Localization of temporal preparation effects via trisected reaction time

STEVEN A. HACKLEY, ANDREA SCHANKIN, ANDREAS WOHLSCHELAEGER, AND EDMUND WASCHER

Abstract

Previous research using nonchronometric measures in humans and animals has shown that warning signals can influence stages of processing throughout the reaction time (RT) interval. However, latency measures indicate that warning effects on RT are not due to the speeding of motor processes, at least not late ones. To better isolate the chronometric effects of temporal preparation, we used lateralized event-related potentials to divide mean RT into three time segments. Foreperiod duration had only a small, nonsignificant influence on the first and last segments (early visual and late motor processes, respectively). The chronometric effect was mainly restricted to the middle interval, which extended from onset of the N2pc component to onset of the lateralized readiness potential. The results imply that temporal preparation primarily speeds late perception, response selection or early motor processes.

Descriptors: Mental chronometry, Reaction time, Event-related potential, Attention, Vision

Efforts to determine the first point in time at which overlaid waveforms for potentials evoked by attended and unattended stimuli differ has played an important role in our understanding of selection based on stimulus attributes such as location, pitch, and color (Hillyard, Hink, Schwent & Picton, 1973; Mangun, 1995). For example, the fact that effects of spatial attention on event-related potentials (ERPs) can occur as early as about 15 ms for audition and 90 ms for vision argues against the late selection view that perceptual analysis is fully automatic (for review, see Hackley, 1993).

Unfortunately, this approach is unlikely to work in the case of temporal attention. For one thing, the effects of selectively attending to a particular point in time appear to lie mainly within decision and motor processes (Coull & Nobre, 1998; Hackley & Valle-Inclán, 2003), processes that are not assessed by modality-specific evoked potentials. Another problem is that it is difficult to precisely identify the onset of warning effects for potentials evoked by the imperative stimulus in a warned reaction time (RT) task because these components are superimposed on the offset of the contingent negative variation (CNV), which varies dramatically across conditions (for review, see Correa, Lupiáñez, Madrid & Tudela, 2006).

Considering the difficulty of comparing evoked potentials that ride upon a rapidly shifting baseline, it is not surprising that the results from previous studies of temporal attention have been inconsistent (Correa et al., 2006). Subtraction components should be relatively immune to shifting baselines and to contamination by extraneous sources. The only study of temporal attention effects to date that examined a subtraction component failed to observe any effects (Rudell & Hu, 2001, studying the lexical “Recognition Potential”).

Here we take a different approach toward chronometrically localizing the effects of temporal attention. We measured the onset of two subtraction components, one perceptual and one motor, that were extracted from the ERP. Specifically, we recorded the N2pc (pc = posterior, contralateral relative to a visual target) and the lateralized readiness potential (LRP). The onsets of these components were then used as landmarks to partition mean RT into three time segments. Our goal was to determine which of these three segments is shortened by temporal preparation. This methodology was independently developed by Ruge, Stoet, and Naumann (2006), who used it to chronometrically localize the effects of a task switching set.

Unlike some ERP components, the N2pc and LRP have well-defined cognitive and neuroanatomical correlates. The N2pc occurs at around the time of the second major negative deflection in the visual evoked potential, with maximum amplitude at a posterior site (PO7/8) contralateral to the hemifield containing...
the target in a visual search task (Luck & Hillyard, 1994; Wascher, 2005). Hence, occurrence of the N2pc indicates that the participant has perceptually analyzed the display sufficiently to determine the side of the display in which the target lies. Dipole modeling studies suggest a single generator for the N2pc, one that lies within lateral extrastriate cortex (Hopf, Boelms, Schonenfeld, Luck, & Heinze, 2004). The time interval extending from stimulus onset until N2pc onset—a dependent measure in the present study—is known to be sensitive to target salience or discriminability and number of distractors (Wascher & Wauschkuhn, 1996; Wolber & Wascher, 2005).

The LRP is a surface-negative waveform with maximum amplitude over motor cortex. It is extracted from the ERP by subtracting potentials recorded at the electrode ipsilateral to the planned response from those recorded at the corresponding contralateral electrode. Occurrence of the LRP indicates that the participant has chosen which hand to respond with. Dipole modeling studies indicate that the primary generator lies within the hand area of M1, with additional contributions from nearby premotor and somatosensory cortices (Boetzl, Plendl, Paulus, & Scherg, 1993). The time interval extending from LRP to response onset is known to be sensitive to response probability, response complexity, and key press force (Masaki, Wild-Wall, Sangals, & Sommer, 2004; Mueller-Gethmann, Rinkenaus, Stahl, & Ulrich, 2000; Smulders, Kok, Kenemans, & Bashore, 1995).

Although trisection of the RT interval has not previously been employed to study temporal preparation, seven previous experiments partitioned mean RT based on LRP onset (Hackley & Valle-Inclán, 1998, 1999; Mueller-Gethmann, Ulrich, & Rinkenaus, 2003, Experiments 1 and 2; Smulders et al., 1995; Tandonnet, Burle, Vidal, & Hashbroucq, 2003, 2006; for review, see Hackley & Valle-Inclán, 2003). Using a variety of methods to manipulate temporal preparation, six of these studies yielded consistent evidence that this form of attention has no effect on the duration of the LRP-to-response (LRP-R) interval. The seventh study did obtain a foreperiod effect on the LRP-R interval, but the effect was small and its variation as a function of foreperiod duration differed from that of RT (Mueller-Gethmann et al., 2003, Experiment 1). Converging evidence for the absence of temporal preparation effects on the duration of late motor processes has recently been obtained using a wholly unrelated method, the psychological refractory period paradigm (Bausenhart, Rolke, Hackley, & Ulrich, 2006).

Based on these findings, we predict that the LRP-R interval will not be modulated by foreperiod duration. The best existing data regarding early visual processing, that of Rudell and Hu (2001), suggest that null effects are also likely for the first of the three time segments. The main chronometric effect of foreperiod duration, therefore, is predicted to lie within the middle interval.

Methods

Participants

Thirty-one paid volunteers (6 men, 25 women; all right-handed; age 20–31, M = 25.5 years) constituted the final sample. The data from an additional participant (male) were rejected from the psychophysiological analyses because he did not exhibit a measurable LRP. Nearly all subjects had participated in previous visuo-motor experiments at this laboratory.

Procedure

Recent work on temporal attention has been dominated by a methodological in which a pre-cue on each trial either validly or invalidly predicts the imperative’s time of arrival (e.g., Coull & Nobre, 1998). Although pre-cue manipulation studies have led to many valuable insights, we chose instead a traditional fore-period-duration manipulation. This allows continuity with the 125-year-old literature on warning effects (which began with Wundt, 1880, described in James, 1890) and permits comparison with similar conditioning, CNV, and reflex modulation studies (Hackley & Valle-Inclán, 2003).

In the present study, there were two blocks of 260 trials in which a short, easy-to-estimate interval of 600 ms separated the onset of the warning and imperative stimuli. During the other two balanced blocks of trials, a longer and hence more difficult-to-estimate interval was used, 3000 ms. The imperative for the choice RT task was the Roman letter “A” or “B” (0.5 x 0.6 in size), randomly presented 1” to the left or right of fixation. As in some previous N2pc studies at this laboratory (Wascher & Wauschkuhn, 1996) the distractor consisted of three horizontal lines, similar to the Greek letter Ξ, presented at the mirror-image location of the opposite hemifield.

With only a single distractor and target, this is certainly an austere search task. However, the paradigm yields N2pc components that are similar in morphology, amplitude, latency, topography, and functional correlates to the N2pc waveforms obtained with more complex tasks (Wascher & Wauschkuhn, 1996).

The warning signal in our study was a 400-ms vibration delivered simultaneously to the left and right ankles. The task was to press the upper key with the thumb of the right hand when they saw an “A” or the lower key with the left thumb when they saw a “B.” As expected, RTs were slower in the 3000- than in the 600-ms condition (M = 83 ms, SD = 43, z[31] = 5.65, p < .001; RT for the 600-ms condition averaged 475 ms, SD = 89 ms). This difference was not due to a speed-accuracy trade-off because errors were more common in the long- than in the short-foreperiod condition (M = 0.030 and 0.023, respectively, z[31] = 14.49, p < .001).

As described in the introduction, the goal of our psychophysiological analysis was to partition this serviceably large behavioral effect—83 ms—into three time segments that roughly correspond to early perception, decision, and late motor stages. The sizable behavioral effect (83 ms), sample size (31 participants), and number of trials per condition (520) would be expected to yield stable parameter estimates and a considerable power to reject the null hypothesis. In addition, a follow-up study (N = 12) was conducted to confirm all visual ERP results. The methods were identical except that subjects responded using two fingers of the same hand, which precluded chronometric LRP analyses. Behavioral results were similar, with a 71-ms difference in RTs across conditions, F(1,12) = 52.75, p < .001, and a higher error rate for the long-foreperiod condition (M = 0.037 and 0.021 for the 3000- and 600-ms foreperiods, respectively; Wilcoxon’s T = 6.0, p < .005).

Recordings and Analyses

Surface electroencephalograms (EEG) and electrooculograms (EOG) were recorded using 64 Ag-AgCl electrodes embedded in an elastic cap. The recording bandpass was DC to 200 Hz, with a 50-Hz notch filter, a digitization rate of 500 Hz, and off-line low-pass filtration at 8 Hz. The 8-Hz cutoff was designed to yield a

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smooth leading edge, thereby enhancing the measurement of onset latency. Ocular artifacts were corrected via a standard subtraction procedure (Gratton, Coles, & Donchin, 1983). Trials with other artifacts (e.g., motion artifacts, amplifier saturation) were removed prior to signal averaging. The N2pc was largest at the PO7/8 electrode sites and the LRP at FC3/4. Only data from these electrode pairs are reported, but findings were similar at nearby sites, and the scalp topographies were comparable to those of previous N2pc and LRP studies.

Lateralisation components were extracted for each participant using the standard, double-subtraction method that gives these measures their well-known invulnerability to volume-conducted contamination from extraneous sources. Specifically, the N2pc was calculated by first subtracting the signal-averaged waveform at PO7 from that at PO8, and then subtracting the resulting average for trials with right-hemifield targets from those with left-hemifield targets. Similarly, LRP was computed by subtracting FC3 from FC4, and then left-hand response trials from right-hand trials. Note that the N2pc and LRP were computed across orthogonal sets of trials, in that the hand responding to the letter was independent of target hemifield. Consequently, the N2pc and LRP should be minimally vulnerable to contamination from one another.

The effects of foreperiod on onset latencies measured at 50% of peak amplitude were assessed using jackknife t tests on the grand average waveforms (Ulrich & Miller, 2001). Similar results were obtained with other methods, including regression-based estimates of absolute onsets for individual subjects and conditions. Supplementary evidence regarding the locus of foreperiod effects was obtained by measuring the peak latencies of N1 and P3 from the presubtraction ERP waveforms.

Results

The three time intervals were estimated by (1) the onset latency of the N2pc, (2) the onset latency of the stimulus-locked LRP minus that of the N2pc, and (3) the response-locked LRP-to-key-press interval. As shown in Figure 1, the interval from stimulus onset until N2pc onset was not affected by foreperiod duration, $F(1,30) = 0.077, p = .783; M_{600} = 205$ ms, $M_{3000} = 209$ ms, $SD = 24.5$. (These time measurements are based on individual subject’s waveforms rather than the grand average). A small effect can be seen for the peak latency, but this difference did not approach significance. The larger amplitude in the short-foreperiod condition was statistically significant, $t(30) = 2.494, p < .02$. Null effects for latency were replicated in the follow-up study. The N2pc waveforms in that study (not shown) overlapped perfectly until 180 ms, or 53% of peak amplitude (mean difference at 50% of peak = 1.6 ms, $SEM = 9.8$). There was no difference in N2pc amplitudes across conditions.

Measurements of the N1 visual evoked potential were suggestive of an effect of foreperiod duration on perceptual analyses. N1 latency appeared to be shorter in the 600-ms condition by about 8 ms, $t(30) = 3.925$ and 3.234 at O1 and O2, respectively, $ps < .005$; see Figure 2. Base-to-peak amplitudes also appeared to be larger in that condition, $t(30) = 1.977$ and 2.098 at O1 and O2, $ps < .06$ and .05. The P3 was larger following long foreperiods but faster following short foreperiods, $t(30) = 6.262$ and 4.354, respectively, $ps < .001$. Each of these effects was replicated in the follow-up study (N1 latency difference at O1 and O2, respectively, $M = 9$ and 6 ms, $t[11] = 3.0$ and 2.4, $ps < .05$; N1 amplitude differences, $M = 0.9$ and 1.1 $\mu V, t[11] = 2.6$ and 2.7, $ps < .05$; P3 amplitude difference at the P3 electrode, $M = 2.3, t[11] = 3.0, p < .02$). As noted earlier, presubtraction evoked potentials are not as trustworthy as lateralisation components because they are superimposed on the offset of the CNV and, in the case of P3, sensorimotor cortex potentials associated with the key-press response.

Consistent with extensive prior research cited in the introduction, the LRP-R interval was not affected reliably by temporal attention, $F(1,30) = 1.252, p = .272; M_{600} = 111$ ms, $M_{3000} = 122$ ms, $SD = 38.5$. Figure 3B shows the response-locked averages for LRP, in which zero on the X axis indicates key-press onset. In contrast, the time from letter onset until stimulus-locked LRP onset was significantly reduced in the short foreperiod condition, $F(1,30) = 77.021, p < .001$ (Figure 3A, in which the origin of the X axis indicates stimulus onset). Based on N2pc and stimulus-locked LRP measurements, the middle time interval is estimated at 104 and 160 ms ($SD = 49$), respectively, for the short- and long-foreperiod conditions.

Discussion

The principal contribution of the present study was to show that the effect of temporal attention on RT lies mainly within an
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respectively). Cortex potentials (13 ms and 4 ms in their 2003 and 2006 studies, respectively) account for only 4 and 11 ms of the RT effect, respectively (1993). This new approach to mental chronometry has much to recommend it. In comparison to the methods of Donders (1868/C0 1/16–7 ms for the first segment and 11 45–79 ms) could be considered the measure of perceptual sensitivity (e.g., Rolke & Hoffman, in press). Electrophysiological and neuroimaging data are congruent. An amplitude effect on at least one modality-specific ERP was obtained in five of the seven studies reviewed by Correa, Lupiñañez, and Tudela (2005). Both positron emission tomography and functional magnetic resonance imaging have documented temporal attention effects within visual cortical areas (e.g., Coull & Nobre, 1998).

Effects of temporal attention on nonchronometric measures of late motor processes are also well established. Measures have included regional hemodynamic activity (e.g., Coull & Nobre, 1998), spinal reflexes (e.g., Scheirs & Brunia, 1985), transcranial magnetic pulse stimulation (Hasbroucq et al., 1999), response force (Ulrich & Mattes, 1996), and Laplacian amplitudes of unilateral motor cortex potentials (Tandonnet et al., 2003, 2006).

In contrast to amplitude measures, findings for latency measures of visual and late motor processes have been inconsistent and of small magnitude. Only one of the seven studies reviewed by Correa and colleagues (2006) obtained a latency effect for an early, modality-specific evoked potential (P1 in this case). Similarly, only one of the seven LRP experiments concerning warning effects found an effect on the LRP-R interval (Mueller-Gethmann et al., 2000, Experiment 1) and, as noted earlier, this modulation was not systematically related to the foreperiod-duration effect on RT. Tandonnet and colleagues (2003, 2006) have reported that foreperiod duration influences the response-locked onset of unilateral motor cortex potentials. However, the effect size was small in both studies (13 and 4 ms, as noted above) and, judging from the published waveforms, might be specific to the particular measurement algorithm they employed.

Because the visual system is highly parallel, a potential criticism of our study is that the N2pc might reflect activity within a pathway that does not determine RT. For example, the N2pc might solely index a process within the dorsal, action-based visual stream, whereas temporal preparation might influence the speed of processing within the ventral, object-recognition visual stream. However, N2pc latency has been found to correlate highly with RT in a number of studies (e.g., Wolber & Wäschler, 2005). Furthermore, the subtraction component studied by Rudell and Hu (2001), the lexical recognition potential, almost certainly originates in the ventral stream. The presence versus absence of a warning signal exerted no effect whatsoever on the amplitude, latency, or morphology of that component.

Given that the locus of chronometric effects lies mainly within the middle time segment (about 200–350 ms after stimulus onset), what are the likely cognitive correlates? We know that this time interval extends from the point at which subjects have determined which side the target is on (N2pc) until the point at which they have chosen which hand to respond with (LRP). Logically, this interval could include late perceptual analyses, response selection, and early motor processes. Neuroimaging studies may help to resolve this question (e.g., Hackley et al., 2007).

The trisection approach employed in this study was independently developed by Naumann’s group (Ruge et al., 2006) and is an extension of the bisection method of Osman and Moore (1993). This new approach to mental chronometry has much to recommend it. In comparison to the methods of Donders (1868/intermediate time segment. To be precise, 67% of the 83-ms RT effect (i.e., 56 ms; 95% confidence interval = 45–79 ms) could be accounted for by modulation of the narrow time window extending from the onset of N2pc at about 200 ms until onset of the LRP at about 350 ms. Numerically, the first and third segments accounted for only 4 and 11 ms of the RT effect, respectively (95% confidence intervals: –16–7 ms for the first segment and 1–21 ms for the second).

Note that these estimates are not expected to exactly sum to the RT effect (4 + 56 + 11 = 71, not 83 ms) due to differences in component morphology, thresholding between stages, and choice of measurement algorithm. The small size of the N2pc latency effect (4 ms at 50% of peak amplitude) is consistent with the apparent modulation of N1 peak latency (8 ms). Similarly, the small, nonsignificant effect on the LRP-R interval (10 ms at 50% of peak amplitude) is comparable to the magnitude of the effect reported by Tandonnet and colleagues for unilateral motor cortex potentials (13 ms and 4 ms in their 2003 and 2006 studies, respectively).

Although the trisection analysis generated null effects for the first and third segments, it is indisputable that warning signals exert some sort of influence on early perceptual and late motor processes. Visual psychophysics research has shown that temporal attention enhances d′, a relatively pure measure of perceptual sensitivity (e.g., Rolke & Hoffman, in press). Time-locking and neuroimaging data are congruent. An amplitude effect on at least one modality-specific ERP was obtained in five of the seven studies reviewed by Correa, Lupiñañez, and Tudela (2005). Both positron emission tomography and functional magnetic resonance imaging have documented temporal attention effects within visual cortical areas (e.g., Coull & Nobre, 1998).

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Figure 3. A: Stimulus-locked lateralized readiness potentials (sLRP) at fronto-central electrode sites (FC3/4) averaged across 31 participants, as a function of short and long foreperiods (600 and 3000 ms, respectively). In stimulus-locked averaging, the EEG is segmented with respect to stimulus onset; hence, the origin of the abscissa indicates stimulus onset. B: Grand average, response-locked, lateralized readiness potentials (LRP) overlying frontocentral cortex (FC3/4) as a function of short and long foreperiod (600 and 3000 ms, respectively). In response-locked waveforms, zero on the X axis indicates response onset.
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McCarthy, G., & Donchin’s (1981) method. We believe that the trisection method merits consideration for application to a broad array of problems in cognitive science.


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