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P300 amplitude is determined by target-to-target interval

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Abstract

P300 event-related brain potential (ERP) measures are affected by target stimulus probability, the number of nontargets preceding the target in the stimulus sequence structure, and interstimulus interval (ISI). Each of these factors contributes to the target-to-target interval (TTI), which also has been found to affect P300. The present study employed a variant of the oddball paradigm and manipulated the number of preceding nontarget stimuli (0, 1, 2, 3) and ISI (1, 2, 4 s) in order to systematically assess TTI effects on P300 values from auditory and visual stimuli. Number of preceding nontargets generally produced stronger effects than ISI in a manner suggesting that TTI determined P300 measures: Amplitude increased as TTI increased for both auditory and visual stimulus conditions, whereas latency tended to decrease with increased TTI. The finding that TTI is a critical determinant of P300 responsivity is discussed within a resource allocation theoretical framework.

Descriptors: P300, Event-related potential (ERP), Sequence effects, Interstimulus interval (ISI), Target-to-target interval (TTI)

Decreases in P300 amplitude with increases in target-stimulus probability have been established for a wide range of target probability and stimulus modality manipulations (Donchin & Coles, 1988; Johnson, 1986, 1988; Picton, 1992; Polich, 1998; Pritchard, 1981). However, in addition to global target probability effects, P300 is also sensitive to the specific order of nontarget (N) and target stimuli (T) that control the local target stimulus probability (e.g., NNNT > NNT > NT > TT). Such stimulus sequence effects are reliable (Gonsalvez et al., 1999), have been used in clinical evaluations (Duncan-Johson, Roth, & Kopell, 1984; Ford, Duncan-Johnson, Pfefferbaum, & Kopell, 1982; Miller, 1996; Polich, Ladish, & Bloom, 1990), and can be elicited across global probabilities (Johnson & Donchin, 1980; Squires, Petuchowski, Wickens, & Donchin, 1977; Squires, Wickens, Squires, & Donchin, 1976), response tasks (e.g., Giese-Davis, Miller, & Knight, 1993; Johnson & Donchin, 1980; Leuthold, & Sommer, 1993; Verleger, 1987), and modalities (e.g., Duncan-Johnson & Donchin, 1982; Johnson & Donchin, 1982; Squires et al., 1976).

Interstimulus Interval

These probability effects have served as the basis for the theoretical interpretation that P300 is generated by task conditions involving working memory (Donchin, Karis, Bashore, Coles & Gratton, 1986), with more recent studies continuing to contribute to the analysis of P300's sensitivity to stimulus sequence processing (e.g., Gonsalvez et al., 1995; Sommer, Leuthold, & Matt, 1998; Sommer, Leuthold, & Soetens, 1999). However, even though stimulus probability is an important determinant of P300, the time between stimulus events or the interstimulus interval (ISI) also has been found to affect P300 magnitude. Several studies have reported that P300 components elicited with relatively short ISIs have smaller amplitudes than those obtained with longer ISIs (Fitzgerald & Picton, 1981; Woods & Courchesne, 1986; Woods, Courchesne, Hillyard, & Galambos, 1980). These effects sometimes have been attributed to "temporal probability," as P300 amplitude appears to be influenced by the temporal frequency with which a target stimulus occurs in a given time interval (Picton & Stuss, 1980). In addition, increases in P300 amplitude with decreases in the temporal frequency of the target stimulus have been observed for both easy and hard stimulus discrimination tasks, suggesting that temporal presentation variables control component variation more than task difficulty (Fitzgerald & Picton, 1984; Polich, 1987). More important, when ISI is about 6 s or longer, the influence of target stimulus probability on P300 amplitude wanes considerably (cf. Donchin et al., 1986; Fitzgerald & Picton, 1981; Polich, 1990a, 1990b), although sequence effects are maintained (Polich & Bondurant, 1997).

One possible explanation for the influence of ISI on P300 is suggested by the similar declines in amplitude observed with decreases in ISI for sensory ERPs (e.g., Davis, Mast, Yoshie, & Zerlin, 1966; Polich, Aung, & Dalessio, 1988; Roth et al., 1976). These effects have been interpreted as the result of "recovery cycle" limitations inherent in the mechanisms responsible for component generation. Relatively small potentials will be produced with short ISIs, because the system requires time to recover from

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very recent ERP production. With longer ISIs, however, the generation processes can reacquire the necessary resources to produce large ERPs because they have "recovered" from their previous use. Response time studies also indicate that the time interval between task stimuli is an important determinant of processing outcomes because decreases in ISI increases recovery cycle time (Kahneman, 1973; Kantowitz, 1974; Keele, 1973; Pashler, 1994). Given the influence of recovery cycle on sensory ERP amplitudes and behavioral responses to the time intervals between stimulus presentations, it is reasonable to suppose that similar effects might be observed for the P300 component as is implied by the presence of relatively small amplitudes for this potential when very short ISIs are employed (Fitzgerald & Picton, 1981; Woods & Courchesne, 1986; Woods, Courchesne, et al., 1980). If a recovery cycle mechanism does contribute to P300 amplitude, changes in target stimulus probability and ISI should interact with one another because P300 size will vary inversely with target stimulus probability and ISI (Polich, 1990a, 1990b).

Target-to-Target Interval

Although P300 is clearly affected by target stimulus probability, stimulus sequence structure, and ISI, each of these factors also varies the target-to-target interval (TTI)—the time between the target that elicits the ERP and the preceding target. Decreasing target-stimulus probability, increasing nontarget sequence length, and increasing the ISI all extend the TTI by increasing the time for nontarget sequence length to prolong TTI. However, few studies have addressed this issue directly, so that the general influence of TTI is as yet unclear because relatively limited ranges of either sequence length or ISI have been employed. Fitzgerald and Picton (1981) held TTI constant (2.5 and 7.5 s), and manipulated target probability and ISI to assess their influence on stimulus sequence: TTI enhanced P300 amplitude more than the other variables. Gonsalvez et al. (1999) found that when TTI (2–8 s) effects were controlled, sequence length and ISI did not influence P300 amplitude, suggesting that target interval was the more potent influence on component size. Katayama, Tanaka, and Morotomi (1998) obtained a similar outcome when standard tone occurrence (none and 1 or 2 s ISIs for all stimuli) and mean TTI (5, 10, 20 s) were manipulated. TTI influenced P300 amplitude more than ISI. Polich (1990b) reported that target probability changed P300 amplitude only with relatively short (<6 s) but not long (6–10 s) ISI conditions, suggesting that the concurrently longer TTI influenced the P300 measures. Leuthold and Sommer (1993) obtained ERPs and response time (RT) for 16 sequence types and three relatively short ISIs (1.6, 2.1, 2.8 s). The comparatively longer ISIs were associated with larger P300 amplitudes, with an interaction between sequence and ISI obtained such that stimulus alternations (NT) produced larger P300 amplitudes than repetitions (TT) for the very short but not longer ISIs. Taken together, these studies indicate that TTI contributes to P300 amplitude across sequences, but whether this factor is the major determinant of component size over a wide range of sequence and ISI lengths and yields similar effects for both auditory and visual stimuli is unknown.

The "single-stimulus" paradigm also has been used to elicit P300 components from target stimuli. In the single-stimulus task, the nontarget stimulus is replaced with either silence or a blank screen whenever a nontarget would normally occur, although the target stimulus is presented with the same temporal frequency, as it would occur in the corresponding oddball task. Hence, the TTI remains identical for both the oddball and single-stimulus tasks, whereas the stimulus sequences is varied—random occurrences of T (low probability) and N (high probability) stimuli for the oddball task but only T (probability = 1.0) stimuli are presented for the single-stimulus task. Despite the lack of nontarget stimulus presentations, comparable P300 components are obtained for both the single-stimulus and oddball tasks across a range of stimulus and task variables (Cass & Polich, 1997; Mertens & Polich, 1997; Polich, Eischen, & Collins, 1994; Polich & Heine, 1996). Indeed, target stimulus amplitude was virtually identical and highly correlated between task types (Katayama & Polich, 1996b). Moreover, when target stimulus "probability" is increased, P300 amplitude decreases for both paradigms even in the absence of a nontarget stimulus because the ISI remains constant so that the TTI is shortened with increases in target probability (Polich & Margala, 1997). Source localization of the P300s generated by the two tasks produces similar waveforms, topographic distributions, and dipole coordinates (Tarkka & Stokic, 1998). These outcomes can be accounted for by assuming that TTI rather than probability, sequence structure, and ISI controls P300 amplitude (cf. Gonsalvez et al., 1999; Johnson, 1986; Polich, 1990a, 1990b, 1998).

Present Study

As the above review suggests, P300 amplitude is influenced by target probability, nontarget sequence length, and ISI. However, the time between target stimuli or TTI appears to underlie the majority of these effects as it produces consistent component amplitude changes that can account for a wide variety of P300 findings. To assess the TTI directly, the oddball tasks employed manipulated stimulus sequence length (TT, NT, NNT, NNNT) and ISI (1, 2, 4 s), but kept target probability constant for both auditory and visual stimulus conditions. The stimulus presentation structure and timing were carefully designed so that TTI was varied systematically from 1 to 16 s (see Table 1). If TTI is a primary determinant of P300 amplitude, then those conditions that maximize the time between target stimuli in the oddball paradigm should produce the largest components regardless of sequence length or ISI.

Methods

Participants

Fourteen young adult (M = 21.2, SD = 1.6 years) undergraduates (7 men, 7 women) from the University of California, San Diego served as participants. All reported normal hearing and (corrected to) normal vision, reported no serious neurological or psychiatric problems, and participated for course credit or remuneration.

Stimuli and Procedure

A series of target (T) and nontarget (N) stimulus sequences was constructed in which equal numbers (25) of four sequence types

Table 1. *Target-to-Target Interval (TTI) Defined by Combinations of Sequence Order (T = Target, N = Nontarget) and Interstimulus Interval (ISI) in Seconds*

	TTI							
ISI	1 s	2 s	3 s	4 s	6 s	8 s	12 s	16 s
1 s	TT	NT	NNT	NNNT				
2 s		TT		NT	NNT	NNNT		
4 s				TT		NT	NNT	NNNT

(TT, NT, NNT, NNNT) were presented in a random order, with the same random sequence series presented using 1-, 2-, or 4-s ISI for both auditory and visual stimuli. Table 1 portrays the combination of these conditions that defined the eight levels of TTI duration (1–16 s). An additional sequence (NNNNNT) was also presented occasionally to prevent subjects from preparing for a target stimulus after three consecutive nontargets. The target stimulus probability was always 0.40. Participants were instructed to press a button when the target stimulus was detected and to refrain from responding when the nontarget was presented. Accuracy and response time (RT) were recorded.

Auditory stimuli were 60-ms (including 10-ms rise/fall times) tones presented at 60 dB SPL through headphones. Target tone frequency was 2000 Hz, and nontarget tone frequency was 1000 Hz. Visual stimuli were white letters on a black background (5 cm wide and tall), with the target defined by "X" and the nontarget by "O" and presented for 60 ms 1 m in front of the participant on a computer screen. Order of the 1-, 2-, and 4-s ISI conditions (yielding experimental conditions of approximately 5.5, 11, and 22 min, respectively) was counterbalanced within each modality condition across gender. Rest intervals were provided between all conditions, and additional breaks given during the 2-s and 4-s conditions to reduce fatigue effects.

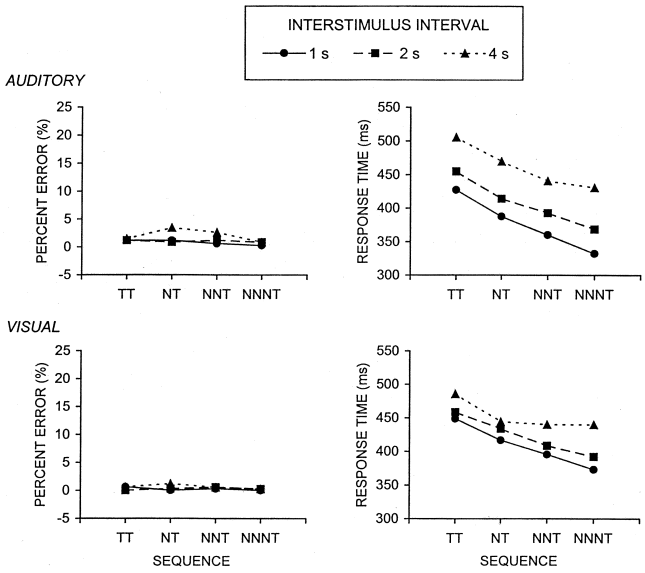

Figure 1. Mean percent error and response time as a function of stimulus (N = nontarget, T = target) sequence for each interstimulus interval and modality condition.

Recording Conditions

Electroencephalographic (EEG) activity was recorded using an electrode cap from the Fz, Cz, and Pz recording sites, referred to linked earlobes, with a forehead ground and impedance at 10 KΩ or less. Additional electrodes were placed at the outer left canthus and below the left eye to measure EOG activity with a bipolar recording. The bandpass was 0.01–30 Hz (6 dB/octave), and the EEG was digitized at 4.0 ms per point for 900 ms, with a 100-ms prestimulus baseline. Waveforms were averaged off-line, and trials on which the EEG or EOG exceeded ±100 μV were rejected. Single trial data were subjected to an EOG correction procedure to remove any remaining artifact (Semlitsch, Anderer, Schuster, & Presslich, 1986). All experimental conditions were recorded with eyes open.

Results

Waveforms for the final target stimulus of each sequence were assessed visually for each subject, with the amplitudes and latencies of the N100, P200, N200, and P300 components identified at each electrode site by locating the most positive or negative component within the latency windows of 70–250, 200–300, 250–400, and 250–600 ms, respectively. As the present study's purpose is to assess TTI effects on P300, only data from the target stimuli will be presented. In addition, only trials that received a correct response were included in the average, with at least 20 artifact-free trials obtained for each condition. Amplitude was measured relative to the prestimulus baseline, with peak latency defined as the time point of maximum positive amplitude. Statistically significant effects were assessed with Newman–Keuls means comparisons using the appropriate mean square error term; descriptions of the detailed outcomes are based on these analyses.

Task Performance

Figure 1 presents the mean error rate and RT for each ISI condition as a function of sequence from each modality. The statistical analyses of the behavioral data were made with a three-factor (4 Sequences × 3 ISIs × 2 Modalities) multivariate analysis of variance. Percent error produced no reliable sequence, ISI, or modality effects. Response time decreased as sequence length increased, $F(3,39) = 35.7$, $p < .0001$, and increased as ISI lengthened, $F(2,26) = 24.8$, $p < .0001$, with these factors yielding a significant interaction, $F(6,78) = 2.4$, $p < .05$, such that the sequence RT was less at the shorter, $p < .005$, but not at the longer, $p < .10$, ISI duration. Auditory stimuli produced larger sequence length RT effects than did visual stimuli, $F(3,39) = 2.9$, $p < .05$, with modality and ISI also interacting, $F(2,26) = 7.1$, $p < .01$, such that auditory stimuli demonstrated a larger increase in RT with increases in ISI, $p < .001$, than did visual stimuli, $p < .03$. In sum, as sequence lengthened and ISI decreased, RT also decreased and more so for the auditory compared to the visual stimulus conditions.

P300 Measurement and Analyses

Figures 2 and 3 illustrate the grand average ERP waveforms for each sequence, ISI, and electrode for the auditory and visual stimulus conditions, respectively. Figures 4 and 5 illustrate the mean P300 amplitude and latency values, respectively, from each ISI condition plotted as a function of sequence type. P300 data were analyzed with a four-factor (4 Sequences × 3 ISIs × 2 Modalities × 3 Electrodes) multivariate analysis of variance. Table 2 summarizes the results of these analyses.

P300 amplitude. Increases in stimulus sequence length produced reliable and strong increases in component size. Increases in ISI demonstrated similar effects, although this variable was less consistent than sequence length in its influence on amplitude magnitude. More important, as TTI increased, P300 amplitude increased significantly as reflected by the pattern of main and interaction effects for sequence length and ISI factors. As is typically observed, P300 was smaller for auditory than visual stimuli and increased from the frontal to parietal electrode sites.

To assess their comparative influence within each modality, separate three-factor analyses (4 Sequences × 3 ISIs × 3 Elec-

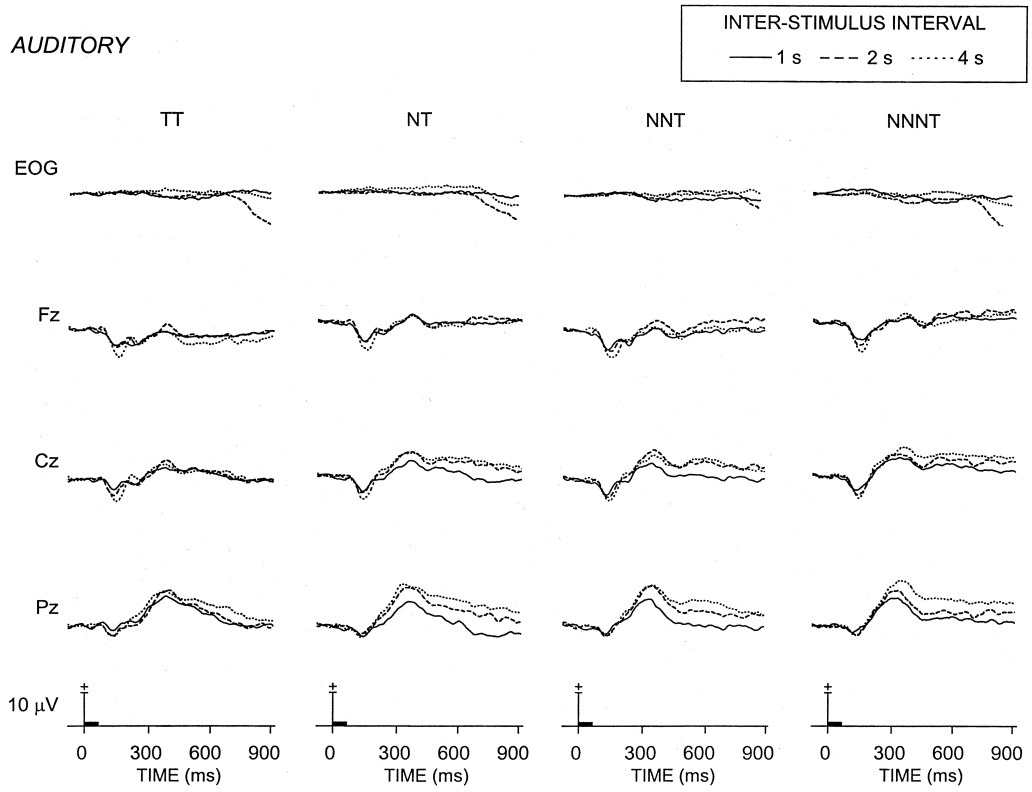

Figure 2. Grand average auditory event-related potentials for each stimulus (N = nontarget, T = target) sequence, interstimulus interval, and electrode site (n = 14).

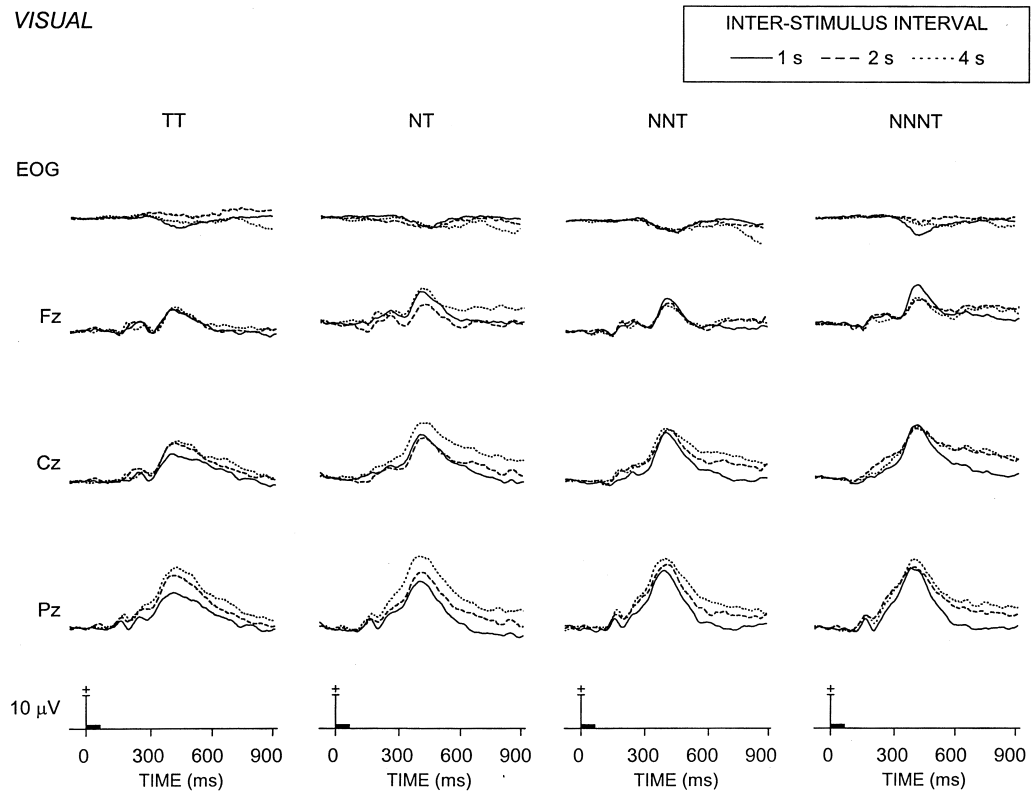

Figure 3. Grand average visual event-related potentials for each stimulus (N = nontarget, T = target) sequence, interstimulus interval, and electrode site (n = 14).

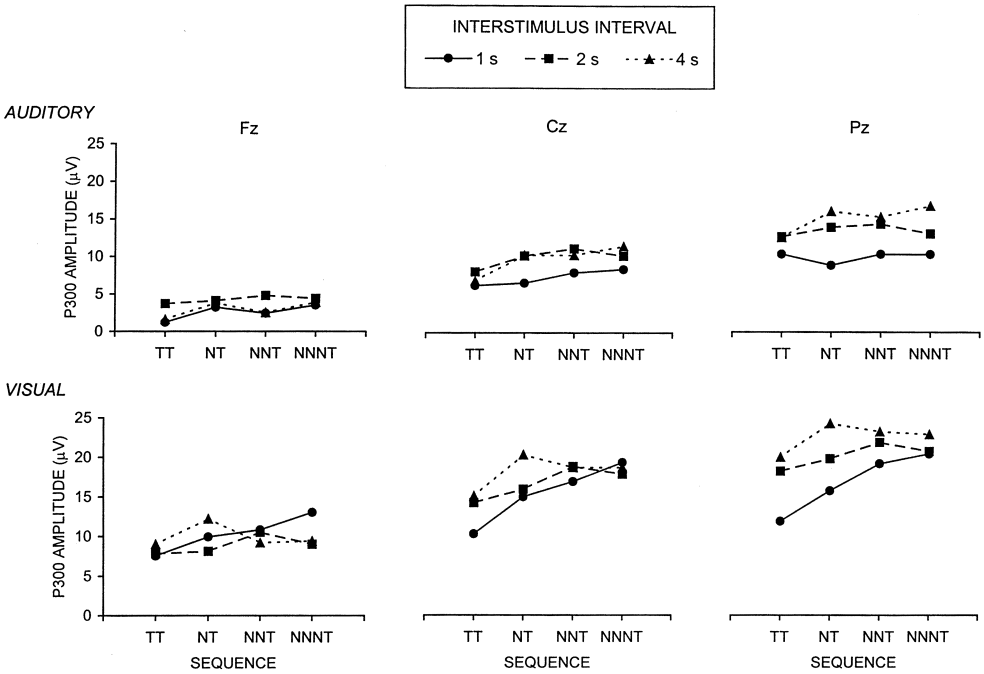

Figure 4. Mean P300 amplitude as a function of stimulus (N = nontarget, T = target) sequence for each interstimulus interval and modality condition from each electrode.

trodes) were conducted on the P300 amplitude data from the auditory and visual stimulus conditions. Auditory stimuli yielded a strong effect for stimulus sequence length, such that longer sequences produced larger component amplitudes, $F(3,39) = 4.7$, $p < .01$. However, the ISI effect was only marginally reliable, $p < .10$. Visual stimuli demonstrated a very strong stimulus sequence effect, such that longer sequences evinced larger P300 amplitudes, $F(3,39) = 12.0$, $p < .0001$, with ISI again yielding a marginal result, $p < .10$. P300 amplitudes increased as both sequence and ISI increased to produce a reliable interaction between these fac-

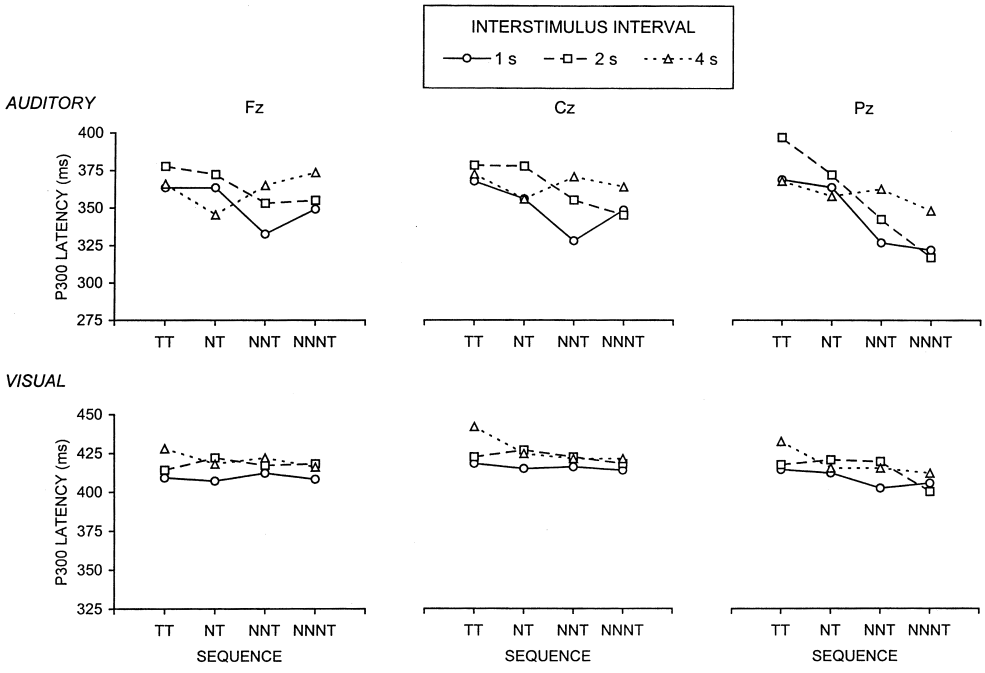

Figure 5. Mean P300 latency as a function of stimulus (N = nontarget, T = target) sequence for each interstimulus interval and modality condition from each electrode.

Table 2. *Summary of the Four-Factor (4 Sequence × 3 Interstimulus Interval × 2 Modalities × 3 Electrode) Multivariate Analysis of Variance Performed on the P300 Amplitude and Latency Data*

	Amplitude		Latency	
Factor (*df*)	*F*	*p*	*F*	*p*
Sequence (3,39)	15.2	.0001	11.1	.0001
ISI (2,26)	4.2	.05	6.2	.01
Modality (1,13)	138.7	.0001	145.8	.0001
Electrode (2,26)	44.5	.0001	9.4	.001
S × I (6,78)	2.6	.05	—	—
S × M 3,39)	—	—	4.4	.01
I × M (2,26)	—	—	—	—
S × E (6,78)	5.2	.001	12.5	.0001
I × E (4,52)	27.1	.0001	—	—
M × E (2,26)	—	—	—	—
S × I × M (6,78)	—	—	2.9	.05
S × I × E (12,156)	—	—	—	—
S × M × E (6,78)	—	—	3.4	.01
I × M × E (4,52)	—	—	—	—
S × I × M × E (12,156)	—	—	—	—

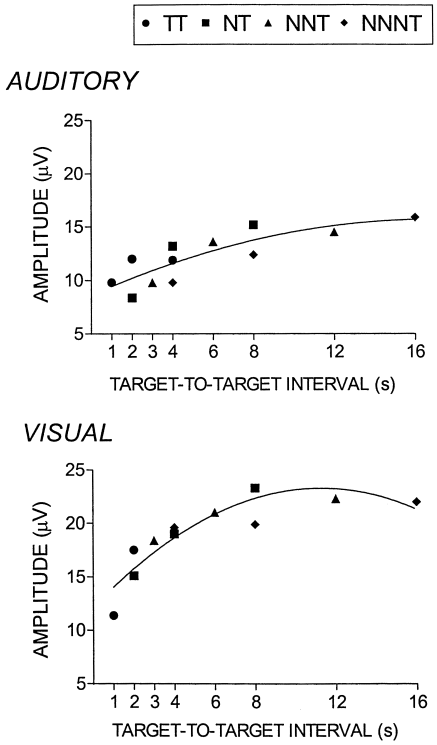

Figure 6. Mean P300 amplitude (Pz) as a function of target-to-target interval (TTI) for each stimulus (N = nontarget, T = target) sequence (see Table 1). The regression line reflects the curvilinear TTI analysis.

tors, $F(6,78) = 3.9$, $p < .002$, such that the shorter ISI conditions, $p < .02$, evinced larger amplitude increases across sequence length than the longer ISI conditions, $p > .50$. In sum, as found for the overall analysis, P300 amplitude from auditory and visual stimulus conditions increased appreciably as sequence length increased, with somewhat weaker effects for ISI observed.

Regression analyses. To evaluate their relative influence on P300 amplitude, the values of each sequence length, ISI, and TTI were used to predict mean P300 amplitude from the Pz electrode in separate linear and curvilinear regressions. Table 3 presents a summary of the analyses. Figure 6 illustrates the scattergrams for the auditory and visual stimulus conditions. The linear regression was computed by regressing P300 amplitude against TTI. The polynomial curvilinear regression includes both linear and second order curvilinear predictor variables, with the significance of the latter indicated in the table. This approach was adopted to provide a means to evaluate the relative strengths of the linear and curvilinear trends, which are correlated as indicated in Figure 6. These findings indicate that the variability of P300 amplitude is very well accounted for by TTI across both modalities, although for auditory stimuli ISI accounts for slightly more variance than TTI. Moreover, as suggested by the patterns in Figure 6, P300 is curvilinearly related to TTI, as component amplitude increases with increasing TTI up to about 6–8 s and then is relatively unaffected by further increases.

Table 3. *Summary of Linear and Second Order Polynomial Regression Analyses of Stimulus Sequence Length, Interstimulus Interval (ISI), and Target-to-Target Interval (TTI) as Predictors for Mean P300 Amplitude (Pz Electrode as Illustrated in Figure 6) from the Auditory and Visual Stimulus Conditions*

	Stimulus sequence length		Interstimulus interval (ISI)		Target-to-target interval (TTI)	
Modality (*df*)	R^2	Beta	R^2	Beta	R^2	Beta
Auditory						
Linear[a] (1,10)	.054	0.23	.686***	0.83***	.659**	0.81**
Curvilinear[b] (2,9)	.065	−0.60	.806***	−2.42*	.701**	−0.79
Visual						
Linear[a] (1,10)	.277	0.53	.486*	0.70*	.546**	0.74**
Curvilinear[b] (2,9)	.340	−1.43	.526*	−1.41	.822***	−2.02**

[a] R^2 and beta values for linear trend.
[b] R^2 values for linear and quadratic trends; beta values reflect curvilinear trend only.
*$p < .05$, **$p < .01$, ***$p < .001$.

P300 latency. Increases in stimulus sequence length produced strong decreases in peak latency. Increases in ISI generally evinced increases in P300 latency, although these effects were somewhat variable across stimulus sequence types. Component latency was shorter for auditory than visual stimulus conditions and decreased overall from the frontal to parietal electrode sites. The shortening of P300 latency with increased sequence length was more robust for auditory than visual stimulus tasks, with stronger ISI effects also obtained to yield a significant (albeit weak) three-way interaction among these factors. Sequence length, modality, and electrode yielded a three-way significant interaction such that the decrease in component latencies with sequence length tended to be more prominent over the parietal electrode within the auditory task.

Separate three-factor analyses (4 Sequences × 3 ISIs × 3 Electrodes) were performed on the P300 latency data from the auditory and visual conditions (with the electrode effects unreported). Auditory stimuli yielded a strong effect for stimulus sequence length, such that longer sequences produced shorter peak latencies, $F(3,39) = 10.3$, $p < .0001$. As ISI increased, component latency increased overall, $F(2,26) = 3.6$, $p < .05$. P300 latency became shorter with increases in sequence length but longer as ISI increased to produce an interaction, $F(6,78) = 3.2$, $p < .001$, such that decreases in peak latency occurred for the short ISI condition, $p < .005$, but not for the long ISI condition, $p > .40$. Visual stimuli demonstrated an overall decrease in peak latency as sequence length increased, $F(3,39) = 3.2$, $p < .05$, although no ISI effects were observed. In sum, as found for the overall analysis, P300 latency decreased as sequence length increased and ISI decreased, with a weaker influence of ISI obtained.

Discussion

P300 Amplitude

The present findings confirm previous stimulus sequence length effects: When ISI is constant, increasing nontarget sequence length increases P300 amplitude (Duncan-Johnson et al., 1984; Ford et al., 1982; Giese-Davis et al., 1993; Gonsalvez et al., 1995, 1999; Johnson & Donchin, 1982; Kilpelainen et al., 1999; Leuthold & Sommer, 1993; Matt, Leuthold, & Sommer, 1992; Sommer, Matt, & Leuthold, 1990; Sommer et al., 1999; Squires et al., 1976, 1977; Verleger, 1991). This outcome was observed for both auditory and visual modalities. Increasing ISIs also increased P300 amplitude, although this effect was only marginally reliable for auditory and visual stimuli over midline electrode positions. Consistent with previous research, the ISI effect was more pronounced for parietal electrode positions (Miltner, Johnson, & Braun, 1991; Polich, 1990b; Polich & Bondurant, 1997).

Increasing nontarget sequence length or ISI necessarily increases TTI, and the present results suggest that TTI provides a comprehensive account of P300 amplitude variability. This conclusion is based on the MANOVA and multiple regression analyses, which found interactive effects between sequence length and ISI as well as relatively large proportions of variance accounted for by the TTI variable. The current results were also stronger for the visual than auditory conditions, perhaps because P300 amplitude is generally more robust for visual stimuli so that it would more readily reflect TTI effects as has been found for a variety of experimental factors (Johnson, 1988; Katayama & Polich, 1998; Polich, Ellerson & Cohen, 1996; Polich & Heine, 1998). Alternatively, at shorter TTIs, visual stimuli may not generate as strong an initial memory trace as do auditory stimuli (cf. Bennington & Polich, 1999; Polich, 1990a, 1990b; Woods, Hillyard, Courchesne, & Galambos, 1980). In either case, the present findings are consistent with previous TTI outcomes and support the hypothesis that TTI underlies the P300 amplitude effects attributed to target probability, sequence length, and ISI (Curry & Polich, 1992; Fitzgerald & Picton, 1981, 1984; Gonsalvez et al., 1995, 1999; Katayama et al., 1998; Polich, 1987).

P300 Latency and Response Time

Increasing nontarget sequence length also demonstrated a reliable decrease in P300 latency for both auditory and visual stimuli, although P300 latencies were somewhat more variable across conditions and modulated by ISI and electrode locations. Response time evinced a similar pattern in the same direction: RT decreased with increases in sequence length and increased with ISI for both auditory and visual stimuli. These findings corroborate previous studies that examined sequence effects on P300 and simple RT (Gonsalvez et al., 1995, 1999; Kilpelainen et al., 1999). However, reports employing equiprobable stimuli and choice paradigms have found that RTs become longer as sequence length increases, although the P300 amplitude findings are the same as those here—as sequence length increases, P300 amplitude increases (Duncan-Johnson et al., 1984; Ford et al., 1982; Leuthold & Sommer, 1993; Sommer et al., 1990, 1999). The inconsistent RT findings most likely stem from the interaction between differing task probabilities and response requirements, as for choice RT paradigms, increasing sequence length induces a repetition of the same response several times, thereby facilitating its execution and inhibiting the competing response when repetition is discontinued. However, in a low probability oddball task, target occurrences after shorter nontarget series are unusual, thereby delaying RT, whereas targets following longer nontarget series are more typical and lead to short RTs in the absence of inhibitory effects from competing responses (cf. Johnson & Donchin, 1980, 1982; Leuthold & Sommer, 1993).

Theoretical Implications

Although the present study does not rule out the possible influence of either "sequential processing" or "temporal probability" effects, the observed influence of stimulus sequence and ISI was likely caused by the increased demands placed on system resources from the relatively rapid stimulus presentation rates used here (Fitzgerald & Picton, 1981; Gonsalvez et al., 1999; Leuthold & Sommer, 1993). These effects, in turn, may originate from limits on memory function that stem from trace decay rate (Donchin et al., 1986; Polich, 1990a; Squires et al., 1976; Woods & Courchesne, 1986). This resource limitation explanation also can account for the apparent ceiling effects observed for P300 amplitude at the longer TTIs. When TTI was greater than 6–8 s, P300 amplitude remained fairly constant as TTI increased to 16 s for both auditory and visual stimuli. With such relatively long TTIs, memory-updating operations could occur in the absence of previous processing requirements to achieve a maximal level regardless of target probability, stimulus sequence structure, or ISI (Fitzgerald & Picton, 1981; Polich, 1990b; Polich & Margala, 1997). Thus, P300 amplitude is governed by an interaction between target probability, sequence length, and ISI—all factors that directly affect TTI (Gonsalvez et al., 1999; Polich, 1999), which conspire to limit processing capacity when stimuli must be evaluated in quick succession (cf. Kantowitz, 1974; Keele, 1973; Pashler, 1994).

The likelihood that the TTI underlies P300 changes attributed to target probability, sequence, and ISI suggests that TTI affects processing of all sequentially presented stimuli. Several studies

have found that longer target sequences increased P300 amplitude to nontargets in the same way as nontarget sequences increased P300 amplitude to targets (Johnson & Donchin, 1980; Sams, Alho, & Näätänen, 1983; Squires et al., 1976, 1977; Verleger, 1987, 1991; Verleger & Berg, 1991). Oddball tasks employing more than one nontarget stimulus also produce larger P300 amplitudes to infrequent versus frequent nontargets (Courchesne, 1978; Courchesne, Hillyard, & Courchesne, 1977; Duncan-Johnson & Donchin, 1982; Katayama & Polich, 1996a; Oades, Zerbin, & Dittmann-Balcar, 1995). In sum, larger nontarget P300 amplitudes occurred when preceded by longer target sequences or extended nontarget intervals, such that P300 amplitude increases appear directly related to and controlled by the interval separating consecutive occurrences of matching (target or nontarget) stimuli.

Finally, a processing resource interpretation of TTI effects also is supported by several ERP studies that have found an interaction between task difficulty and target stimulus probability. When target items are difficult to process, P300 amplitude is reduced and probability effects are attenuated or eliminated compared to when target items are relatively easy to process even though task performance is constant across conditions (Kramer, Schneider, Fisk, & Donchin, 1986; Polich, 1987; Ruchkin, Sutton, & Mahaffey, 1987). This interaction between target probability and task difficulty again implies that P300 amplitude is sensitive to the allocation of available processing resources used to perform the eliciting task (Isreal, Wickens, Chesney, & Donchin, 1980; Kramer, Wickens, & Donchin, 1985; Wickens, Kramer, Vanasse, & Donchin, 1983). Hence, when target stimulus events occur frequently because of high target probability (short TTI), few preceding nontarget stimuli, or short temporal ISI, more resources are consumed in a given amount of time than with less frequently occurring events, and relatively small P300 amplitudes are produced. When stimulus events occur infrequently (long TTI), the P300 generation system can recover more fully and relatively large P300 amplitudes are produced. By assuming that resource limitations generally determine P300 amplitude, the obtained interaction between nontarget sequence length and ISI could have occurred for the same reasons that an interaction between task difficulty and target probability has been observed. As noted, this interpretation is consistent with a context updating or memory restoration P300 theory (Donchin & Coles, 1988; Gonsalvez et al., 1999). The present findings indicate that P300 updating processes are primarily influenced by the interval between stimuli rather than the sequence structure context.

Conclusions

The present findings confirm and extend the importance of TTI for P300 measures: The longer the time between consecutive target occurrences within the typical oddball task, the larger is P300 amplitude and the shorter is its peak latency. Although P300 generation may reflect memory-updating operations, when stimuli are presented using relatively short ISIs as occurs in most P300 studies, manipulations of target probability, sequence structure, or ISI determine the TTI and, therefore, P300 amplitude. Given that attention allocation processes are reflected by P300 size, the temporal interlude between target events appears to be a primary determinant of P300 values as it directly affects attentional resource allocation during task performance. Thus, during the relatively simple stimulus discrimination paradigm typically employed to elicit the P300, the time between target stimuli is a major influence because it governs how efficiently the neural system can process the critical information.

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