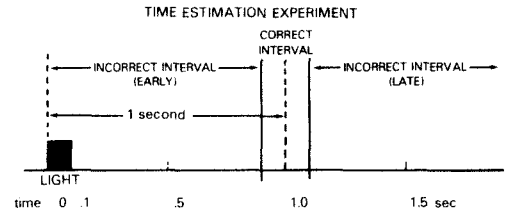


Figure 6. Diagrammatic representation of the events in the Time Estimation paradigm used by Johnson and Donchin (1978).

having correctly perceived an event. The complement of equivocation is, of course, the proportion of transmitted information.

The seed for this model came from a study on the effects of stimulus discriminability on P300 (Johnson & Donchin, 1978). Our finding that P300 amplitude and task performance were inextricably linked to stimulus discriminability revealed the nature and overriding importance of the information transmission dimension. In this experiment, subjects estimated the passage of one second while two equally probable tones provided feedback about whether the estimate was "correct" or "incorrect" (see Figure 6). Stimulus discriminability was manipulated by varying the intensity difference between the two feedback tones in different series. The data revealed that both P300 amplitude and task performance were positively correlated with discriminability (Figure 7A and B). In a second experiment, the same stimuli were presented in an identical manner except that the subjects were instructed to count one of the tones. In contrast to the results of Experiment 1, P300 amplitude and counting accuracy were constant across all levels of discriminability as evident in panels C and D of Figure 7.

The only difference between these two experiments was that the subjects had an alternative source of information in the time estimation task. That is, as their uncertainty increased about which stimulus was presented, the subjects could supplement the external feedback provided by the tones with internal feedback from having practiced the task. This interpretation was supported by the data from the series in which both feedback tones were of equal intensity when, despite a reduction in accuracy, subjects continued to make estimates. The subjects could not, however, correctly count the stimuli without completely processing the tones. Although the stimuli in both experiments were meant to convey equivalent amounts of information, this did not obtain. Rather, it appeared that the subjects, at their option (cf. Sutton, 1969), determined the extent to which they used the information contained in the feedback stimuli according to the difficulty of the

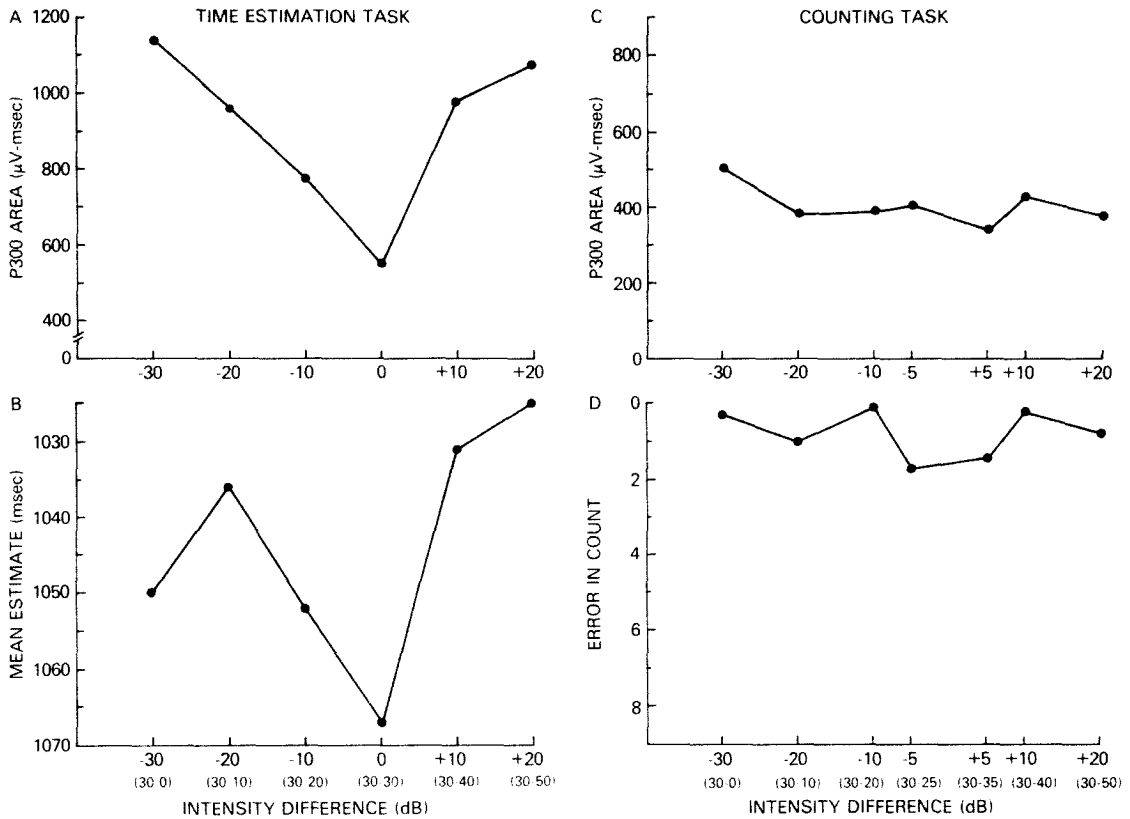


Figure 7. **A**) Grand-mean (over 14 subjects and two types of feedback) P300 areas at six levels of stimulus discriminability. **B**) Performance data, in terms of the mean time estimate, accompanying the P300 data in A. **C**) Grand-mean (over 10 subjects) P300 areas for the counted stimulus at seven levels of stimulus discriminability. **D**) Counting performance for the data in C. P300 areas were measured at the electrode where amplitude was maximal: C_z for the Time Estimation task and P_z for the Counting task. The areas were obtained by integrating the activity in the interval between 280 and 360 ms poststimulus after subtracting the mean activity in the 280-ms baseline (see Johnson & Donchin, 1978, for further details). Note that the scales on the ordinate in B and D are inverted and that lower values are indicative of better performance.

discrimination. As shown in Figure 7, these strategy differences were accompanied by concomitant changes in both P300 amplitude and task performance.

It could be argued that the amplitude changes in this experiment have little or nothing to do with variations in the proportion of transmitted information. In fact, Rosler (1980) suggested that subjects process only those stimuli of whose category they are certain. If Rosler were correct, the proportion of trials with a P300 response would vary directly with discriminability. This fact, coupled with the nature of the averaging process, would produce P300 amplitude results identical to those reported by Johnson and Donchin (1978). This all-or-none hypothesis was tested recently by analyzing the P300 activity in the single trials. This analysis revealed that P300s were elicited on a *constant* percentage of trials at all levels of stimulus discrimin-

ability in the time estimation experiment (Johnson & Donchin, 1985). These results therefore confirm that subjects did indeed process each stimulus and that the effects of information transmission operated on the ERP responses to individual events by modulating their amplitudes. Other experimental manipulations that affect equivocation are signal detection paradigms and memory paradigms.

P300 Amplitude and Attention

The preceding definition of equivocation does not cover instances in which stimulus information is lost due to inattention and thus these cases form the second category of variables on this dimension.

In general, "task relevance" is the term most frequently used to explain the results of experiments using "attend" vs. "ignore" instructions. By instructing the subject about which stimuli are relevant and which are irrelevant, the experimenter

directs the subject's attention and thereby defines which stimuli do and do not transmit information. A testament to the arbitrary nature of such instructions, at least as far as the subject is concerned, is the observation that P300s can be elicited by "irrelevant" (i.e., unattended) stimuli (e.g., Roth, Ford, Lewis, & Kopell, 1976; Vaughan, & Ritter, 1970). In such studies, however, P300s were present when the subjects had no other task to perform. The data from these "passive-ignore" conditions conflict with those showing an absence of P300 activity when subjects are forced to ignore stimuli (i.e., "active-ignore" conditions) by requiring them to perform another task (e.g., Duncan-Johnson & Donchin, 1977).

Given the relation between information transmission and task performance, the model would predict that performance in passive- and active-ignore conditions would be quite different. For example, had the subjects been debriefed, it is likely that more accurate estimates of the event probabilities would have been obtained following a passive-ignore series than following an active-ignore series. Moreover, it is reasonable to expect that P300 amplitude would have been modulated by the preceding sequence of stimuli during passive-ignore conditions but not in active-ignore conditions. While neither of these hypotheses has been evaluated experimentally, positive results would support the assertion that information is indeed being transmitted and processed during passive-ignore series. The direct relation between attention and P300 amplitude and task performance is also evident in the data from studies using signal detection and dual-task paradigms.

Summary of the Information Transmission Dimension

The information transmission dimension describes the effects on P300 amplitude when subjects do not receive all of the information contained in a stimulus. Because information is lost, the amplitude contributions of the subjective probability and stimulus meaning dimensions are modulated by variables on the information transmission dimension. Moreover, since task performance is linked directly to the proportion of transmitted stimulus information, changes in P300 amplitude associated with this dimension will be accompanied by changes in task performance.

The two variables on this dimension, equivocation and attention, each affect the perception of the stimulus. To date, only the multiplicative relation between equivocation and the variables on the other two dimensions has been confirmed (Johnson, 1984). However, it seems reasonable to

assume that attentional variables will operate on P300 amplitude in the same fashion as those that affect equivocation. Similarly, equivocation and attentional variables appear to be independent of one another since, whereas equivocation is determined by external conditions, attention is determined by internal conditions. Given this independence, it follows that these two categories of variables will have multiplicative effects on one another. Finally, as with the other two dimensions, equivocation has been demonstrated to affect the P300s elicited by individual stimuli.

APPLYING THE MODEL

Having presented the basic tenets of the model, the question of how the respective amplitude effects of the three dimensions can be separated needs to be addressed. The data suggest that this problem can be solved with an additive factors approach. For example, the P300s elicited by the uncounted stimuli in an oddball task appear to provide the clearest approximation of the effects of global probability on P300 amplitude since there is no task attached to these events (i.e., they are not counted).⁵ Moreover, for uncounted stimuli with probabilities greater than or equal to .50, the data reviewed above reveal that the effect of global probability is so minimal that it can be ignored (Duncan-Johnson & Donchin, 1977; K. Squires et al., 1977). Even at these probabilities, however, sequential expectancies still influence P300 amplitude. Thus, when stimuli are *equally probable* and there is no information loss (i.e., no performance decrement), the respective effects of the stimulus meaning and subjective probability dimensions can be determined simply by performing a sequential analysis on the data. This analysis accomplishes two things. First, the amplitude *difference* between the repetition (i.e., AA, AAA, etc.) and non-repetition (i.e., BA, BBA, etc.) stimulus sequences represents the amount of P300 activity due to subjective probability. Second, because the effects of subjective probability are effectively eliminated in the averages of stimulus repetitions, the amplitude remaining in the repetition averages represents the contribution made by variables on the stimulus meaning dimension. Since probability is a factor at values less than .50, the effect of stimulus meaning variables is defined as

⁵The subject must, of course, attend to and identify both stimuli. However, once the decision is made to count or not to count, processing of the uncounted stimulus ceases. In contrast, processing of the target stimulus continues until the subject's count has been incremented. This continued processing is presumably responsible for the "target effect": the observation that counted stimuli always elicit larger P300s than uncounted stimuli.

the amplitude difference between the P300s elicited in two different tasks at the same level of probability. When information transmission is varied, the amplitude contributions of both the subjective probability and stimulus meaning dimensions are altered by the proportion of information that is lost.

In the next two sections, evidence supporting the additive and multiplicative relations in the model is presented. One difficulty in demonstrating the accuracy of the proposed relations is that the amplitude measurements necessary to separate the respective contributions of the subjective probability and stimulus meaning dimensions are rarely made. Rather, P300 amplitude has been treated as a simple entity for which an overall measure of amplitude (or area) is sufficient. Thus, while there have been studies in which the same subjects have performed in different tasks, the statistics necessary to demonstrate additivity have not been reported. That is, to show that the amplitude contributions of these two dimensions are independent and additive requires an ANOVA with significant main effects of subjective probability and task along with a non-significant interaction between the two. Since non-significant effects are rarely, if ever, noted, such a combination of results has not, to the best of my knowledge, been reported.

The Evidence for Additivity in P300 Amplitude

Despite the lack of statistical evidence, observations on the data from a variety of studies support the assertion that variables on the subjective probability and stimulus meaning dimensions make independent and additive contributions to overall P300 amplitude. The data from paradigms in which task complexity was varied within a series were discussed above. Further examples can be found in experiments in which conditional probability was varied and those in which the same subjects performed different tasks over a range of event probabilities.

Manipulations of conditional probability serve to change the randomness of events by altering the subject's uncertainty about the identity of the following event. Experiments have demonstrated that sequential expectancies are developed only when events occur randomly: when an explicit source of information about the events in a series is available, it will be used as the principal datum for generating expectancies (Kornblum, 1973). Therefore, P300 amplitude should decrease as the amount of available sequential information increases. The data in Figure 8 reveal that P300 amplitude indeed varies inversely as a function of conditional probability in a prediction task (Tueting et al., 1970). In this experiment, P300 amplitude decreased as condi-

tional probability increased whether the subjects knew (Certain condition) or did not know (Uncertain condition) the identity of the next event. A sequential analysis on these data revealed that P300 amplitude decreased for non-repetitions in both conditions as conditional probability increased, although there was no clear relation for stimulus repetitions. The small P300s elicited in the Certain condition at low conditional probabilities were approximately equal in magnitude (i.e., 3–5 μ V) to those observed to be due to the processing of sequential expectancies. Thus, although the stimuli in the Certain condition conveyed no feedback, the fact that sequence effects were present at all levels of conditional probability confirms that the subjects continued to process the probability content of these events. These data demonstrate that experimental manipulations known to reduce the magnitude of stimulus sequence effects (see Kornblum, 1973) also result in reductions in P300, thereby demonstrating the additivity of subjective probability effects on P300 amplitude.

A second point illustrated by the Tueting et al. data is that the effects of conditional probability operate equally on the P300s elicited in both conditions. The constant amplitude difference between the Certain and Uncertain conditions presumably reflects the increased task complexity when the stimuli delivered feedback. Although not reported, it would be surprising, given the nature of these data, if the interaction of conditional probability with task were significant. Another example of the additive effect of task complexity variables is shown in Figure 9. These amplitude data are from an odd-ball paradigm in which subjects either counted the number of low-pitched tones or made a choice RT response to both stimuli (see Figure 1 for the ERP waveforms from this condition). The usual inverse relation between P300 amplitude and event probability is clearly evident in both cases although the curve for the RT task is displaced upwards from that for the Counting task. An ANOVA revealed significant main effects of both Task ($F(1/6)=9.3$, $p<.05$) and Probability ($F(4/24)=63.5$, $p<.001$) with a non-significant interaction of Task \times Probability ($F(4/24)=1.3$, $p=.30$). Similar results were reported by Duncan-Johnson and Donchin (1977) in comparisons of the P300s elicited by counted and uncounted stimuli at probabilities from .10 to .90. They found significant main effects for both Task (counted vs. uncounted) and Probability, although the Task \times Probability interaction was not significant (Connie C. Duncan, personal communication, August, 1985).

In summary, the data from these studies support the hypothesis that it is possible to vary either the

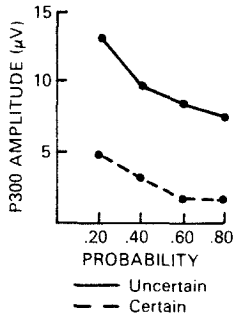


Figure 8. Data from Tueting et al. (1970) showing P300 amplitude as a function of conditional probability in a prediction task in which subjects ($N=4$) were either Uncertain (solid line) or Certain (dashed line) of the identity of the stimulus they were predicting. Data used with permission.

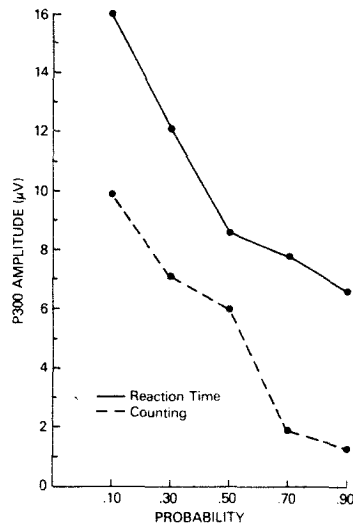


Figure 9. Grand-mean ($N=7$) base-to-peak P300 amplitude data for an odd-ball paradigm under Reaction Time (solid line) and Counting (dashed line) instructions as a function of a priori probability.

subjective probability or stimulus meaning portions of P300 amplitude independently of one another. Moreover, such manipulations can result in either a loss of P300 amplitude, as in the case of conditional probability manipulations, or in a gain of P300 amplitude, as with the manipulation of task complexity. Such results strongly support the assertion that these two dimensions have additive effects on overall P300 amplitude.

The Evidence for a Multiplicative Relation

While the subjective probability and stimulus meaning dimensions have independent and additive effects, the amplitude contributions of *both* these dimensions depend on the proportion of transmitted information. This is a logical consequence of the fact that lost information about the identity of an event must affect any processing that is dependent on the accuracy of stimulus identification, such as the evaluation of expectancies and meaning. Consequently, changes in the proportion of transmitted information must result in *proportional* (i.e., multiplicative) changes in the amplitude contributions of the other two dimensions.

Evidence for the multiplicative relation can be found in the data from the experiment mentioned earlier in which P300 amplitude was directly related

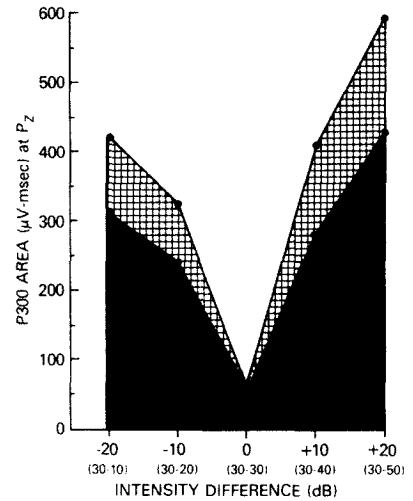


Figure 10. Grand-mean (over 10 subjects and two types of feedback) values of P300 area at P_z for the repetition (lower curve) and non-repetition (upper curve) stimulus sequences as a function of stimulus discriminability. The amplitude contributions for the subjective probability and stimulus meaning dimensions are represented by the cross-hatched and filled areas, respectively. Data from Johnson (1984).

to the discriminability of the feedback tones (Johnson & Donchin, 1978). The results of the sequential analysis performed on these data (Johnson, 1984) are shown in Figure 10 where the amplitudes (measured here in terms of area) of the P300s elicited by stimulus repetitions (lower curve) and non-repetitions (upper curve) are graphed. Since these stimuli were equally probable, the cross-hatched area between the two curves represents the contribution of subjective probability to P300 amplitude while the filled area under the repetition curve represents the portion of the P300 associated with stimulus meaning variables.

The multiplicative effect of information transmission can be seen in the *relative* amplitude changes for the two dimensions as stimulus discriminability was varied. It is clear that, whereas the amplitude contributions of both dimensions varied directly with discriminability, the portion of P300 amplitude attributed to stimulus meaning is much greater than that due to subjective probability in every series. Since the magnitude of the subjective probability portion of P300 is rather small, changes on this dimension accounted for only a small part of the overall changes in P300 area at each level of discriminability. In contrast, changes in the portion of P300 area due to stimulus meaning are much

larger from one level of discriminability to the next except when both tones were of equal intensity. The apparent disparity between the changes in P300 area for these two dimensions is eliminated when these amplitude changes are expressed in terms of proportions. For example, between the -20dB and -10dB levels of discriminability, the changes in P300 area for the subjective probability and stimulus meaning dimensions are 18% and 24%, respectively. Thus, the amplitude decrements for both dimensions were consistent with their relative contributions to overall amplitude. As discussed earlier (see Figure 7), these changes in P300 amplitude were paralleled by changes in the subjects' task performance. The nature of the multiplicative relation between subjective probability and equivocation has been replicated recently by Ruchkin, Sutton, and Mahaffey (1986). In summary, these data demonstrate that manipulations of information transmission do indeed cause proportional changes in the amount of information processing activity on the subjective probability and stimulus meaning dimensions.

ADDITIONAL CONSIDERATIONS

P300 Latency and the Proposed Model

Since the initial report by Ritter, Simson, and Vaughan (1972), much evidence has accumulated to show that P300 latency provides an accurate index of the time required to evaluate and categorize an event (e.g., Donchin, 1979; Duncan-Johnson, 1981; Ford, Roth, Mohs, Hopkins, & Kopell, 1979; Johnson et al., 1985; Kutas et al., 1977). Since experiments on P300 latency also frequently reveal amplitude variations, the relation between these two measures merits a brief discussion. On the subjective probability dimension, any experimental manipulation that increases the likelihood of a particular event also appears to result in a decrease in P300 latency (cf. Figure 1). In contrast, manipulations that decrease the proportion of transmitted information always seem to be accompanied by increases in P300 latency (e.g., Johnson & Donchin, 1985). Similarly, on the stimulus meaning dimension, increases in stimulus complexity result in latency increases (e.g., McCarthy & Donchin, 1981; Ritter, Simson, & Vaughan, 1983). In fact, the only variables that change P300 amplitude but do not appear to consistently affect latency are those that increase task complexity (cf. Figure 4) and stimulus value. This seemingly paradoxical situation suggests that these variables are fundamentally different from all others that influence P300 amplitude. Although the nature of this difference remains to

be determined, it is notable that these two variables are the only ones in the model that cannot be linked to information theory.

Automatic vs. Controlled Processing

In recent years, much emphasis has been placed on determining which cognitive operations are performed automatically and which require effortful activity. The distinction between automatic and controlled processing was proposed by Shiffrin and Schneider (1977; Schneider & Shiffrin, 1977). They defined these two qualitatively different kinds of cognitive processes as follows: 1) Automatic processes are those that function continuously and at optimal levels independently of intention, and 2) Controlled processes, which depend on the subject's intent, are easily monitored by introspection and, since they can vary in the amount of capacity they require, they interfere with other simultaneous controlled processing. Some investigators, however, have argued that even automatic processes require that the subject attend to the stimulus (e.g., Hasher & Zacks, 1984).

Rosler (1980, 1983) argued that the P300 is elicited only when subjects must perform "controlled" processing and that P300 amplitude therefore indexes the amount of controlled processing performed by the subject. Contrary to this position, the definitions of automatic and controlled processing appear intuitively to fit the subjective probability and stimulus meaning dimensions, respectively. In fact, there is ample evidence to support this assertion. Hasher and Zacks (1984) presented a wealth of data showing that frequency of occurrence is encoded automatically for virtually every type of experimental and naturally occurring event. Similarly, the substantial body of findings demonstrating a relation between P300 amplitude and subjective probability is consistent with all five of Hasher and Zacks' criteria for automatic encoding.

It seems equally clear that the variables on the stimulus meaning dimension belong to the category of controlled processing. The fact that P300 amplitude varies directly with variables on the stimulus meaning dimension fits well with the definition of controlled processing. Thus, it appears reasonable to suggest that the probability and stimulus meaning dimensions, respectively, provide functional indices of the amounts of automatic and controlled processing that subjects perform in response to a stimulus.

Potential Problems

There are a few experimental manipulations that have yielded results that are not readily explained

by the proposed model. In each case, these manipulations could be considered to be at the limits of a particular variable. For example, Roth et al. (1982) reported that very loud, 115dB stimuli elicit large P300s under any circumstances. Similarly, extremely rare stimuli, such as the novel stimuli used by Courchesne, Hillyard, and Galambos (1975), also elicit larger P300s than would be expected on the basis of the relation between probability and P300 amplitude. In each of these examples, it could be argued that the effect of these particular experimental manipulations is to create a situation in which the stimuli become biologically relevant. This would result in their being endowed with additional value just as when monetary rewards are substantial. This interpretation, if correct, also suggests that, in the case of extremely rare stimuli, the independence of the subjective probability and stimulus meaning dimensions may fail to hold. These problems at extreme values do not, however, detract from the model's ability to account for variations in P300 amplitude under more customary experimental conditions. Moreover, it should be pointed out that, even in extreme cases, the model would provide for instances in which past experience results in value becoming associated with a stimulus. That is, when, as a result of learning, value is attached to a rare event (e.g., a fire alarm), a larger P300 will be elicited than for rare events for which there is no associated value. This principle would apply for a wide variety of stimuli and stimulus attributes (e.g., loudness, directionality).

SUMMARY OF THE PROPOSED MODEL

The data reviewed above are consistent with the idea that P300 reflects endogenous, cognitive processes. This substantial body of research is sufficient to begin to construct models that will both predict and explain the amplitude results of P300 studies. I have proposed a testable model that reduces the large number of variables known to influence P300 to only three dimensions: subjective probability, stimulus meaning, and information transmission. For the subjective probability dimension, the unexpectedness of the stimulus appears to be the primary determinant of P300 amplitude: unexpected events elicit larger P300s than expected events. On the stimulus meaning dimension, P300 amplitude increases directly with stimulus and task complexity and stimulus value. Lastly, P300 amplitude is directly proportional to the extent to which the full amount of stimulus information is transmitted to the subject. Evidence has been presented to support the contention that, whereas the first two dimensions have independent and additive effects on P300

amplitude, their contributions to P300 are modulated by variables on the information transmission dimension. The respective amplitude contributions due to variables on the subjective probability and stimulus meaning dimensions in any given task can be assessed with an additive factors approach. The available data further show that the effects of variables on all three dimensions affect P300 amplitude not only in averages, but also in the responses to individual events. Finally, it follows from the independence of the subjective probability and stimulus meaning dimensions that, in all likelihood, each is the product of an anatomically separate neural generator (see Johnson, in press, for a more thorough discussion on this point). The relations among these three dimensions are summarized in Figure 11.

As asserted above, each dimension of the model consists of a relatively small number of fundamental experimental variables. For the information transmission dimension, there are two categories of experimental variables, equivocation (EQ) and attention (AT), whose effects are linked by a multiplicative relation. Thus:

$$\text{Information Transmission (T)} = f(1 - EQ \times AT) \quad (1)$$

The subjective probability dimension is also comprised of two experimental variables: those that affect global probability (GP) and those that affect sequential expectancies (SE). These variables are linked by an additive relation. Thus:

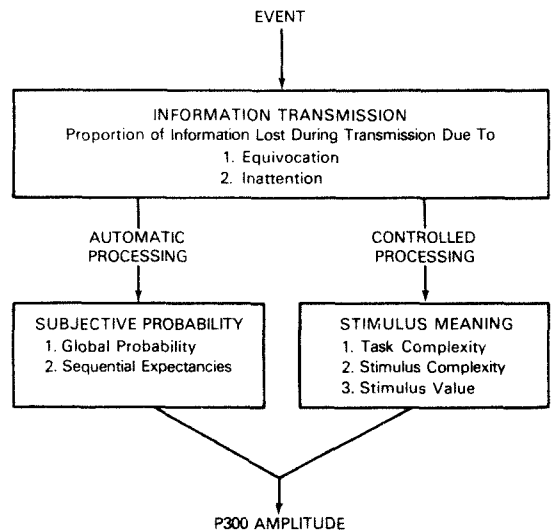


Figure 11. Summary of the three dimensions and their interactions in the proposed model of P300 amplitude.

Subjective Probability (P) = $f(\text{GP} + \text{SE})$ (2)

As described by Squires et al. (1976), sequential expectancies are influenced by three factors: 1) the subject's memory for the preceding sequence of events, 2) an alternation factor for a particular subset of stimulus sequences, and 3) the ratio of stimulus repetitions to non-repetitions at each level of global probability (note: this last factor was not a part of the Squires et al. formulation).

Finally, the stimulus meaning dimension includes three experimental variables, i.e., task complexity (TC), stimulus complexity (SC), and stimulus value (SV), which are linked by additive relations. Thus:

Stimulus Meaning (M) = $f(\text{TC} + \text{SC} + \text{SV})$ (3)

Therefore, when the simplified description of the factors affecting P300 amplitude presented in the beginning of the paper:

P300 Amplitude = $f[\text{T} \times (1/\text{P} + \text{M})]$ (4)

is expanded to include equations (1), (2), and (3), the final result is:

P300 Amplitude = $f((1 - \text{EQ} \times \text{AT}) \times$
 $[(\text{GP} + \text{SE}) + (\text{TC} + \text{SC} + \text{SV})])$

With this equation, the outcomes of particular experimental manipulations can be more readily predicted in advance.

CONCLUSIONS

In the preceding review, I have endeavored to summarize the current state of our knowledge of the factors that determine the occurrence and magnitude of the P300 component of the ERP. A key attribute of this model is that it provides a basis for understanding the nature of amplitude variations in a wide variety of situations. While no model can account for all of the experimental variance, it is my contention that the proposed formulation will account for a very substantial portion of P300 amplitude results. Nevertheless, a number of aspects of the stimulus meaning and information transmission dimensions still require experimental verification—particularly in regard to methods of quantification and the interactions among variables. As a result, the proposed model is merely descriptive rather than quantitative: except for the probability term, it is still too early to attach weights to any of the other terms. Yet, this model extends previous conceptualizations of the factors affecting P300 amplitude, and the mathematical relations

among the variables on each dimension provide fertile ground for experimentation.

Whether or not the present formulation is correct in whole or in part, increased efforts must be made to understand the factors underlying P300 amplitude. Testing the accuracy of this formulation means that ERP researchers will have to modify their experimental procedures. For example, it is particularly important that P300 amplitude not be viewed as a single entity. This will require that the amplitude contributions of the subjective probability and stimulus meaning dimensions be assessed separately or that the significance level of the interaction of these two factors in an ANOVA be reported. Also, the importance of collecting data from subjects in more than one paradigm cannot be overstated. Such designs provide a much more detailed context in which to place the results of any single paradigm and could, presumably, provide a variety of new and valuable insights into the relation between P300 amplitude and variables on the stimulus meaning dimension.

There is also a pressing need for more parametric studies of P300 amplitude in order to achieve a more thorough understanding of how different variables influence P300 amplitude. Many ERP experiments consist of relatively few manipulations of a single experimental variable. Such studies at best provide a relatively limited picture of the behavior of P300 and, at worst, can mask the true nature of the relation between P300 and the experimental variables. For example, most studies of the oddball paradigm use only two complementary probabilities which masks the differences in processing between the counted and uncounted stimuli. Moreover, such limited experimental manipulations are too restricted to obtain an accurate estimate of their relation to P300 amplitude.

The precise specification of how different variables influence P300 amplitude is becoming increasingly important as this component of the ERP is used as an index of normal and abnormal cognitive processing. The need for an increased understanding of the variations in P300 amplitude is best illustrated by the fact that the vast majority of clinical studies have used the oddball paradigm to elicit a P300. Although there are undoubtedly many instances in which other paradigms might provide more useful information, this task has been used most frequently presumably because the effects of probability on P300 amplitude are by far the most clearly understood. As our knowledge of the effects of the other variables is extended, the diagnostic utility of measures of P300 amplitude should be greatly enhanced. For example, by sorting out the

respective amplitude contributions made by each of the three dimensions, the proposed model should provide additional information on the source of the amplitude reductions frequently observed in studies of patient groups.

In conclusion, the P300 component of the ERP appears to manifest an important cognitive oper-

ation. The data reviewed in this paper attest to the richness of the information that may be gleaned from the measurement of its amplitude. The proposed model provides a reasonable and testable framework in which to conceptualize P300 results and should add to the utility of the P300 as a tool in the study of cognition.

REFERENCES

- Begleiter, H., Porjesz, B., Chou, C.L., & Aunon, J.I. (1983). P3 and stimulus incentive value. *Psychophysiology*, *20*, 95-101.
- Campbell, K.B., Courchesne, E., Picton, T.W., & Squires, K.C. (1979). Evoked potential correlates of human information processing. *Biological Psychology*, *8*, 45-68.
- Chesney, G.L., & Donchin, E. (1979). Predictions, their confirmations, and the P300 component [Abstract]. *Psychophysiology*, *16*, 174.
- Courchesne, E. (1978). Changes in P3 waves with event repetition: Long-term effects on scalp distribution and amplitude. *Electroencephalography & Clinical Neurophysiology*, *45*, 754-766.
- Courchesne, E., Hillyard, S.A., & Courchesne, R.Y. (1977). P3 waves to the discrimination of targets in homogeneous and heterogeneous stimulus sequences. *Psychophysiology*, *14*, 590-597.
- Courchesne, E., Hillyard, S.A., & Galambos, R. (1975). Stimulus novelty, task relevance and the visual evoked potential in man. *Electroencephalography & Clinical Neurophysiology*, *39*, 131-143.
- Donchin, E. (1979). Event-related brain potentials: A tool in the study of human information processing. In H. Begleiter (Ed.), *Evoked potentials and behavior* (pp. 13-88). New York: Plenum Press.
- Donchin, E., Kubovy, M., Kutas, M., Johnson, R., Jr., & Herning, R.I. (1973). Graded changes in evoked response (P300) amplitude as a function of cognitive activity. *Perception & Psychophysics*, *14*, 319-324.
- Duncan-Johnson, C.C. (1981). P300 latency: A new metric of information processing. *Psychophysiology*, *18*, 207-215.
- Duncan-Johnson, C.C., & Donchin, E. (1977). On quantifying surprise: The variation in event-related potentials with subjective probability. *Psychophysiology*, *14*, 456-467.
- Duncan-Johnson, C.C., & Donchin, E. (1982). The P300 component of the event-related brain potential as an index of information processing. *Biological Psychology*, *14*, 1-52.
- Eason, R.G., Harter, M.R., & White, C.T. (1969). Effects of attention and arousal on visual cortical evoked potentials and reaction time in man. *Physiology & Behavior*, *4*, 283-289.
- Ford, J.M., Roth, W.T., Mohs, R.C., Hopkins, W.F., & Kopell, B.S. (1979). Event-related potentials recorded from young and old adults during a memory retrieval task. *Electroencephalography & Clinical Neurophysiology*, *47*, 450-459.
- Friedman, D., Hakerem, G., Sutton, S., & Fleiss, J.L. (1973). Effect of stimulus uncertainty on the pupillary dilation response and the vertex evoked potential. *Electroencephalography & Clinical Neurophysiology*, *34*, 475-484.
- Friedman, D., Simson, R., Ritter, W., & Rapin, I. (1975). The late positive component (P300) and information processing in sentences. *Electroencephalography & Clinical Neurophysiology*, *38*, 255-262.
- Hasher, L., & Zacks, R.T. (1984). Automatic processing of fundamental information: The case of frequency of occurrence. *American Psychologist*, *39*, 1372-1388.
- Horst, R.L., Johnson, R., Jr., & Donchin, E. (1980). Event-related brain potentials and subjective probability in a learning task. *Memory & Cognition*, *8*, 476-488.
- Johnson, R., Jr. (1979). Electrophysiological manifestations of decision making in a changing environment (Doctoral dissertation, University of Illinois, 1979). University Microfilms No. 79-15372. *Dissertation Abstracts International*, *40*, 485B.
- Johnson, R., Jr. (1984). P300: A model of the variables controlling its amplitude. In R. Karrer, J. Cohen, & P. Tueting (Eds.), *Brain and information: Event-related potentials*. *Annals of the New York Academy of Sciences*, *425*, 223-229.
- Johnson, R., Jr. (in press). The amplitude of the P300 component of the event-related potential: Review and synthesis. In P.K. Ackles, J.H. Jennings, & M.G.H. Coles (Eds.), *Advances in psychophysiology* (Vol. III, in press). Greenwich, CT: JAI Press.
- Johnson, R., Jr., & Donchin, E. (1978). On how P300 amplitude varies with the utility of the eliciting stimuli. *Electroencephalography & Clinical Neurophysiology*, *44*, 424-437.
- Johnson, R., Jr., & Donchin, E. (1980). P300 and stimulus categorization: Two plus one is not so different from one plus one. *Psychophysiology*, *17*, 167-178.
- Johnson, R., Jr., & Donchin, E. (1982). Sequential expectancies and decision making in a changing environment: An electrophysiological approach. *Psychophysiology*, *19*, 183-200.
- Johnson, R., Jr., & Donchin, E. (1985). Second thoughts: Multiple P300s elicited by a single stimulus. *Psychophysiology*, *22*, 182-194.
- Johnson, R., Jr., & Kopell, B.S. (1980). P300 and expectancies for linguistic stimuli. *Psychophysiology*, *17*, 309.
- Johnson, R., Jr., Pfefferbaum, A., & Kopell, B.S. (1985). P300 and long-term memory: Latency predicts recognition time. *Psychophysiology*, *22*, 498-507.

- Johnston, V.S. (1979). Stimuli with biological significance. In H. Begleiter (Ed.), *Evoked brain potentials and behavior* (pp. 1-12). New York: Plenum Press.
- Kornblum, S. (1973). Sequential effects in choice reaction time: A tutorial review. In S. Kornblum (Ed.), *Attention and performance IV* (pp. 509-546). New York: Academic Press.
- Kramer, A.F., Wickens, C.D., & Donchin, E. (1983). An analysis of the processing requirements of a complex perceptual-motor task. *Human Factors*, 25, 597-622.
- Kutas, M., McCarthy, G., & Donchin, E. (1977). Augmenting mental chronometry: The P300 as a measure of stimulus evaluation time. *Science*, 197, 792-795.
- McCarthy, G., & Donchin, E. (1981). A metric for thought: A comparison of P300 latency and reaction time. *Science*, 211, 77-79.
- Munson, R., Ruchkin, D.S., Ritter, W., Sutton, S., & Squires, N.K. (1984). The relation of P3b to prior events and future behavior. *Biological Psychology*, 19, 1-29.
- Picton, T.W., Campbell, K.B., Baribeau-Braun, J., & Proulx, G.B. (1978). The neurophysiology of human attention: A tutorial review. In J. Requin (Ed.), *Attention and performance VII* (pp. 429-468). Hillsdale, NJ: Erlbaum.
- Picton, T.W., & Hillyard, S.A. (1974). Human auditory evoked potentials. II. Effects of attention. *Electroencephalography & Clinical Neurophysiology*, 36, 191-200.
- Ritter, W., Simson, R., & Vaughan, H.G., Jr. (1972). Association cortex potentials and reaction time in auditory discrimination. *EEG Journal*, 33, 547-555.
- Ritter, W., Simson, R., & Vaughan, H.G., Jr. (1983). Event-related potential correlates of two stages of information processing in physical and semantic discrimination tasks. *Psychophysiology*, 20, 168-179.
- Rosler, F. (1980). Event-related positivity and cognitive processes. In M. Koukkou, D. Lehmann, & J. Angst (Eds.), *Functional states of the brain: Their determinants* (pp. 203-222). Amsterdam: Elsevier.
- Rosler, F. (1983). Endogenous ERPs and cognition: Probes, prospects, and pitfalls in matching pieces of the mind-body problem. In A.W.K. Gaillard & W. Ritter (Eds.), *Tutorials in ERP research: Endogenous components* (pp. 9-35). Amsterdam: Elsevier.
- Roth, W.T., Blowers, G.H., Doyle, C.M., & Kopell, B.S. (1982). Auditory stimulus intensity effects on components of the late positive complex. *Electroencephalography & Clinical Neurophysiology*, 54, 132-146.
- Roth, W.T., Ford, J.M., Lewis, S.J., & Kopell, B.S. (1976). Effects of stimulus probability and task-relevance on event-related potentials. *Psychophysiology*, 13, 311-317.
- Ruchkin, D.S., & Sutton, S. (1978). Equivocation and P300 amplitude. In D. Otto (Ed.), *Multidisciplinary perspectives in event-related potential research* (pp. 175-177). Washington, DC: U.S. Government Printing Office/EPA.
- Ruchkin, D.S., Sutton, S., & Mahaffey, D. (1986). *Functional differences between members of the P300 complex: P3E and P3b*. Manuscript submitted for publication.
- Ruchkin, D.S., Sutton, S., & Tueting, P. (1975). Emitted and evoked P300 potentials and variation in stimulus probability. *Psychophysiology*, 12, 591-595.
- Schneider, W., & Shiffrin, R.M. (1977). Controlled and automatic human information processing I: Detection, search, and attention. *Psychological Review*, 84, 1-66.
- Shannon, C.E., & Weaver, W. (1963). *The mathematical theory of communication*. Urbana, IL: University of Illinois Press.
- Sheridan, T.B., & Ferrell, W.R. (1974). *Man-machine systems: Information, control, and decision models of human-performance*. Cambridge, MA: Cambridge University Press.
- Shiffrin, R.M., & Schneider, W. (1977). Controlled and automatic human information processing II: Perceptual learning, automatic attending, and a general theory. *Psychological Review*, 84, 127-190.
- Snyder, E., Hillyard, S.A., & Galambos, R. (1980). Similarities and differences among the P3 waves to detected signals in three modalities. *Psychophysiology*, 17, 112-122.
- Squires, K.C., Petuchowski, S., Wickens, C., & Donchin, E. (1977). The effects of stimulus sequence on event-related potentials: A comparison of visual and auditory sequences. *Perception & Psychophysics*, 22, 31-40.
- Squires, K.C., Wickens, C., Squires, N.K., & Donchin, E. (1976). The effect of stimulus sequence on the waveform of the cortical event-related potential. *Science*, 193, 1142-1146.
- Squires, N.K., Donchin, E., Squires, K.C., & Grossberg, S. (1977). Redundant information in auditory and visual modalities: Inferring decision-related processes from the P300 component. *Journal of Experimental Psychology: Human Perception and Performance*, 3, 299-315.
- Steinhauer, S.R. (1981). *Emitted and evoked pupillary responses and event-related potentials as a function of reward and task involvement*. Unpublished doctoral dissertation, City University of New York.
- Stuss, D.T., & Picton, T.W. (1978). Neurophysiological correlates of human concept formation. *Behavioral Biology*, 23, 135-162.
- Stuss, D.T., Toga, A., Hutchison, J., & Picton, T.W. (1980). Feedback evoked potentials during an auditory concept formation task. In H.H. Kornhuber & L. Deecke (Eds.), *Motivation, motor and sensory processes of the brain. Progress in Brain Research* (Vol. 54, pp. 403-409). Amsterdam: Elsevier.
- Sutton, S. (1969). The specification of psychological variables in an average evoked potential experiment. In E. Donchin & D.B. Lindsley (Eds.), *Average evoked potentials: Methods, results and evaluations* (pp. 237-298). Washington, DC: NASA.
- Sutton, S., Braren, M., Zubin, J., & John, E.R. (1965). Evoked-potential correlates of stimulus uncertainty. *Science*, 150, 1187-1188.
- Sutton, S., & Ruchkin, D. (1984). The late positive complex: Advances and new problems. In R. Karrer, J. Cohen, & P. Tueting (Eds.), *Brain and information: Event-related potentials. Annals of the New York Academy of Sciences*, 425, 1-23.

- Sutton, S., Tueting, P., Zubin, J., & John, E.R. (1967). Information delivery and the sensory evoked potential. *Science*, 155, 1436-1439.
- Tueting, P., & Sutton, S. (1976). Auditory evoked potential and lift/no-lift reaction time in relation to uncertainty. In W.C. McCallum & J.R. Knott (Eds.), *The responsive brain* (pp. 71-75). Bristol, England: John Wright & Sons.
- Tueting, P., Sutton, S., & Zubin, J. (1970). Quantitative evoked potential correlates of the probability of events. *Psychophysiology*, 7, 385-394.
- Vaughan, H.G., Jr., & Ritter, W. (1970). The sources of auditory evoked responses recorded from the human scalp. *Electroencephalography & Clinical Neurophysiology*, 28, 360-367.
- Verbaten, M.N. (1983). The influence of information on habituation of cortical, autonomic and behavioral components of the orienting response. In A.W.K. Gaillard & W. Ritter (Eds.), *Tutorials in ERP research: Endogenous components* (pp. 201-216). Amsterdam: Elsevier.
- Wilkinson, R.T., & Morlock, H.C., Jr. (1967). Auditory evoked response and reaction time. *Electroencephalography & Clinical Neurophysiology*, 23, 50-56.

Announcements

Staff Psychophysicologist

The Washington University Behavior Research Lab is presently recruiting a staff psychophysicologist with skills in computer programming (VAX 750, PDP 11/23) and experimental design. Current laboratory focus is on issues of cognitive psychophysiology, "work-load," and fatigue assessment. Position available June 1986.

Contact: Dr. J.A. Stern, Washington University Behavior Research Lab at Malcolm Bliss Mental Health Center, 1420 Grattan Street, St. Louis, Missouri 63104 (telephone (314) 621-4211).

Nominations for Editor-in-Chief of *Psychophysiology*

With the impending expiration of David Shapiro's extended term as Editor-in-Chief of *Psychophysiology*, the Board of Directors of the Society seeks nominations for the next Editor of the journal. A decision on the editorship will be taken by the Board at its meeting in October. Nominations of suitably qualified individuals should be sent to: Jasper Brener, Department of Psychology, The University, Hull HU6 7RX, England.

Psychophysiology-Research Assistant Professor

The Psychology Department of the State University of New York at Stony Brook is recruiting a new faculty member for a non-tenure track three-year appointment to do full-time research and development in a new psychophysiology laboratory to be directed by Edward S. Katkin. Salary is competitive depending on qualifications. Experience using hardware and software in psychophysiological research is essential. Send resume and have three letters of recommendation sent to Ruth Sheppard, Assistant to Chair, Psychology Department, SUNY Stony Brook, Stony Brook, New York 11794. SUNY Stony Brook is an affirmative action/equal opportunity educator and employer.

Science Report Requests Film Footage of Psychophysiological Research

The Society for Psychophysiological Research has received a request from *Science Report*, to publish an announcement asking individuals who have 16mm film footage or videotape illustrating psychophysiological research, to contact their editors regarding possible use of this material in their science news program.

Individuals who have film or videotape, or would be interested in pursuing the possibility of producing a film or videotape for this purpose, should contact: Norman Kagan, Ph.D., *Science Report*, 408 East 64th Street, New York, New York 10021.

This document is a scanned copy of a printed document. No warranty is given about the accuracy of the copy. Users should refer to the original published version of the material.