Stimulus presentation rate dissociates sequential effects in event-related potentials and reaction times

HARTMUT LEUTHOLD AND WERNER SOMMER
Department of Psychology, University of Konstanz, Konstanz, Germany

Abstract

The present study explored the impact of the stimulus presentation rate on sequential effects in event-related potentials (ERPs) and reaction times (RTs). Random series of equiprobable tones were presented at interstimulus intervals (ISIs) of 1.3, 2.1, and 2.9 s. Fast and accurate choice responses to the tones were required. Although sequential effects in RTs were stable across all ISIs, the common first-order repetition effect in P300 amplitude was only observed at the 1.3-s ISI and not at the slower presentation rates. This dissociation between the first-order effects in RTs and ERPs speaks against an explanation of both effects by a common expectancy mechanism. In addition, sequential effects were observed as early as about 100 ms after stimulus onset in the lateralized readiness potential. Together with similar sequential effects in P300 latency, this finding supports a continuous flow model of information processing.

Descriptors: Event-related potentials, P300, Reaction times, Interstimulus interval, Sequential effects, Lateralized readiness potential

Responses to stimuli in random (Bernoulli) series are strongly affected by the sequence of events that precedes a given stimulus. These sequential effects have been observed both in reaction times (RTs) and in event-related brain potentials (ERPs). We investigated the dependency of sequential effects on the stimulus presentation rate and attempted to localize these effects within the flow of information processing by means of ERP measures. The first report of sequential effects in ERPs was published by Squires, P. Wickens, Squires, and Donchin (1976). Most of the variance of the ERP amplitudes to any given stimulus could be explained by an “expectancy” factor, resulting from the a priori (global) probability of the stimulus and the exponentially decaying contribution of preceding like stimuli at specific sequential positions. Thus, a given stimulus was held to induce an expectation for its repetition, which decays over successive trials. This basic expectancy for repetitions may be modulated by the expectancy for the continuation of any alternation patterns in the preceding sequence. The observed ERP amplitudes (mainly the P300 component but also the N200 and slow wave) were inversely proportional to this expectancy variable.

These sequential effects have been replicated not only during counting, as in the study of Squires et al. (e.g., Johnson & Donchin, 1980; Squires, Petuchowski, Wickens, & Donchin, 1977), but also for prediction tasks (e.g., Chesney & Donchin, 1979; Munson, Ruchkin, Ritter, Sutton, & Squires, 1984) and when choice reactions were required (Duncan-Johnson, Roth, & Kopell, 1984; Ford, Duncan-Johnson, Pfefferbaum, & Kopell, 1982; Sommer, Matt, & Leuthold, 1990).

Although the effects of recent and remote stimuli on ERPs differ only in strength and not in direction, two types of sequential effects are distinguished for RTs. First-order effects are attributed to the immediately preceding event, whereas higher order effects are caused by events earlier in the sequence (Kirby, 1980; Soetens, Boer, & Hueting, 1985). First-order effects in RTs are dependent on the interval from the preceding response to the next stimulus presentation, the response-stimulus interval (RSI). At RSIs shorter than 500 ms, typically first-order repetition effects have been reported, that is, RTs are shorter for stimulus repetitions (R) than alternations (A). With increasing RSIs, the repetition effects decrease (e.g., Bertelson & Renkin, 1966) or even change into alternation effects, that is, shorter RTs for alternations than for repetitions (e.g., Hale, 1967; Kirby, 1976).

As for first-order effects, the RSI is also a determinant of the higher order sequential effects in RTs. At RSIs shorter than 500 ms, higher order effects appear to be due to the cumulation of the (automatic) facilitating effects of successive stimulus rep-
etition, s. For RSIs longer than 500 ms, however, there is a cost-benefit pattern (e.g., Audley, 1973). When runs of stimulus repetitions (RRRR) or stimulus alternations (AAAA) are continued, RT decreases with the length of the run. In this case, RTs are fast (benefit) as the actual event matches the expectancy of the benefit pattern (e.g., Audley, 1973). When runs of stimulus repetitions (RRRR) or stimulus alternations (AAAA) are continued, RT increases (cost) if the expectation is disconfirmed by the current event (RRRA, AAAR).

There are no published studies concerning the question of whether sequential effects in ERPs also may depend on the rate of stimulus presentation. Most ERP studies used interstimulus intervals (ISIs) between 1.3 and 1.6 s. In two prediction task studies with longer subject-controlled ISIs (Chesney & Donchin, 1979; Munson et al., 1984), the usual first-order repetition effects in P300 amplitude were found. Johnson and Donchin (1980, note 1) mentioned an unpublished study of McCarthy, Kutas, and Donchin, in which the ISI was varied from 1,000 to 3,000 ms, presumably in a counting task, and where the usual sequential effects appeared to hold at all ISIs.

Influences of the presentation rate on sequential effects in P300 amplitude might be expected because the ISI does modulate the effect of the global or prior stimulus probability (Polich, 1990a, 1990b). Together with sequential effects, prior probability is one of the factors in the Squires et al. (1976) expectancy model, and both have been subsumed under the heading of subjective probability in Johnson’s (1988) model of the P300 amplitude. Polich (1990a, 1990b) examined the relationship between the prior probability of target stimuli, the ISI, and the P300 component in auditory discrimination tasks. P300 amplitude in response to the targets was inversely proportional to prior probability only for ISIs of up to 3 s but not at longer ISIs. Miltnner, Johnson, and Braun (1991) reported an enhancement in P300 amplitude with increasing ISIs for rare targets but even more so for frequent nontargets.

Fitzgerald and Picton (1981, 1984) found increasing P300 amplitudes with increasing ISIs (0.25–4 s) but only for their target stimuli. This finding cannot be explained by habituation or refractoriness because P300 seems to be fully recovered at ISIs of less than 1 s (e.g., Woods, Courchesne, Hillyard, & Galambos, 1980). The authors suggested that the temporal probability, that is, the probability of an event within a period of time, rather than the prior probability is the main determinant of the probability effects on P300 amplitude. However, because there were no effects of the ISI for the nontargets, Johnson (1988) suggested an alternative interpretation: more value was assigned to the targets in the long ISI (low temporal probability) condition than in the short ISI condition, causing an increase of the target-elicited P300.

The present study investigated the effect of the ISI on sequential effects in RTs and ERPs. The range of ISIs explored was from the repetition of perceptual identifications up to repetitions of response executions (e.g., Rabbitt & Vyas, 1973, 1974). For longer RSIs, sequential effects are modulated by stimulus-response compatibility (Bertelson, 1963; Kornblum, 1969; Soetens et al., 1985) but not by stimulus quality (Hansen & Well, 1984). Thus, the locus of sequential effects at longer RSIs may be situated in late rather than early stages of processing.

An alternative approach toward the localization of sequential effects uses ERP measures. The latency of the P300 component is affected by stimulus discriminability but much less by stimulus–response compatibility (e.g., Magliero, Bashore, Coles, & Donchin, 1984; McCarthy & Donchin, 1981). Therefore, P300 latency appears to index the duration of stimulus evaluation but seems to be insensitive to the duration of response-related processes (e.g., Kutas, McCarthy, & Donchin, 1977). Because P300 latency shows sequential effects similar to those of RTs (Duncan-Johnson et al., 1984; Ford et al., 1982; Sommer et al., 1990), categorization processes also seem to contribute to sequential effects.

A second chronometric ERP measure to be employed here is the lateralized readiness potential (LRP). Lateralized negative potentials accompany overt responses and are maximal over the motor areas of the brain contralateral to the responding hand (Kutas & Donchin, 1980; Vaughan, Costa, & Ritter, 1968). The readiness potentials lateralizes as soon as a particular response channel (left or right hand) is activated (e.g., Coles, 1989; Gratton, Coles, Sirevaag, Erikson, & Donchin, 1988).

In measuring P300 latency and the LRP, we may be able to assess effects of the stimulus sequence at two levels of information processing, stimulus evaluation and activation of response channels.

Method

Subjects

Five women and one man (M = 26.3 years of age) participated in this study and were paid 10 DM per hour. All subjects were strongly right handed, as indicated by a laterality quotient of +66 or more in the Edinburgh Inventory for Handedness (Oldfield, 1971).

Stimuli and Apparatus

Auditory stimuli were equiprobable sinusoidal tones of 1,000 and 1,500 Hz, both of 78 dB (A) intensity and 65 ms duration, including 8 ms rise/fall times. The stimuli were presented in random order via loudspeaker in front of the subject. ISIs of 1,300, 2,100, and 2,900 ms were used, and the ISI condition was held constant within a block of 660 trials. A room ventilator provided a masking noise of 42 dB (A). Two buttons mounted 20 cm apart on a horizontal response panel served for the recording of RTs. The index fingers of the left and right hand operated the left and right keys, respectively. The subjects were instructed to press one of the keys in response to the low tone and the other key to the high tone. The relation between tone pitch and response key was counterbalanced across subjects.

Procedure

Each subject was tested in two identical sessions, 1–2 days apart. Subjects were instructed to make fast and accurate choice responses to the two tones. The ordering of the ISI conditions was completely permuted about the subjects. For any given subject, the same ordering was used in both sessions. Under each ISI condition, a total of 660 stimuli were presented. After every 165 trials each, there was a short rest.
Subjects were instructed in writing as to the experimental procedure and advised to avoid eye movements or blinks during the experiment.

Recording and Data Analysis

The electroencephalogram (EEG) from Fz, Cz, Pz, C3', and C4' (4 cm to the left and right of Cz, respectively) referenced to the right mastoid and the electrooculogram (EOG) from above the right eye were recorded with Grass E55H Ag/AgCl electrodes and Beckman Electrode Electrolyte paste. All signals were amplified with time constants of 5.5 s and low-pass filters set to 40 Hz (−3 dB attenuation, 12 dB rolloff/octave). The EOG and EEG were digitized at 100 Hz for 1,100 ms, starting 400 ms prior to stimulus onset. Any trial exceeding a range of 75 μV in the EOG channel was considered to be EOG contaminated.

In both sessions, only correct (RTs >100 ms and <800 ms) and EOG-artifact-free trials were considered. To gain resolution for the higher order sequences, the data were collapsed over pitch and pooled over sessions. This permitted a differentiation of 16 stimulus sequences, defined by the actual tone and all possible combinations of the four preceding tones.

RTs and ERPs were averaged according to the three ISI conditions, whether the presented tone repeated its predecessor or not (first-order stimulus sequence; R vs. A) and according to eight higher order stimulus sequences (RRR, ARR, RAR, AAR, RRA, ARA, RAA, AAA). The averaged ERPs were digitally low-pass filtered at 8.8 Hz (−3 dB; Ruchkin & Glaser, 1978). The average activity during a 90-ms prestimulus baseline was subtracted from each wave shape, and an area measure of the P300 component of the ERP (300–400 ms after stimulus onset) and the slow wave (500–700 ms) was taken. This voltage integral was divided by the number of time points involved, resulting in a measure representing the average amplitude during the component interval in microvolts. P300 latency was measured with the following procedure. A 2-Hz half sine-wave template was aligned with the averaged ERP wave shapes from the Pz electrode. The center of the template was moved across the ERP from 250 ms after stimulus onset to 750 ms in steps of 10 ms, and cross products between template and ERP were calculated at each lag. At the lag of the maximum cross product, P300 latency was taken as the time point in the ERP corresponding to the center of the template.

The LRP was derived by computing difference waves for the C3' and C4' electrodes between the electrode contralateral to the corresponding hand in a given trial and the ipsilateral electrode, that is, C3' – C4' for right-hand response trials and C4' – C3' for left-hand response trials. Then, the two types of difference waves were averaged within each of the 16 stimulus sequences and the ISI conditions, thus eliminating response-independent ERP asymmetries. The prestimulus LRP was quantified by measuring the average amplitude during the 380-ms interval preceding stimulus onset. For the analysis of poststimulus LRP activity, a 90-ms prestimulus baseline was subtracted from each LRP wave shape and average amplitudes were calculated for the intervals 10–50 ms, 60–100 ms, and 110–150 ms after stimulus onset.

All dependent variables were subjected to repeated measures analyses of variance (ANOVAs) with ISI and first-order and higher order stimulus sequence. For the analysis of P300 amplitude, electrode site (Fz, Cz, Pz) was included in the ANOVA as well. If any main effect or interactions were significant, the linear trends across the levels of this variable was also considered. Conservatory (Huynh-Feldt) F tests were used throughout.

Results

Table 1 presents an overview of the ANOVAs.

Reaction Times

Higher order sequences affected the RTs as a main effect \((F[7,35] = 5.4; \epsilon = .20, MS_e = 3,261.8, p < .05; F[linear: 1.5] = 8.4, MS_e = 11,590.9, p < .05)\) and in interaction with the first-order stimulus sequence \((F[7,35] = 18.0; \epsilon = .44, MS_e = 435.31, p < .001; F[linear: 1.5] = 26.1, MS_e = 11,052.9, p < .01)\); Figure 1). This result demonstrates the presence of the common sequential effects at RSIs greater than 500 ms, namely that RTs increased if runs of repetitions or alternations were discontinued by the actual stimulus as compared with the continuation of runs. There was a trend for an increase of RTs with the ISI \((M[1.3–2.9 s] = 311, 321, and 337 ms; F[2,10] = 3.4, \epsilon = 1.00, MS_e = 4,685.2, p = .07; Figure 2)\). However, no main effect of the first-order stimulus sequence was obtained, and first-order and higher order sequential effects were not modulated by the ISI.

Figure 1. Sequential effects in error rates, reaction time, and P300 amplitude and latency superimposed for the three ISI conditions. The variables are plotted separately for first-order repetitions and alternations (R and A, left and right side of each panel, respectively). The eight higher order sequences within each first-order sequence are ordered from three repetitions (RRR) to three alternations (AAA).

The choice of the right mastoid for a reference is justified because usually the P300 is symmetrically distributed and for the calculation of the LRP the choice of reference site is irrelevant.
Table 1. ANOVA Results for Error Rates, Reaction Times (RT), and the P300 Component

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Error rates</th>
<th>RT</th>
<th>Amplitude</th>
<th>Latency</th>
</tr>
</thead>
<tbody>
<tr>
<td>Electrode site (E)</td>
<td>2,10</td>
<td>1.52</td>
<td>3.43</td>
<td>32.44***</td>
<td>5.35</td>
</tr>
<tr>
<td>Interstimulus interval (I)</td>
<td>2,10</td>
<td>4.87</td>
<td>0.59</td>
<td>9.41**</td>
<td>0.88</td>
</tr>
<tr>
<td>First-order sequence (FO)</td>
<td>1,5</td>
<td>0.40</td>
<td>0.39</td>
<td>0.40</td>
<td>0.88</td>
</tr>
<tr>
<td>FO × E</td>
<td>2,10</td>
<td>3.66*</td>
<td>5.37</td>
<td>4.75***</td>
<td>2.39</td>
</tr>
<tr>
<td>Higher order sequence (HO)</td>
<td>7,35</td>
<td>1.71</td>
<td>1.71</td>
<td>8.50**</td>
<td>2.05</td>
</tr>
<tr>
<td>HO × E</td>
<td>14,70</td>
<td>0.46</td>
<td>0.46</td>
<td>2.11</td>
<td>0.88</td>
</tr>
<tr>
<td>I × FO</td>
<td>2,10</td>
<td>7.97***</td>
<td>18.00***</td>
<td>7.87**</td>
<td>7.11*</td>
</tr>
<tr>
<td>I × FO × E</td>
<td>4,20</td>
<td>4.38**</td>
<td>4.38**</td>
<td>0.81</td>
<td>1.20</td>
</tr>
<tr>
<td>P300 Amplitudes (Pz)</td>
<td>7,35</td>
<td>1.17</td>
<td>1.07</td>
<td>1.60</td>
<td></td>
</tr>
<tr>
<td>P300 Latencies</td>
<td>14,70</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*p < .05. **p < .01. ***p < .001.

**Error Rates**
The sequential effect in the RTs cannot be explained by speed-accuracy trade-off because error rates were similarly affected by the higher order sequence (Figure 1; \(F[3,33] = 3.7, \epsilon = .36, MS_e = 2.875.6, p < .05\); Table 1, source: 1 | 5) = 14.1, MS_e = 97.619.9, \(p < .05\) and in interaction with the first-order stimulus sequence \(F[3,33] = 8.0, \epsilon = .56, MS_e = 1,928.1, p < .001; F[linear: 1,5] = 19.1, MS_e = 71.713.7, p < .01\).

**Event-Related Potentials**
P300 amplitude showed a parietocentral scalp topography \(M[Fz to Pz] = 3.1, 0.9, 11.5 \mu V; F[2,22] = 32.4, \epsilon = .54, MS_e = 16,267.3, p < .01; F[linear: 1,5] = 5.9, MS_e = 24,652.0, p = .06\) and interaction with the first-order stimulus sequence \(F[7,35] = 7.9; \epsilon = .41, MS_e = 1.027.9, p < .01; F[linear: 1,5] = 16.2, MS_e = 59,956.4, p < .01; Figure 1\). P300 amplitude was larger after discontinued runs of repetitions or alternations than after the continuation of such runs, and this effect was more pronounced at the Pz electrode \(F[14,70] = 4.4; \epsilon = .51, MS_e = 88.5, p < .01\). Unlike RTs, however, the ISI modulated the first-order stimulus effect in P300 amplitude (Figures 2 and 3; \(F[2,10] = 8.5; \epsilon = .90, MS_e = 637.2, p < .01\)). At the short ISI, the familiar first-order repetition effect \(M[R] = 6.5 \mu V, M[A] = 7.7 \mu V; F[1,5] = 8.2, MS_e = 54,896.6, p < .05\) was obtained, but the effect vanished for the 2.1-s ISI condition \(8.6 \mu V vs. 8.6 \mu V; F[1,5] = 0.2\) and turned into a small but not significant alternation effect at the long ISI \(8.2 \mu V vs. 7.7 \mu V; F[1,5] = 0.8)\.

As can be seen in Figure 1, higher order sequential effects were not modulated by the ISI and showed the typical cost-benefit pattern, that is, opposite slopes for the repetition and alternation curve indicating the working of subjective expectancies. With longer ISIs, as compared with the 1.3-s ISI, an increase of about \(3 \mu V\) was obtained in P300 amplitude for the Pz electrode as indicated by the ISI × Electrode Site interaction \(F[4,20] = 9.4; \epsilon = .68, MS_e = 955.0, p < .01; Figure 3\).

Furthermore, Figure 3 reveals a parietocentral slow wave \(M[Fz to Pz] = 0.16, 3.5, 3.8 \mu V; F[2,22] = 44.7, \epsilon = .88, MS_e = 262,793.2, p < .001\) for which a first-order repetition effect \(M[R] = 2.2 \mu V, M[A] = 2.8 \mu V; F[1,5] = 21.8, MS_e = 38,339.0, p < .01\) was obtained. Contrary to the P300 amplitude, the first-order effect in the slow wave was not modulated by the ISI \(F = 1.1)\.
**P300 Latency**

P300 latency tended to be globally affected by the ISI in the same direction as RTs ($\bar{M}[I = 1.3-2.9\ s] = 325, 350, \ and\ 353\ ms$; $F[2,10] = 5.4, \ e = .59, MS_e = 43.9, p = .06$; Figure 2). Similarly, P300 latencies increased for discontinued runs of stimulus repetitions and alternations as indicated by the First-Order x Higher Order interaction ($F[7,35] = 7.1, \ e = .25, MS_e = 16.8, p < .05$; $F[linear: 1.5] = 20.6, MS_e = 181.3, p < .01$).

**Lateralized Readiness Potential**

The prestimulus LRP ($-380$ to $0\ ms$) was not affected by any of the experimental variables (see Table 2).

The poststimulus LRP (Figure 4) was affected by the first-order stimulus sequence throughout all three poststimulus time segments. LRPCs were more pronounced following stimulus alternations than repetitions ($\bar{M}[A] = -0.09, -0.20, \ and\ -0.53\ \mu V$ vs. $\bar{M}[R] = 0.06, 0.07, \ and\ -0.17\ \mu V$; $F[1,5] = 19.5, 62.1, \ and\ 7.9, MS_e = 30.4, 32.0, \ and\ 471.4, p < .01, p < .001, \ and\ p < .05$, respectively; Figures 4 and 5).

Further, the higher order stimulus sequence as a main effect ($F[7,35] = 4.0, e = 1.00, MS_e = 324.0, p < .01; F[linear: 1.5] = 11.1, p < .05$) and in interaction with the first-order stimulus sequence (Figure 5; $F[7,35] = 2.7, \ e = 1.00, MS_e = 79.2, p = .05; F[linear: 1.5] = 15.8, p < .01$) began to influence the LRP at the 60-100-ms time segment. Even larger stimulus sequence-dependent LRP amplitude differences were seen during the 110-150-ms time segment; here, the repetition and alternation curves revealed opposite slopes as indicated by the First-Order x Higher Order interaction ($F[7,35] = 8.2, e = 1.00, MS_e = 86.5, p <

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Table 2. ANOVA Results for the Lateralized Readiness Potential

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>-380-0</th>
<th>10-50</th>
<th>60-100</th>
<th>110-150</th>
</tr>
</thead>
<tbody>
<tr>
<td>Interstimulus interval (I)</td>
<td>2,10</td>
<td>1.97</td>
<td>4.79</td>
<td>0.25</td>
<td>1.56</td>
</tr>
<tr>
<td>First-order sequence (FO)</td>
<td>1.5</td>
<td>0.00</td>
<td>19.45*</td>
<td>62.09**</td>
<td>7.93*</td>
</tr>
<tr>
<td>Higher order sequence (HO)</td>
<td>7.35</td>
<td>1.13</td>
<td>1.21</td>
<td>3.97**</td>
<td>3.83**</td>
</tr>
<tr>
<td>I x FO</td>
<td>2.10</td>
<td>3.34</td>
<td>0.84</td>
<td>3.82</td>
<td>0.22</td>
</tr>
<tr>
<td>I x HO</td>
<td>14.70</td>
<td>2.01</td>
<td>1.07</td>
<td>0.93</td>
<td>0.71</td>
</tr>
<tr>
<td>FO x HO</td>
<td>7.35</td>
<td>2.86</td>
<td>1.59</td>
<td>2.66*</td>
<td>8.23***</td>
</tr>
<tr>
<td>I x FO x HO</td>
<td>14.70</td>
<td>1.57</td>
<td>1.05</td>
<td>0.95</td>
<td>1.76</td>
</tr>
</tbody>
</table>

*p < .05, **p < .01, ***p < .001.
Presentation rate and sequential effects

1.3 s
2.1 s
2.9 s

Figure 4. Wave shapes of the lateralized readiness potential averaged for the three ISI conditions and for first-order stimulus repetitions (solid line) and alternations (broken line). Tick marks denote intervals of 100 ms.

Poststimulus LRP

Figure 5. Sequential effects in the poststimulus lateralized readiness potential (LRP) for the three time segments, plotted separately for first-order repetitions and alternations (R and A, left and right side of each panel, respectively). The eight higher order sequences within each first-order sequence are ordered from three repetitions (RRR) to three alternations (AAA).

Discussion

The present study examined the influence of stimulus presentation rate on sequential effects in RTs, the P300 component, and the lateralized readiness potential. Confirming previous reports, the higher order sequential effects in RTs, P300 amplitudes, and latencies resembled each other (Duncan-Johnson et al., 1984; Ford et al., 1982; Sommer et al., 1990). All higher order effects observed in the present study were unmodulated by the ISIs. Their similarity across variables is compatible with the notion of a common underlying expectancy mechanism. The stability of sequential effects in P300 across an ISI range of 1.3–2.9 s indicates that they are determined by structural aspects of the stimulus sequence rather than by a purely time-dependent memory decay, as proposed by Fitzgerald and Picton (1981).

Although the higher order sequential effects in P300 amplitude were unaffected by the ISI, the familiar first-order repetition effect was only obtained at the short ISI (e.g., Duncan-Johnson et al., 1984; Ford et al., 1982; Johnson & Donchin, 1980). This effect was completely abolished for the 2.1-s ISI, and there was a nonsignificant tendency toward an alternation effect at the long ISI.

This ISI effect appears to be specific for the processes reflected in the P300 component, because the first-order repetition effect in the subsequent slow wave is unaffected by the ISI. The stable first-order effect in the slow wave may be interpreted as a sign of increased task demands under the condition of stimulus and/or response alternation (Matt, Leuthold, & Sommer, 1992; Roth, Ford, & Kopell, 1978).

The contrast of our results with reports of a first-order repetition effect in P300 amplitude at longer ISIs (Chesney & Donchin, 1979; Munson et al., 1984) may be due to prediction tasks used in those studies, which may have induced a different mode of processing. Whereas there are few demands on the quality of performance in prediction tasks, appropriate motor responses must be selected and executed and response speed and accuracy must be monitored in reaction time tasks (cf. Donchin, Kubovy, Kutas, Johnson, & Herning, 1973).

The ISI dependency of the first-order effect in our data fits with the disappearance of the probability effect for targets at longer ISIs, as reported by Polich (1990a, 1990b). Polich suggested that the increase in P300 amplitude with the ISI is due to the recovery of processing resources specifically for targets. This explanation, however, is unsuitable for the present data because it would require the unlikely assumption of a resource pool specific for alternations. Similarly, our ISI effect on P300 amplitude cannot be attributed to changes in subjects' strategies of information processing because the first-order effects in RTs and P300 latencies and in error rates were unaffected by the ISI.

A parsimonious explanation of the ISI effect on P300 amplitude may be provided within the framework of Donchin's context-updating hypothesis (Donchin & Coles, 1988). The context-updating hypothesis states that P300 amplitude is proportional to the amount of the revision of a mental model or schema. If one assumes that each stimulus is represented by such a schema and that schemata decay over time, the representation for a stimulus that has just been presented, that is, a repetition, should be available to a greater degree than representations of...
stimuli that have not been shown on the immediately preceding trial (alternations). Thus representations for repetitions should require less updating than should representations for alternations and therefore should elicit smaller P300 amplitudes. This effect should be more pronounced for short ISIs, because at long ISIs the representations for repetitions also may have decayed to some floor level and may therefore require the same amount of updating as the representations of alternating stimuli. This decay may explain why the P300 amplitude for stimulus repetitions grows as large as that for alternations with increasing ISI.

The dissociation between first-order effects in RTs and P300 amplitude by the stimulus presentation rate is in line with similar dissociations reported previously. Sommer et al. (1990) found a stable first-order alternation effect in RTs throughout four experimental sessions, while the first-order repetition effect in P300 amplitude gradually disappeared over sessions. Matt, Leuthold, and Sommer (1992) found that only the first-order effects in RTs but not in P300 amplitudes could be modulated by voluntary expectancies for either repetitions or alternations. When first-order effects in P300 amplitude and RTs can be dissociated, a common expectancy explanation for both effects is clearly unsuited. On the basis of these findings, Matt et al. (1992) suggested that the first-order effect in P300 amplitude is generated by an automatic and largely uncontrollable process. In contrast, the processes responsible for first-order RT effects at long RSIs may be under the control of the subjects' conscious expectancies.

The present study also attempted to localize sequential effects within the flow of information processing by means of ERP measures. The prestimulus LRP yielded no evidence for specific activation of motor cortices in advance of the stimulus. However, there were clear first-order alternation effects in the poststimulus LRP as early as 10–50 ms after the stimulus. Therefore the motor cortex corresponding to the responding hand must have been activated earlier after stimulus alternations than after repetitions. The very early onset of these differential motor cortex responses may be explained in two ways. The results from the evaluation of stimulus alternations may have been available to the motor cortex earlier than those for stimulus repetitions. However, one would also expect shorter P300 latencies—supposedly reflecting stimulus evaluation time—for the alternations, which was not the case. Alternatively, following a response the executing motor cortex may be temporally inhibited and the mere presentation of any stimulus—repetition or alternation—may activate the motor cortices of both hemispheres. In this case, responses to stimulus alternations are mediated by a relatively uninhibited motor cortex, yielding more negative LRPVs than responses to repetitions.

Higher order effects in the LRP appear somewhat later than the first-order effects, but they are still surprisingly early, with first signs between 60 and 100 ms after stimulus onset. The finding of similar sequential effects in P300 latency indicates that the sequential effects in motor preparation (LRP) are secondary to those in stimulus evaluation. However, the early onset of sequential effects in the motor preparation stage supports the concept of a continuous flow model of information processing where partial information is transmitted to subsequent stages of processing.

REFERENCES


Presentation rate and sequential effects


(Received November 7, 1991; accepted December 3, 1992)
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