

INVITED COMMENTARY

On the neural generators of the P300 component of the event-related potential

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Abstract

The triarchic model of P300 amplitude (Johnson, 1986, 1988a) postulated that the overall amplitude of the P300 recorded at any given electrode site represented the summation of activity from different neural generators, each related to the processing of a different type of information. However, neither of these original accounts provided an explicit description of the methods required to establish experimentally the presence of multiple neural sources. This paper reviews the triarchic amplitude model, the subsequently obtained data that support the postulated presence of multiple generators underlying the P300, and the methods used to demonstrate the presence of these multiple sources. These methods are straightforward because it is only necessary to show that the portions of P300 amplitude associated with different experimental variables have different scalp distributions. The implications of the multiple-generator basis of P300 on such factors as component definition, neural source analyses, and the cognitive processes underlying its activity are discussed.

Descriptors: Event-related potential, P300, Neural generators, Topographic analyses, Memory

Historically, the P300 component of the event-related brain potential (ERP) generally has been conceptualized as arising from a single neural generator. This outlook has shaped virtually every aspect of P300 research, from the types of explanations proposed for its functional significance, to the lack of attention to detailed topographic analyses, to the way it is used in clinical studies. However, converging evidence from a number of recent studies analyzing scalp topography data have now demonstrated that significantly different combinations of neural generators contribute to the P300 activity elicited by different combinations of experimental variables. These data indicate that the P300 is not a monolithic component. These findings further suggest that the different P300 generators appear to be activated essentially simultaneously, possibly sharing a common cellular architecture and with each responsible for processing a specific aspect of the stimulus or task information. The different contributions to overall P300 amplitude may represent the activation of the stored memories required to process the stimulus and task information. Thus, these recent results indicate that the P300 is a considerably more complex and informative ERP component than previously thought, and consequently it must be analyzed in new ways. The intent of this paper is to review the

rationale for the triarchic model of P300 amplitude and the procedures for analyzing topographic data. This review will be followed by a discussion of the implications of recent results for component definition, neural source analyses, and the cognitive processes underlying P300 activity.

The Triarchic Model

Based on a review of the P300 literature, I argued (Johnson, 1986, 1988a) that the many experimental variables known to affect P300 amplitude could be described by three general factors.¹ This triarchic formulation stated that overall P300 amplitude represents the summation of effects due to two independent categories of psychological variables, labeled *subjective probability* (*P*) and *stimulus meaning* (*M*), and that the P300 amplitude contributions made by the subjective probability and stimulus meaning factors were modulated by a third factor that accounted for the proportion of the overall stimulus information transmitted to the subject (*T*). Thus,

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

The multiple generator nature of P300 was further emphasized by the fact that, based on data available at that time, sub-

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¹This model was designed specifically to describe the P300, or P3b, component of the late positive complex and not related components, such as the P3a, novelty P3, or P3e. The relations between these different members of the "late positive complex" remain to be determined.

categories of experimental variables, each making their own independent contributions to P300 amplitude, were also identified. Thus, subjective probability was posited to be a function of the effects of both global stimulus probability (*GP*) and sequential expectancies (*SE*), and stimulus meaning was defined as the sum of experimental variables affecting task complexity (*TC*), stimulus complexity (*SC*), and stimulus value (*SV*). Thus, the original formulation specified the existence of at least five different contributors to P300 amplitude:

P300 amplitude

$$= f\{T \times [(1/GP + 1/SE) + (TC + SC + SV)]\}.$$

The rationale for proposing an additive relation between the subjective probability and stimulus meaning factors was based on two kinds of results: (a) those showing that the effects of stimulus meaning variables on P300 amplitude were constant across all probability levels, and (b) those showing that the effects of subjective probability variables were constant across variations of stimulus meaning (see Johnson, 1986, 1988a, for extensive examples). Because each factor had no apparent effect on the portion of P300 amplitude related to the processing of variables belonging to the other factor (i.e., they did not interact), the experimental manipulations of each factor could only be described as having independent, additive effects (i.e., they had different generators). Similarly, data showing that experimental manipulations of variables affecting information transmission produced equivalent reductions in the portion of P300 amplitude related to subjective probability (Johnson, 1984; Ruchkin, Sutton, & Mahaffey, 1987) and stimulus meaning (Johnson, 1984) support the postulated multiplicative relation in the formulation. In this formulation, only those experimental variables linked with an additive relation (i.e., all those belonging to the subjective probability and stimulus meaning factors) contribute to P300 amplitude. In contrast, because each variable in the information transmission category is expressed as the proportion of the total information received by the subject (i.e., with values between 0 and 1), experimental manipulations that increase the subject's equivocation can only reduce P300 amplitude. In addition, the multiplicative relation requires that variables in this category have equal effects on the P300 amplitude contributions made by the subjective probability and stimulus meaning variables.

The additive relations in the model imply that different neural generators are activated by each of the different variables associated with the subjective probability and stimulus meaning factors.² Logically, this is obtained because the fundamental differences in the cognitive activity for each of the variables in the subjective probability and stimulus meaning categories are incompatible with the idea that all these processes could occur simultaneously in the exact same neurons. The selective nature of these neural generators means that each can be thought of as a distinct information processor. For example, one processor/generator would evaluate global probability information,

and a different processor/generator would evaluate sequential probability information. The independence of these processors means that each can be activated selectively and in different combinations. Therefore, in any given situation, the total number and configuration of active processors/generators depends on the nature of the stimulus information and the subject's task. Given that the generators possess the correct configuration, differences in their spatial locations mean that the effects of each on P300 amplitude will have its own characteristic scalp distribution. Thus, the total amount of P300 activity elicited by any given stimulus will represent a summation of the outputs from all the activated processors/generators. Because of volume conduction, the amplitude of P300 at any given electrode site will be the sum of the activity from all of the spatially overlapping, simultaneously generated electrical fields from all the activated processors.

Topographic Profile Analyses

Validating the existence of additive effects on P300 amplitude is a straightforward process, although a recent paper by Verleger and Berg (1991) reflected a fundamental misconception in this regard. It is only necessary to show that the portions of P300 amplitude associated with different experimental variables have different scalp distributions. Such differences normally appear first as a significant interaction between the experimental variable and the electrode factor (e.g., Task \times Electrode) in an analysis of variance (ANOVA). Thus, the fact that Verleger and Berg observed significantly different scalp distributions in their experiment constitutes unequivocal support for the presence of multiple neural sources for P300. In claiming that their data did not support the additive hypothesis, these authors may have been confused by the apparent similarity between the concept of additivity, as exemplified in the Additive Factors Method (Sternberg, 1969), and the concept of additivity as it is used here. In the Additive Factors Method, an interaction between two task variables (each with two or more levels) in an ANOVA on reaction time data is taken as evidence of nonadditivity in the effects of the two variables. In contrast, in the case of P300, an interaction between a task variable and the electrode factor in an ANOVA on amplitude data constitutes evidence that the different tasks do indeed have different scalp distributions.

However, because the simple ANOVA procedure provides necessary but not sufficient evidence for topographic differences, a further test is required. These interactions may be significant because of differences in absolute amplitude across conditions rather than differences in topography (see McCarthy & Wood, 1985). Thus, a second ANOVA must be performed on normalized component amplitudes. If there are more than two experimental conditions, these tests would consist of post hoc tests between pairs of normalized amplitude measurements obtained in two different experimental conditions at the electrode sites where the activity is largest (i.e., topographic profile comparisons). Amplitude normalization removes any between-condition differences (i.e., the average amplitude remaining in each experimental condition is equated) so that only topographic differences remain. Normalization can be accomplished using different methods (as described thoroughly by McCarthy & Wood, 1985). If the intracranial source configuration is identical in different conditions, then the scalp topographies will be the same. However, if the overall pattern of P300 scalp activity is the result of multiple neural generators, then the experi-

²At present, it is not known whether, for any particular manipulation, the neural structure(s) responsible for generating its specific portion of P300 activity consists of one or more groups of neurons. Consequently, it may be more accurate to describe this as a pattern of generator activity. However, to avoid circumlocution, the term *generator* will be used.

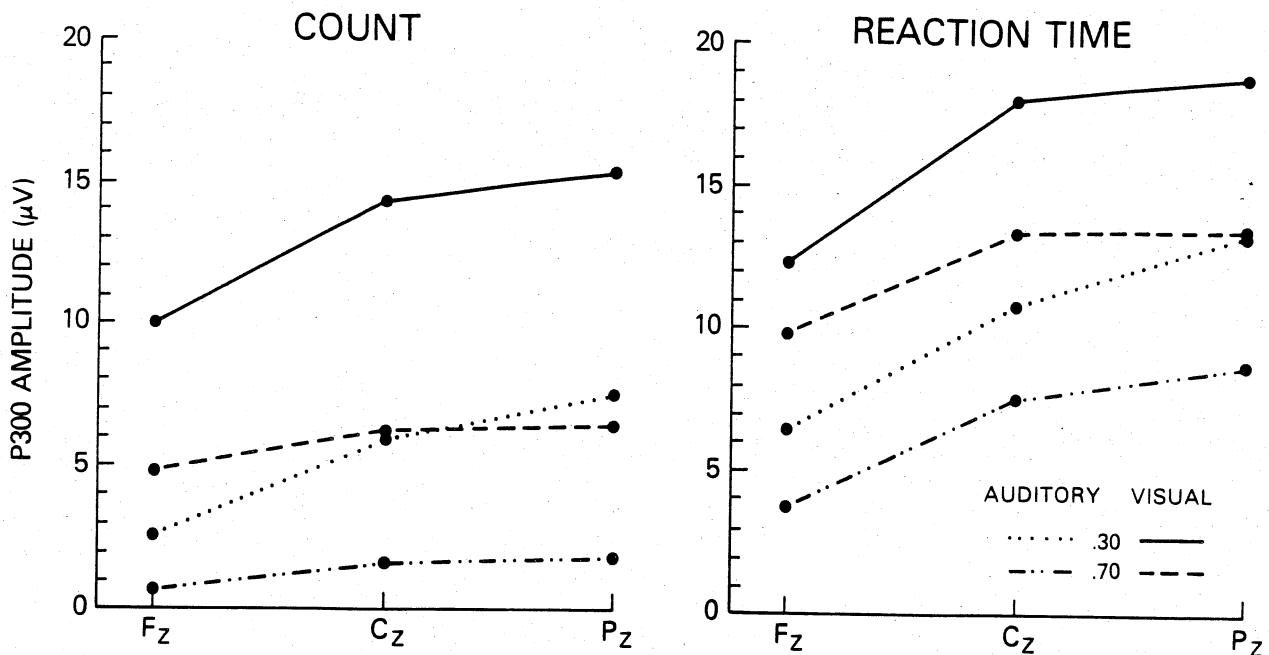


Figure 1. Grand mean raw P300 amplitudes elicited at the three midline electrode sites by stimuli in two stimulus modalities (auditory, visual), at two levels of stimulus probability (.30, .70), and in two tasks (count, reaction time) from the experiment by Johnson (1989a).

mental variable should still interact significantly with the electrode factor in an ANOVA. Thus, a difference in scalp topography is evidence that more than one intracranial generator contributed to the ERP measurements in the different conditions. Such findings constitute unambiguous confirmation of the additivity expressed in the amplitude model.

The methods for isolating and studying these different sub-components of the P300 are best illustrated by reviewing the procedures followed in a recent paper (Johnson, 1989a). In that experiment, subjects were presented with a Bernoulli series of stimuli (.30/.70) that, in separate series, were presented in one of two stimulus modalities (auditory, visual) while the subjects performed two different tasks (count, choice reaction time [RT]). The overall ANOVA on the baseline-to-peak P300 amplitudes (Figure 1) revealed significant interactions between the electrode factor and each manipulation (Probability \times Electrode, Task \times Electrode, Modality \times Electrode), suggesting that the P300 activity associated with each variable had its own distinct neural generator.

These findings were replicated in another form of topographic analyses, *regional ANOVAs*. In these analyses, different ANOVAs were done on the P300 amplitudes from electrodes in small non-overlapping scalp regions (i.e., P3, Pz, P4; C3, Cz, C4; F3, Fz, F4). These regional ANOVAs revealed the presence of multiple neural generators for P300 by showing clear differences in the pattern of significant effects for the different variables over the different scalp regions. Thus, there were significant effects of stimulus modality on P300 amplitude over frontal scalp but not over central or parietal scalp. In contrast, the task variable produced its largest effects over parietal and central scalp and had no significant effect over frontal scalp. There was a third pattern of significant results for the probability variable because significant effects were obtained over all three scalp regions (see Johnson, 1989a, Table 2).

To determine whether the significant interactions with electrode were due to real differences in topography or simply to differences in absolute amplitude across conditions, the amplitudes were normalized. Because there were more than two different experimental conditions in this experiment, an overall ANOVA was done first on the normalized amplitudes followed by post hoc tests for each variable. Thus, for the overall ANOVA, the raw data were normalized by converting all P300 amplitudes to a percentage of the across-subject mean amplitude obtained at the Pz electrode for the infrequent stimulus in the RT condition separately for each stimulus modality (Figures 2A and B). This transformation removed the differences in overall amplitude between modalities while preserving any modality-specific differences in scalp distribution and any differences in response to the other experimental variables. In this ANOVA, the Modality \times Electrode interaction remained significant, indicating that the P300 activity elicited by the stimuli in each modality were generated by different neural sources. To evaluate the Probability and Task interactions with Electrode, post hoc tests were done after the data were renormalized for each of these two comparisons (see the data in Figures 2B and C for the task comparison). All post hoc topographic profile comparisons were done after the raw data were scaled such that the root-mean-square (RMS) amplitudes of the means of the measurements (averaged across subjects) were the same. This series of topographic profile tests revealed that (a) there were modality-specific neural generators for auditory and visual P300s, (b) there was one generator for the task effects on P300 amplitude, (c) there was another generator for the probability effects on P300 amplitude, and (d) the task and probability P300 generators were modality independent (see Johnson, 1989a, pp. 639-640, for additional details).

One final aspect of the P300 amplitude variations still remained to be characterized: whether different experimental ma-

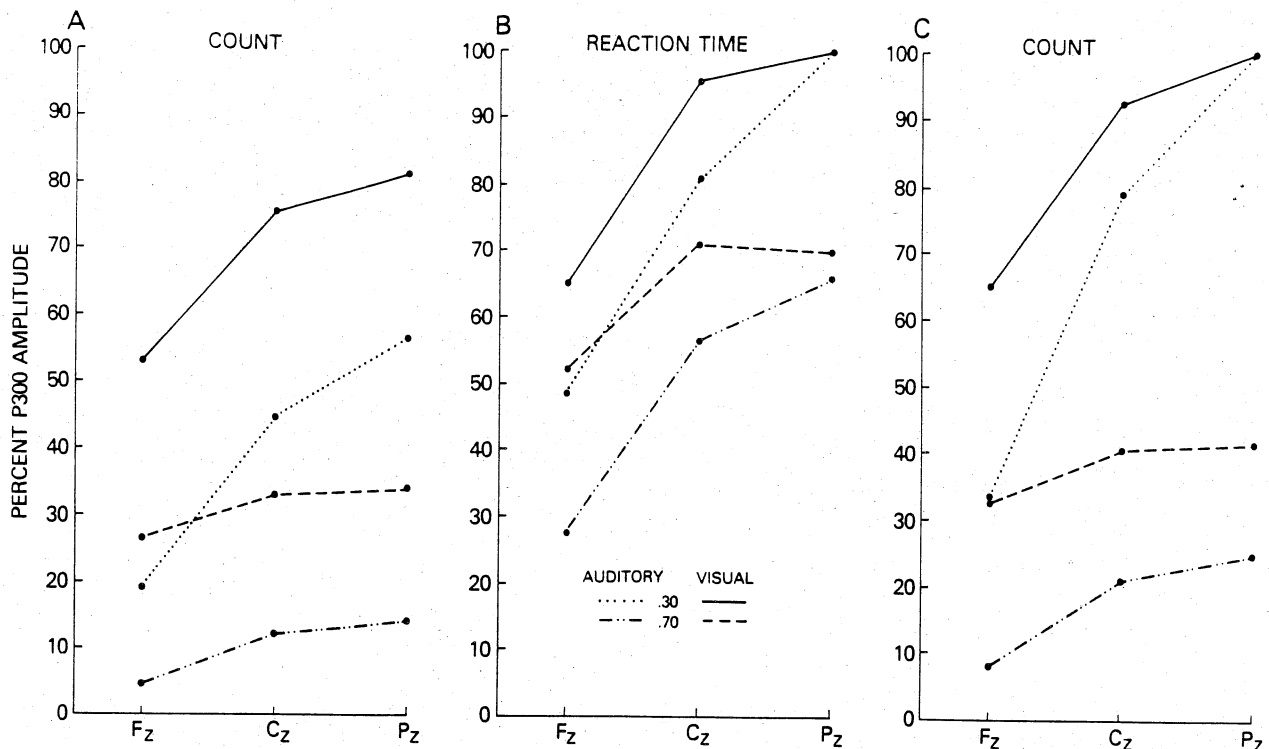


Figure 2. Grand mean normalized P300 amplitudes elicited by stimuli in both modalities as a function of task, stimulus probability, and electrode. Panels A and B show P300 amplitude for the count and reaction time tasks, respectively, when the data were normalized separately for each stimulus modality on the mean amplitude of the P300 elicited by the infrequent stimulus in the reaction time task. Panel C shows the same data as in panel A, except that amplitude was renormalized on the P300 elicited by the infrequent stimulus in the count task. *Source:* Johnson, 1989a; © 1989 Society for Psychophysiological Research. Reprinted with permission.

nipulations activate different neural generators. To address this issue, it is necessary to determine whether the portion of P300 amplitude associated with (i.e., elicited by) a particular manipulation or comparison is different from that of the remaining, possibly unrelated P300 activity. To illustrate this point, examine the hypothetical results from a memory experiment in which the P300 activity elicited at the Pz, Cz, and Fz electrodes by items that were later recognized (larger waveforms, labeled "A" in Figure 3A) is compared with that elicited by items that were later unrecognized (smaller waveforms, labeled "B"). If these amplitude results are graphed in the customary fashion, using overall P300 amplitudes, then both curves A and B (Figure 3B) show the usual P300 scalp distribution (i.e., Pz maximum and decreasing in the anterior direction). However, when the P300 activity specifically related to the memory manipulation is isolated from that due to all other variables by subtracting the subsequently unrecognized amplitudes from the subsequently recognized amplitudes (A - B curve in Figure 3B), a different picture emerges. This *memory effect* P300 activity represented by the A - B amplitude difference curve (often referred to as *Dm*; Paller, Kutas, & Mayes, 1987) clearly shows that, in contrast to the measures of overall amplitude, the scalp distribution of the memory effect P300 is such that equally large P300s are found at the three midline electrode sites. Presumably, this difference is due to the fact that the B waveform (i.e., the "base" P300) also contains P300 activity reflecting the processing of the ever-present other factors that affect P300 amplitude (e.g., stimulus probability, sequential effects, the subjects' task).

If the differences in these scalp distributions are large enough to produce a significant interaction in an ANOVA, it would be evidence that the memory effect has a different pattern of intracranial generator activity than either of the "parent" P300 waveforms. If, after proper normalization (Figure 3C), significant differences in scalp distribution are found in the post hoc tests, then this difference would constitute unambiguous evidence that the memory effect on P300 amplitude has its own distinct pattern of generator activity.

Using this subtraction procedure, the portion of P300 amplitude related to any experimental manipulation can be isolated from that due to any other factors. Clearly, subtractions must be performed on quantified amplitudes (rather than subtracting one waveform from another) in comparisons where there is latency variability or latency differences as a function of experimental conditions (e.g., normal vs. degraded stimuli, auditory vs. visual). Although a single variable is being manipulated in an experiment, it cannot be assumed there is only one pattern of neural generator activity responsible for eliciting all of the observed P300 amplitude. Thus, the subtraction procedure should always be used to isolate the portion of P300 amplitude elicited by the variable being manipulated.

Thus, this subtraction procedure was used to resolve the question of whether the probability and task portions of P300 amplitude in the Johnson (1989a) study had scalp distributions that were different from one another. The answer to this question bears on the specific issue of whether probability and task variables described in the triarchic model make their own dis-

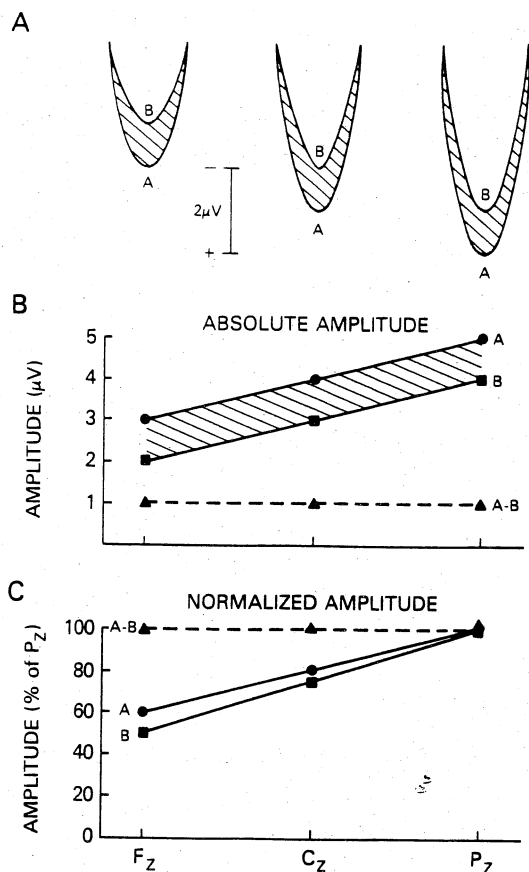


Figure 3. Hypothetical data from a memory experiment to illustrate the analysis of P300 scalp distribution. Panel A shows the P300s elicited at the Pz, Cz, and Fz electrode sites by items that were separated on the basis of their subsequent recognition performance. In this example, the larger (A) and smaller (B) waveforms were elicited by subsequently recognized and unrecognized items, respectively. Panel B shows the overall (curves A, B) and difference (A - B) P300 amplitudes obtained from the waveforms in panel A using the baseline-to-peak method. Panel C shows the same amplitude data as in panel B after the P300 amplitudes from each electrode site were normalized by adjusting each to be a percentage of the amplitude obtained at the Pz site separately for each condition.

tinct contributions to overall P300 amplitude. Therefore, the probability portion of P300 amplitude was isolated by collapsing over conditions and subtracting the P300 activity elicited by the .70 stimulus from that elicited by the .30 stimulus. The same procedure was followed to isolate the effects of task (RT minus Count). The scalp distributions of these task and probability P300 amplitudes were then normalized to have equal RMS amplitudes and tested in a topographic profile comparison. Because this comparison produced a significant difference, the results indicated that the portion of P300 amplitude related to the probability and task manipulations each arose from distinct patterns of neural generator activity.

Another possible, but considerably less powerful, method of demonstrating additivity consists of testing the model equation directly by showing the absence of a significant interaction between the effects of two experimental variables in an ANOVA (e.g., Probability \times Task). There are, however, severe problems with this method. For example, although a significant interac-

tion in an ANOVA is necessary to show the presence of different generators, the presence of a nonsignificant interaction is not sufficient evidence to rule out the presence of different generators because a nonsignificant interaction can result from a variety of factors (e.g., noisy data) that are unrelated to the experimental manipulations. Moreover, even when a nonsignificant interaction is obtained, its interpretation is still ambiguous because failure to reject the null hypothesis does not assure the validity of the null hypothesis. Even after obtaining a significant interaction, the absence of statistically significant additive effects on P300 amplitude at individual electrode sites (in post hoc statistical tests) can occur because of the placement of the electrodes relative to the sources or because of irrelevant properties of the overlapping fields (e.g., amplitude, spread, generator locations relative to one another). Thus, in Pritchard's (1989) results, significant additive P300 amplitude effects for subjective probability and stimulus meaning manipulations were found at most, but not all, electrode sites.

A key assumption underlying tests of scalp distribution differences for any ERP component is that all the component measurements are free from any substantial component overlap that could create spurious differences where there are none. The possibility that any or all of the distributional changes in a particular component could be due to changes in a spatially or temporally adjacent component is fundamental enough that it must be dealt with in any topographic analysis. The problem of spatial overlap between components is the easiest to deal with because the electrode sites selected for the profile comparisons can be restricted to those where the overlap is minimal. Temporal overlap by components (e.g., slow wave in an analysis of P300) is a more difficult problem, and thus the possibility of component overlap can never be ruled out entirely. The main method for dealing with temporal overlap is to perform the same series of analyses on any component(s) that might overlap the component of interest. In both cases, however, it is possible to reduce the likelihood that overlap is responsible for any topographic changes by demonstrating the presence of major differences in the behavior of the potentially overlapping components. If the measurements of a component's amplitude are contaminated to a substantial degree by the activity of an overlapping component, then both components will respond in substantially similar ways to the experimental variables. Thus, in the Johnson (1989a) example, the identical series of ANOVAs and post hoc analyses were performed on measures of the slow wave component because it can overlap temporally with the P300. These tests revealed a number of important differences in the responses of the P300 and slow wave to the experimental manipulations. For example, there were no modality effects for slow wave; there were different patterns of hemispheric symmetry for slow wave and P300; and the effects of stimulus probability and task produced different scalp distributions for each component (e.g., stimulus probability produced large amplitude increments at all electrodes for P300 but only over parietal scalp for slow wave). Thus, although the possibility that slow wave activity confounded the P300 amplitude measurements in that experiment cannot be ruled out definitively, the overall pattern of results argues strongly against the idea that such confounds were the source of the differences in P300 scalp distribution.

There is a growing list of studies from different laboratories that, as a result of including topographic analyses, have already validated the additivity expressed in the triarchic model (John-

son, 1986, 1989a; Pritchard, 1989). In addition, the existence of the postulated subcategories within the subjective probability and stimulus meaning factors has also been validated by demonstrations of different scalp distributions for the P300 activity elicited by experimental variables within the stimulus meaning factor (Friedman, 1990; Johnson, 1990, 1992; Johnson & Donchin, 1985; Johnson & Fedio, 1987; Ruchkin, Johnson, Canoune, Ritter, & Hammer, 1990). Clearly, however, the realization of statistically significant additive effects on P300 amplitude in any given situation will depend on the locations and orientations of the neural generators activated by the particular experimental manipulations.

Implications of Multiple P300 Generators

The triarchic model and the recent proliferation of different P300 scalp distributions observed in different conditions challenge current notions of how an ERP component is defined. In general, P300 has been defined simply as an endogenous positive component with a Pz-Cz maximum and a latency of between 280 and 1,000 ms. This definition implies that (a) P300 is a monolithic component with a single, fixed pattern of scalp activity and (b) that all P300 activity observed at electrode sites away from the point of maximal amplitude does not provide additional information. These two properties may explain why the scalp distribution of P300 rarely has been quantified in a rigorous fashion. Paradoxically, despite this clear and simple definition, there is no explicit requirement for experimenters to demonstrate that their data set did not contain any significant differences in P300 scalp distribution across stimuli or conditions before asserting that the component under study is indeed the P300. Thus, in the memory experiment example, it should be necessary for the experimenter to demonstrate that the scalp distribution of the memory-related portion of P300 amplitude is the same as the scalp distribution of the base portion. Despite the fundamental nature of such demonstrations, P300 investigators have been generally quite insensitive to the scalp distribution issue.

The inadequacy of the current topography-based definition of P300 is best illustrated by the combination of the results of Johnson (1989a) and those of Ruchkin et al. (1990). Together, the findings of these two studies demonstrated the presence of six distinct P300 topographies—all meeting the Pz-Cz maximum criterion—in response to six different experimental manipulations. These data show that there is no topographic basis to support the idea that the P300 is a monolithic ERP component with an invariant pattern of scalp activity. These topographic variations, along with others showing that P300 is modality dependent (Barrett, Nishige, & Shibasaki, 1987; Johnson, 1989a, 1989b; Johnson, Miltner, & Braun, 1991), provide strong evidence that the P300 is indeed a composite of the activity arising from different brain processors/generators, as asserted in the amplitude model. In an explicit memory paradigm (Johnson, 1990), the P300 elicited at Pz by words (category probability = .50) could be manipulated independently of the P300 elicited simultaneously at Fz (i.e., not P3a or the novelty P3). This result raises the possibility that, more generally, the P300 activity observed at Fz may not always be a simple volume-conducted manifestation of the P300 activity observed at Pz. This conclusion is bolstered by another recent finding (Ruchkin, Johnson, Grafman, Canoune, & Ritter, 1992), in which the P300s (or P3b-like potentials) elicited at Pz and Cz

in a working memory paradigm had latencies that were separated from one another by more than 100 ms, and each showed different patterns of significant effects in response to the stimulus manipulations. The combined results of these two memory studies suggest that as more complex paradigms are used to elicit the P300, more complex P300 scalp topographies are likely to be observed.

The absence of any requirement for all experimenters to demonstrate the invariant nature of their P300 scalp distributions across stimuli and conditions means that despite assertions to the contrary scalp topography was never either the absolute or even the essential defining characteristic of P300. In the scalp distribution information available in one form or another in the P300 literature, the amount of variability across experimental manipulations is startling. Nevertheless, investigators have consistently identified this activity as the P300. In practice, then, the one property of P300 that has been tested in all experiments is its response to psychological variables. Thus, in reality this property, and no other, has been accepted as the single true defining characteristic of the P300.

Some investigators may want to retain a topography-based definition and argue that the potentials recorded in these other studies do not represent P300 activity. However, if this position is taken, then the topographic definition of P300 must be specified to the degree necessary to eliminate any possible future confusions among investigators. Presumably, such a definition would entail something like a specification of the percentages of Pz amplitude that must be found at every other scalp recording site (at least in the 10–20 system). Such a normalized definition would be necessary to eliminate differences in absolute effects from one experimental manipulation to another. This level of detail would be the only way in which the ERP activity associated with the probability and task manipulations in the above example could be separated. Presumably, strict compliance with this prototypical pattern of scalp activity would have to be demonstrated in every study before the investigator could claim to be studying the P300. It would also be necessary for adherents of a topography-based definition to ensure that the psychological constructs ascribed to their P300 are exclusively supported by the activity of the P300 with this particular topography. Even so, the problem remains of what to call (and how to interpret) the other components that look like P300, behave like P300, have a latency like P300, and even contribute to the overall amplitude at Pz but that may be slightly larger at other electrode sites than specified in the definition. A new nomenclature would be required so that the components not fitting this definition could be labeled. In addition to the usual polarity and latency information, such a labeling system would have to incorporate the percentage of maximal amplitude found at a constellation of electrodes.

The lack of a topography-based anchor raises the question of how the P300 component should be defined. The fact that P300 papers regularly survive the peer review process, regardless of their scalp distribution, or even the absence of any distributional analyses, suggests that there is a general agreement as to which components are P300s and which are not. However, the criteria used to define the P300 component must be stipulated much more precisely. One starting point is to use the triarchic formulation because it provides a summary of the interactions of the cognitive variables that affect the P300. As indicated by the number of different subcategories within the triarchic model, there is a wide variety of cognitive processes

that elicit P300 activity. In each case, a subcategory was identified only when there were data that had been replicated in more than one experiment. Using this model as a frame of reference should alleviate some of the chaos that will inevitably arise from the recognition that there is no current, generally accepted, workable definition of P300.

The different aspects of stimulus information described in the triarchic model are conveyed simultaneously by the stimulus. In response, most combinations of psychological variables appear to produce a single P300 peak, rather than a series of small peaks that are each related to a different variable. Such data suggest that the different generators/processors are activated simultaneously, apparently in parallel, and that their outputs occur at about the same time. Thus, these generators take a relatively constant amount of time to process the information, regardless of the type of information being processed. There are, however, instances in which more than one P300-like peak is found with only minimal latency differences; for example, the P3a/P300 combination (Squires, Squires, & Hillyard, 1975). Although incompletely characterized, the P3a appears to be primarily sensitive to stimulus probability in the same way as the P300. Therefore, the main distinguishing feature of the P3a, compared with the P300, is its more frontal scalp distribution and its slightly shorter latency. Given that P3as are not seen in all situations and experiments, the P3a may represent the activity of a P300 processor whose appearance is dependent on the delayed output of the remaining information processors. Such an interpretation is consistent with the fact that the P3a appears to reflect the simplest of all P300 processes (i.e., some form of probability information). Given constant stimulus parameters, the time required to process probability information should be relatively invariant from one task to another. This stability is in contrast to the presumably more highly variable amounts of processing time required by tasks of various degrees of complexity. Thus, different P300 generators may be distinguished on the basis of their temporal and spatial characteristics.

The nature and variability of P300 scalp distribution has important implications for the nature of the P300 neural generators and thus for its functional significance. The apparent specificity of P300 scalp distribution to the type of information being processed suggests that P300 activity is generated in a large number of *specific-purpose cortical processors*. These processors constitute a system of parallel processors that are distributed throughout the cerebral cortex and appear to have three general properties: (a) each is responsible for performing a particular cognitive operation, (b) each is similar in design and nature, and (c) each is bound to a particular anatomical location. These characteristics allow the processors to be combined in an essentially infinite number of patterns to form a powerful and extremely fluid computational network. Functionally, the nature and apparent ubiquity of these processors suggests that they may represent a form of memory access in which activation of any given processor is dependent solely on which stored memories are required for task performance. In this scheme, P300 amplitude and latency provide measures of the extent and timing of processor activation, respectively, whereas P300 topography provides an indication of which processors are activated during task performance.³ The assertion that P300 is

generated in the cerebral cortex derives from the distributional specificity found in the studies described above, along with other factors (e.g., the relatively large magnitude of these potentials). Although deep sources could produce localized fields at a distance, it is unlikely that such occurrences would be as common as is apparently the case for the P300. The other aspects of this conceptualization are also consistent with the distributional data obtained to date.

The distributional findings can also provide an invaluable guide for other methods of neural source localization (e.g., Nunez, 1990; Scherg, 1990). For example, the scalp analyses can be used in any experiment to provide an estimate of the minimum number of neural sources involved in the generation of a particular pattern of P300 scalp activity. At least some information on the number of possible sources for P300 in a given situation is extremely useful and is certainly better than no such information when using any method of source localization based on backward computations. It would also be mandatory to use the subtraction procedure when looking for the neural sources of the P300 activity associated with a specific experimental manipulation. As for any scalp distribution analyses, source analyses on unsubtracted data from an electrode array with insufficient spatial resolution will produce a solution that will be an average of all the sources because the unsubtracted waveform will reflect the activity of an unknown number of sources. Thus, analysis of scalp distribution data can be a useful adjunct to the other methods of source analyses.

Suggestive evidence in support of the existence of multiple P300 generators has been obtained from studies of different patient groups. Provided that the P300-like activity found in indwelling electrode studies of epilepsy patients (e.g., Halgren, Squires, Rohrbaugh, Babb, & Crandall, 1980) is related to the scalp P300, the fact that this activity does not appear to be a major contributor to the scalp-recorded P300 activity in temporal lobectomy patients (Johnson, 1988b, 1989a; Johnson & Fedio, 1986, 1987; Rugg, Pickles, Potter, & Roberts, 1991; Smith & Halgren, 1989; Stapleton, Halgren, & Moreno, 1987) suggests that P300 is generated in multiple brain sites. In addition, McCarthy and Wood (1987) reported a possible candidate P300 generator in the frontal lobe that was active in an oddball task using auditory, visual, and somatosensory stimuli. In a series of studies, Knight and his colleagues showed that different brain lesions produce different patterns of P300 amplitude reduction and that the parietal P300 and the frontal novelty P300 have different neural generators (Knight, 1990; Yamaguchi & Knight, 1991). However, because all of these other experimenters have generally treated P300 as a monolithic component, their experiments were designed primarily to look for multiple generators of the late positive complex, rather than for multiple generators of the P300, such as those that might be responsible for the variations in scalp topography. Therefore, further studies will be necessary to determine how, and even whether, the activity of these different putative generators and brain regions affect the familiar scalp-recorded P300. Nevertheless, studies of neurological patients may provide unique information about the generator mechanisms underlying the P300.

Conclusions

A major reassessment of the nature of the P300 component is required. Currently, our knowledge of the antecedent conditions necessary for eliciting a P300 greatly exceeds our knowledge of the functional significance of this ERP component. In

³See Johnson (1988a, pp. 116-122) for a discussion of how such a system of processors of fixed design and anatomical specificity can be linked to the anatomical and electrophysiological properties of the cortex.

contrast to past characterizations of the P300 as a monolithic component with a relatively invariant pattern of scalp activity, more recent data suggest the presence of a richer, much more complex component that is capable of providing more detailed information on the actions of different, simultaneously active brain processes. Increased efforts at characterizing the apparently quite numerous variations in P300 scalp distribution

should increase our understanding of the brain and cognitive processes underlying this important component of the ERP. Such efforts should lead to new and testable theoretical and functional interpretations of the P300, such as the memory access hypothesis advanced here, that take into account the multifaceted nature of this activity.

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