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Dissociation of brain ERP topographies for tonal and phonetic oddball tasks

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Abstract

ERP topographies for 30 scalp electrodes were examined in 26 healthy right-handed volunteers during oddball tasks (20% targets) using binaurally presented consonant-vowel syllables or complex tones. Response hand was counterbalanced across participants. Both window averages and a principal components analysis (PCA) with Varimax rotation revealed task-related (tonal/phonetic) hemispheric asymmetries for N2, early P3, and particularly for N2-P3 amplitude. In the tonal task, N2 was maximal over right lateral-temporal regions, and early P3 over right medial-parietal regions. For the phonetic task, N2 was maximal over the left lateral-parietal regions, and late P3/N3 over left medial-parietal regions. A response-related frontal negativity (N3) interacted with task-related asymmetries in an unbalanced fashion. The distinct, asymmetric N2 and P3 topographies for tonal and phonetic tasks presumably reflect differential involvement of cortical structures in pitch (right frontotemporal) and phoneme (left parietotemporal) discrimination.

Descriptors: ERP asymmetry, N2 (N200), P3 (P300), Tonal/phonetic oddball, Principal components analysis (PCA), Response hand

Event-related potentials (ERPs) as diverse as mismatch negativity, P1, P2, N2, P3, slow wave, and stimulus preceding negativity have been reported to be greater over the right than left hemisphere during a variety of nonverbal tasks, for example, matching and memorizing of faces (Barrett, Rugg, & Perrett, 1988; Schweinberger & Sommer, 1991), processing emotionally relevant stimuli (Kayser et al., 1997), estimation of time (Brunia & Damen, 1988), auditory spatial discrimination (Bruder et al., 1992), selective attention to pure tones (Giard, Perrin, Pernier, & Bouchet, 1990), or dichotic listening to complex tones (Tenke, Bruder, Towey, Leite, & Sidtis, 1993). In contrast, tasks involving the processing of linguistic stimuli have shown greater amplitudes of N1, P3 or slow wave over the left hemisphere (reviewed by Molfese, 1983), for instance, during reading (Curran, Tucker, Kutas, & Posner, 1993; Nelson, Collins, & Torres, 1990; Neville, Kutas, & Schmidt, 1982), or dichotic listening to consonant-vowel syllables (Ahonniska, Cantell, Tolvanen, & Lyytinen, 1993) or digits (van de Vijver, Kok, Bakker, & Bouma, 1984). Although hemispheric asymmetries of ERPs to phonetic stimuli, such as /da/ or /ta/, appear to evolve within a few months of maturation (e.g., Novak, Kurtzberg, Kreuzer, & Vaughan, 1989), it is unclear to what extent the direction and topography of these lateral asymmetries are uniquely related to linguistic processing rather than to other acoustic stimulus features (see reviews by Molfese, 1983; Simos, Molfese, & Brenden, 1997). Taken together, these findings suggest that hemispheric asymmetries of ERPs are dependent on specific cognitive task demands requiring different hemispheric processing resources (see reviews by Allen, 1983; Friedman & Polson, 1981), with greater amplitudes over the hemisphere that is predominantly involved in attending to and discriminating the stimuli.

Few studies have, however, compared ERP asymmetries for verbal and nonverbal tasks in the same individuals. Employing a semantic categorization task in a divided visual field paradigm, Kok and Rooyakkers (1986) found contrasting late positive asymmetries for words (left hemisphere larger than right) and pictures of objects (right larger than left), although these effects were restricted to ipsilateral (indirect) rather than contralateral (direct) hemispheric stimulations. Using a visual matching paradigm with either letter strings or nonverbal graphical patterns, Gevins, Cutillo, and Smith (1995) reported several topographic differences between the two conditions for both stimulus encoding and decoding. For verbal processing, they reported larger late negative ERP components (e.g., N470) over the left temporal region, whereas processing of nonverbal patterns was associated with larger late positive ERP components (e.g., P475) over right frontal and temporal regions. As these asymmetries were in agreement with the well-known neuroanatomic lateralization of cognitive processes, the authors concluded that processing of verbal and nonverbal stimuli relies on a regionalized, functionally specific network of subprocessors involved in the required stimulus-specific cognitive operations.

Other recent studies with a montage covering the whole scalp have also reported hemispheric differences in P2, N2, and P3

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amplitude for nonlateralized stimuli in simple "oddball" tasks. Most notably, Alexander and co-workers found larger P3 amplitude over right than left frontocentral sites in healthy adults to nonverbal stimuli in a visual oddball task (Alexander et al., 1995), and also reported larger N2 and P3 amplitudes over right frontocentral sites to tonal stimuli in an auditory oddball task (Alexander et al., 1996). The same direction of hemispheric asymmetry for N2 and P3 has also been found for binaural complex tones in an oddball task (Bruder et al., 1998). Although N2 and P3 may each reflect task-related processing asymmetries, additional components are known that have a time course that overlaps them, for example, the mismatch negativity (MMN). The MMN to deviant tones (Giard et al., 1990) or complex sounds (Alho et al., 1996, using left ear stimulation) was most prominent over the right than left supratemporal auditory cortex, but its topography was reported to be distinct from that of N2 (Ritter et al., 1992). On the other hand, MMN to phonemes was most prominent for the auditory cortex of the left hemisphere, and appeared to be specific to a native language (Näätänen et al., 1997). Also, no MMN was found for synthetic vowels in patients with left temporoparietal lesions, which contrasts with their MMN response to pure tones (Aaltonen, Tuomainen, Laine, & Niemi, 1993). Thus, hemispheric asymmetries of MMN related to stimulus type are in accordance with those seen for other components, that is, N2 and P3.

To our knowledge, no study has directly compared ERP asymmetries for tonal and phonetic oddball tasks in the same individuals using a recording electrode montage adequate to study differences in ERP topography. If asymmetries of endogenous ERP components observed in simple oddball tasks are related to lateralized cognitive processing, oddball tasks that require either tonal or phonetic processing would be expected to show an opposite asymmetry direction. The present study was designed to evaluate this prediction by recording ERPs from 30 scalp electrodes during oddball tasks with either complex tones or consonant-vowel syllables. The rationale for the selection of these tonal and phonetic stimuli was based on a long line of prior behavioral studies that have used these stimuli in dichotic listening tasks, which have clearly shown that complex pitch discrimination yields a left ear (right hemisphere) advantage, whereas identification of consonant-vowel syllables yields a right ear (left hemisphere) advantage (e.g., Berlin, Hughes, Lowe Bell, & Berlin, 1973; Bruder, 1991; Sidtis, 1981; Speaks, Niccum, & Carney, 1982). The extent to which hemispheric asymmetries are present for earlier ERP components (N1, P2, N2) and subcomponents of the late positive complex (P3, slow wave) was examined by using principal components analysis (PCA) to derive orthogonal factors corresponding to known ERP components (for a recent review, see Chapman & McCrary, 1995). A direct comparison of tonal and phonetic stimuli is reasonable, because a similar component structure across stimulus classes has been observed previously (Klein et al., 1995).

One important methodological issue when examining hemispheric asymmetries of ERPs in oddball tasks is the response required, and, as a related issue, subjects' handedness (e.g., Bryden, 1988, emphasized the significance of handedness for cerebral organization). Some studies have had participants respond with their preferred hand (e.g., Ford et al., 1994b; Karniski & Blair, 1989; Polich & Heine, 1996), some have counterbalanced response hand across participants (e.g., Alexander et al., 1995, 1996; Bruder et al., 1998), and yet others have had participants silently count the oddballs (e.g., Naumann et al., 1992; O'Donnell et al., 1993). Responding with the preferred hand will introduce an asymmetry over frontocentral regions because negative movement-related potentials are maximal contralateral to the response hand (Kutas & Donchin, 1980; Neshige, Luders, & Shibasaki, 1988; Singh & Knight, 1990). Counterbalancing response hand has been used to control these response-related asymmetries, but responding with the nonpreferred hand may not be equivalent to responding with the preferred hand, and motor-related asymmetries may interfere with task-related asymmetries in an unbalanced fashion (cf. Rizzolatti, Bertoloni, & De Bastiani, 1982). Silent counting of oddballs avoids response-related asymmetries, but this introduces additional cognitive demands that themselves may have an effect on cortical activity, especially when linguistic processing is required (for a review on dual-task effects in the context of hemispheric specialization, see Friedman & Polson, 1981). The influence of response hand in a right-handed sample was therefore systematically examined in the context of this study.

Method

Participants

Twenty-six healthy volunteers (12 female, 14 male), aged 21–60 years (*Mdn* = 33), being paid US$10 per hour for participation, were recruited from the New York metropolitan area. All participants were screened for hearing loss using a standard audiometric evaluation. Participants were required to have less than 10 dB difference between ears and a hearing loss no greater than 30 dB at 500, 1000, or 2000 Hz. Mean hearing threshold across ears at these frequencies were 7.9 dB (*SD* = 5.3, range −5 dB to 20 dB), 5.7 dB (*SD* = 6.7, range −5 dB to 22.5 dB), and 4.3 dB (*SD* = 6.4, range −7.5 dB to 22.5 dB), respectively. Participants were excluded if they had a current or past neurological problem or substance abuse disorder. Prior to the session, participants were given a baseline questionnaire to verify that, at the time of testing, they were not taking any medication, alcohol, caffeine, nicotine, nor that they were distressed because of mental (e.g., academic tests) or physical (e.g., exercise) demands.

All participants were administered the *Edinburgh Handedness Inventory* (EHI) (Oldfield, 1971). Following the suggestions of Bryden (1977), a handedness score was calculated varying from 10 (extremely right-handed) to 50 (extremely left-handed). Participants with a handedness score above 30 (corresponding to an EHI Laterality Quotient [LQ] cut-off point of zero) were not included in the study. Mean values revealed the sample to be strongly right-handed (*M* = 14.5, *SD* = 3.4; LQ = 84.8, *SD* = 12.8).

Stimuli and Procedure

Two analogous auditory "oddball" tasks, each consisting of 60 target (20%) and 240 nontarget (80%) stimuli, were designed to provoke predominantly right or left lateralized cognitive processing. For the tonal task, six complex tones with a duration of 250 ms were used. Tones consisted of square waves with fundamental frequencies between 264 and 485 Hz, corresponding to the major notes C, D, E, G, A, and B in the octave between middle C and C5, and were linearly tapered over the first and last 10% (i.e., rise and decay times were 25 ms).

For the phonetic task, three consonant-vowel syllables (/da/, /ta/, /ka/) spoken by a male voice were selected from a larger stimulus set (for a description of the physical properties of these stimuli, see Berlin et al., 1973) to match the discriminability level of the complex tone stimuli. For the two stimuli including a voiceless consonant, /ka/ and /ta/, voice onset time (VOT) was 56 ms and 57 ms, respectively; for the voiced consonant syllable /da/, VOT was 10 ms (for a definition of VOT, see Simos et al., 1997).

Whereas the phonetic stimuli were already matched for duration and intensity for use in a dichotic listening task, they were digitized from these audio tapes using the STIM software package (NeuroScan, Inc., 1994) and further edited to match the duration and root mean squared (RMS) amplitude of the tonal stimuli. All stimuli were presented binaurally at 72 dB SPL via a matched pair of TDH-49 earphones that were calibrated for loudness. Earphone orientation and task order were counterbalanced across participants.

Participants listened to a series of either tones or syllables, always starting with at least three frequent events (nontargets), using an interstimulus interval of 1,750 ms. Participants were instructed to respond as quickly as possible to the infrequent events (targets) with a button press. Response hand was counterbalanced across participants, but was the same for both tasks (i.e., 6 females and 7 males responded with their left hand, and 6 females and 7 males responded with their right hand). To reduce ocular artifacts, participants were also instructed to fixate on a cross on a video monitor while they were listening to the stimuli.

Trials were arranged in six 50-trial blocks. For the tonal task, each of the six complex tones served once as a target in one block, and once as a nontarget in another block. In three blocks, the target had a higher pitch than the nontarget, and a lower pitch in the remaining three blocks. For the phonetic task, each of the three consonant-vowel syllables served as a target twice and was paired with either of the remaining two syllables as the nontarget.

ERP Recording

Electroencephalograms (EEGs) were recorded from 4 midline (Fz, Cz, Pz, Oz) and 26 homologous scalp placements from both hemispheres (Fp1/2, F3/4, F7/8, FT9/10, FC5/6, C3/4, T7/8, TP9/10, CP5/6, P3/4, P7/8, P9/10, O1/2) using a nose reference with a Fpz ground and impedances maintained at 5 kΩ or less. EEG gain was 5,000, with a .01–30 Hz band pass (-6 dB/octave). Data were sampled for 1,280 ms at 100 Hz (200 ms prestimulus baseline), and low pass filtered off-line at 20 Hz (-24 dB/octave). Horizontal electrooculograms (EOGs) were recorded differentially from the outer canthi of each eye (horizontal bipolar) and from supra- and infraorbital sites (vertical bipolar).

Data Reduction and Analysis

Trials contaminated by artifacts were eliminated when EEG and horizontal EOG data exceeded $\pm 100\ \mu$V following vertical EOG reduction (linear regression; Semlitsch, Anderer, Schuster, & Presslich, 1986). Average ERP waveforms were computed for each participant and both tasks (tonal/phonetic) and both conditions (target/nontarget) for valid trials with correct responses only, resulting in 49.8 ($SD = 11.9$) and 53.6 ($SD = 6.2$) trials for targets (range 19–60 trials), and 200.5 ($SD = 40.2$) and 211.0 ($SD = 25.3$) trials for nontargets (range 113–237 trials) for tonal and phonetic tasks, respectively. The combined number of valid trials across tasks ranged from 67 to 120 for targets, and from 293 to 471 for nontargets. Thus, the number of valid trials for all subjects exceeded 50% of all target and nontarget trials.[1]

To determine the sources of variance in the ERP waveforms, the averaged ERP waveforms were submitted to a principal components analysis (PCA) derived from the covariance matrix, followed by a Varimax rotation (Chapman & McCrary, 1995; Donchin, Kutas, & McCarthy, 1977; Kayser et al., 1997). The factor analysis was computed using BMDP statistical software (BMDP4M; Dixon, 1992). Columns of the data matrix represented time (110 sample points from -100 ms to 1000 ms), and rows consisted of participants (26), tasks (2), conditions (2), and lateral electrode sites (26). The number of orthogonal factors extracted by the PCA was limited by a criterion of Eigenvalues greater than 1.0. PCA factor scores were submitted to repeated measures analyses of variance (ANOVA) with response hand (left/right) and gender (female/male) as between-subjects factors, and task (tonal/phonetic), condition (target/nontarget), hemisphere (left/right), and site (13 symmetric pairs of electrodes, excluding midline electrodes) as within-subjects factors. Significant condition effects were followed by repeated measures ANOVA for targets only. Greenhouse–Geisser epsilon (ϵ) correction was used to evaluate F ratios for within-subject effects involving more than 2 degrees of freedom (Jennings, 1987; Vasey & Thayer, 1987). Significant interactions involving site were examined through simple effects at each site to locate the source of the interaction. Significant topographic effects involving task and hemisphere were also evaluated after scaling the amplitudes for each task by the vector amplitude measured across electrodes (hemisphere and site) in each participant (McCarthy & Wood, 1985).

Finally, to confirm significant effects for PCA factor scores, N2 and P3 components were also analyzed with conventional techniques for ERP component abstraction. Firstly, N2 and P3 were defined as the mean voltage area within the latency windows of 180–270 and 280–480 ms, respectively. Secondly, peak latencies were measured by locating the most negative or positive deflection within these latency windows at electrode locations where the respective component was most prominent. These locations included sites common to both N2 and P3 over frontocentral and temporal-parietal brain regions (FC5/6, C3/4, T7/8, CP5/6, P7/8), sites over temporal-parietal areas (TP9/10, P9/10) for N2 only, and sites over medial-parietal areas (P7/8, P3/4) for P3 only. All conventional ERP component measures were also submitted to repeated measures ANOVA as described above, and topographic effects were also evaluated after vector scaling the window amplitude measures (McCarthy & Wood, 1985).

For the analysis of the behavioral data, responses latency (mean reaction time of correct responses) was submitted to a repeated measures ANOVA with response hand (left/right) and gender (female/male) as between-subjects factors, and task (tonal/phonetic) as a within-subjects factor.

For all analyses, gender was entered as a control factor into the ANOVA design, but this variable will not be considered further in this report. No significant main effects for gender or task-related topographic interactions with gender were observed in any of the analyses.

Results

Performance was close to perfect for both tasks, with a mean hit rate of 98.1% and a false alarm rate below 0.5% across participants. Mean response latency for correct responses was significantly slower for phonetic ($M = 486.5$ ms, $SD = 80.5$) than for tonal targets ($M = 442.6$ ms, $SD = 76.5$), as confirmed by a task main effect, $F(1,22) = 10.3$, $p < .01$. No significant differences in response time were found for left versus right hand responding, nor did response hand interact with task.

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[1] To assess whether or not the number of valid trials was a critical factor, additional analyses of variance were performed on ERP components measures using a median-split on the combined number of valid trials as a grouping factor. All effects reported in the results section were unaffected in these analyses.

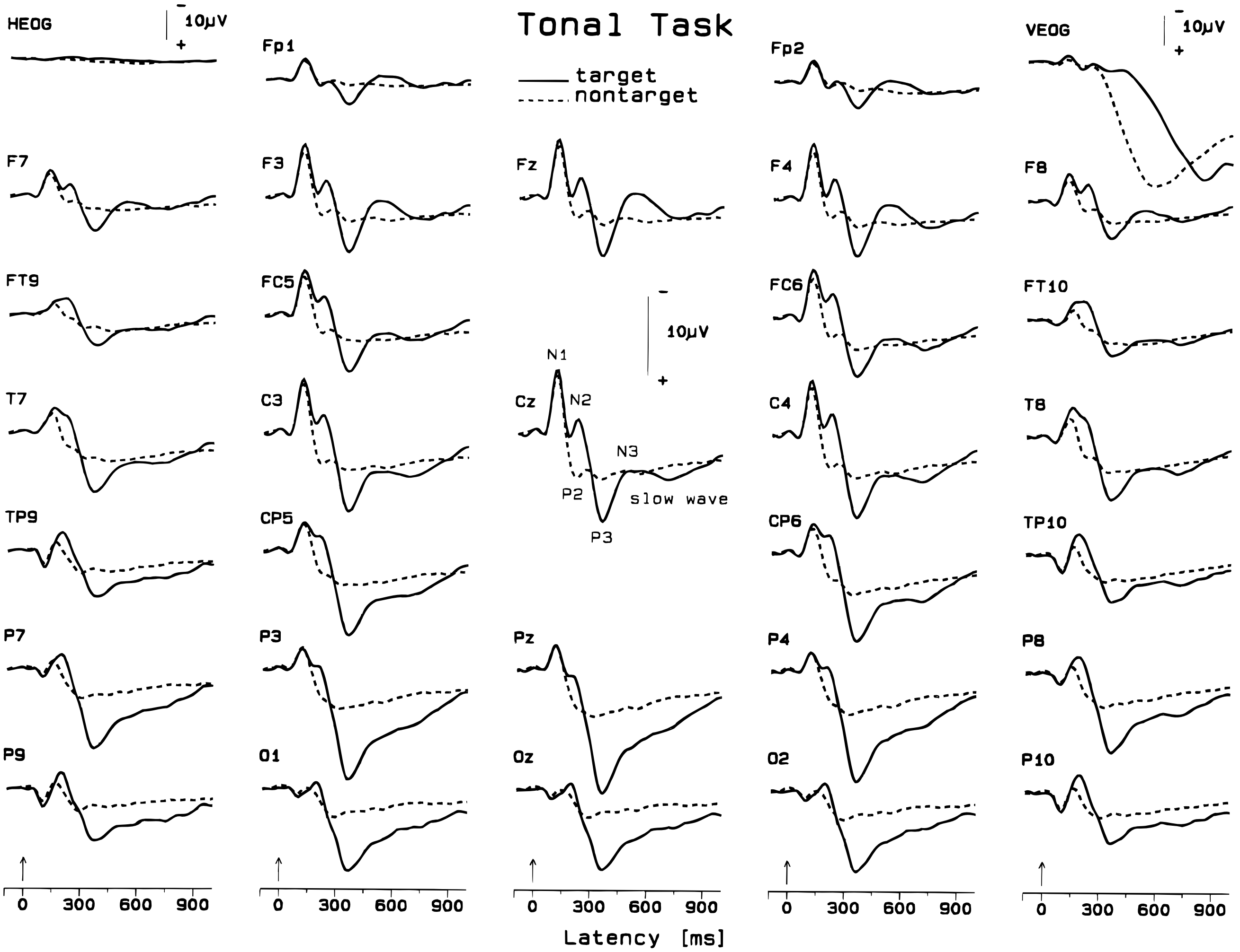

Figure 1. Grand average event-related potentials (ERPs) for the tonal task for targets (solid line) and nontargets (dashed line) for all recording sites, averaged across response hand and gender ($n = 26$). ERP components are indicated at Cz. Note the different scaling for electrooculogram (EOG) channels showing vertical EOG averages (VEOG) before artifact removal.

Average Waveforms and ERP Component Structure

Grand average ERP waveforms for tonal and phonetic tasks are shown in Figures 1 and 2, respectively, comparing levels of condition (target/nontarget). Across tasks, distinctive ERP components were identified as N1 (peak latency 100 ms), N2 for targets, and P2 for nontargets (220 ms), P3 (360 ms), a negative peak labeled N3 (540 ms), and slow wave (beyond 700 ms). N1 was present at all electrode sites but most prominent centrally, that is, at Cz (see Figures 1 and 2). N2 was most prominent at central and temporal sites for both tasks, and also at parietal sites for the phonetic task. P3 and slow wave were broadly distributed but P3 showed a maximum over parietal regions, whereas slow wave was maximal at posterior sites and did not return to baseline by the end of the recording epoch. N3 was most prominent at frontocentral sites. Because the present study focused on hemispheric asymmetries, data from the midline electrode sites will not be considered further.

PCA Factors and ERP Components

The first five principal components extracted by the PCA accounted for 88.8% of the ERP variance. Figure 3 shows a plot of the factor loadings at each time point, together with selected grand average ERP waveforms for both tasks, which illustrates the correspondence of each factor with ERP components. Figure 4 depicts the topographical distribution of the corresponding factor scores for target stimuli in both tasks. Hence, the degree of association of each factor with the temporal locus and the scalp region of activity can be inferred from Figures 3 and 4, respectively.

PCA factors largely correspond to the identified ERP components, and are described in the order of their peak latencies. Factor 5 (4.4% explained variance) peaked at 100 ms and almost entirely overlapped N1 (see Figure 3). Its amplitude was most negative at medial-central sites, particularly for the tonal task (see Figure 4), which is consistent with the central maximum of N1, and the difference in N1 amplitude between tasks (see Figures 1 and 2). For these reasons, Factor 5 was labeled ‘N100’.[2]

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[2] To distinguish between event-related potential (ERP) components present in the averaged ERP waveforms and principal components analysis (PCA) factors believed to represent these ERP components, factor names are put in single quotes throughout the manuscript.

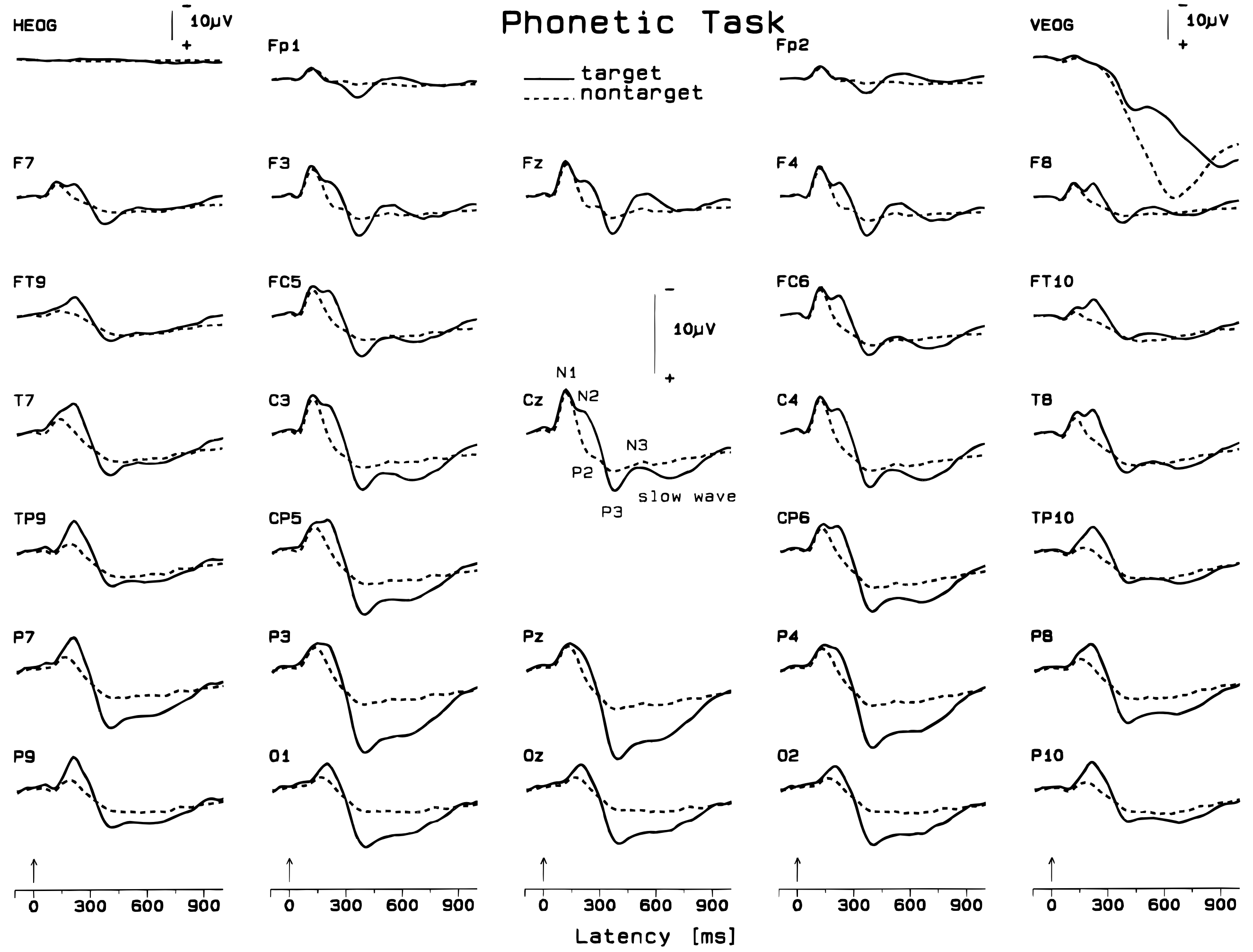

Figure 2. Grand average event-related potentials for the phonetic task for targets (solid line) and nontargets (dashed line) for all recording sites, averaged across response hand and gender ($n = 26$). Component indications and channel scalings are as in Figure 1.

Analogously, Factor 4 (7.9% explained variance) peaked at 210 ms and had a topography similar to N2 (see Figures 3 and 4). Factor 4 amplitude was most negative at lateral-temporal and parietal sites, which is consistent with a modality-specific distribution of N2 for an auditory task, being larger over temporal areas (Hillyard & Picton, 1987). Importantly, pronounced hemispheric asymmetries were present in Factor 4 amplitude, being larger over right lateral-temporal areas for the tonal task, and larger over left temporal-parietal areas for the phonetic task (see Figure 4). Factor 4 was labeled 'N210.'

Factor 3 (14.8% explained variance) amplitude was greatest at 320 ms, corresponding to the early phase of the P3 component (see Figure 3). The respective factor scores were positive over posterior regions for the tonal task (see Figure 4), whereas for the phonetic task factor scores were close to zero. For the tonal task, Factor 3 amplitude was broadly distributed but maximal over parietal sites, comparable to the distribution of P3 typically observed in auditory oddball paradigms (Johnson, 1993; Picton, 1992). This positivity tended to shift towards the right hemisphere in the tonal task. Factor 3 was labeled 'P320'.

Factor 1 (34.6% explained variance) extended over a relatively long time period, with more than 50% of its amplitude from 320 to 710 ms, and peaking between 380 and 490 ms (see Figure 3). Factor 1 amplitude was most positive over posterior regions but negative over anterior regions (see Figure 4). Because the time course of Factor 1 was consistent with both the late phase of the P3 component and an overlapping frontal negativity, identified as N3 (see Figure 3), the factor was named 'late P3/N3'. Unlike factor 'P320', the topography displayed by factor 'late P3/N3' was marked by a posterior positivity that inverted frontally, and this topography was present for both the phonetic and tonal task. Because contributions of multiple P3 generators vary with stimulus and task conditions (Johnson, 1993; Molnár, 1994; Picton, 1992), such differences may be responsible for the topographic differentiation of factors 'P320' and 'late P3/N3'.

Factor 2 (27.2% explained variance) was a long latency component characterizing the later time period of the recording interval (see Figure 3). Factor 2 showed a broad scalp distribution with a right posterior maximum and a left frontal minimum (see Figure 4), compatible with positive slow wave (Ruchkin & Sutton, 1983). Factor 2 was therefore labeled 'slow wave'.

The relevance of the factors extracted by the PCA is apparent from the temporal and topographic distinctiveness of all factors. The percentage of explained variance for each of the PCA factors

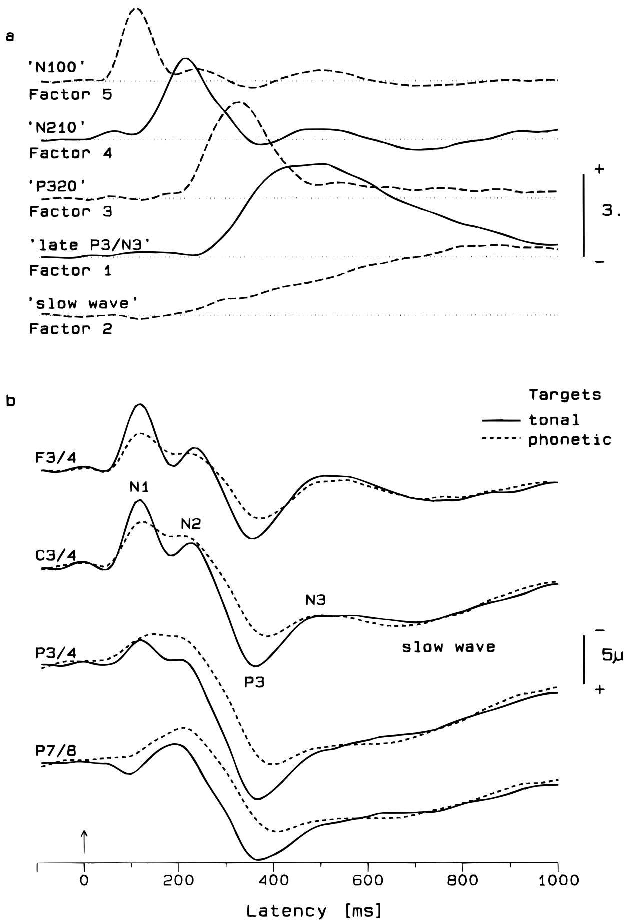

Figure 3. Varimax rotated factor loadings plotted over time for five orthogonal factors extracted by principal components analysis (PCA) (a), and grand mean event-related potential (ERP) waveforms at selected sites averaged across hemispheres for tonal (solid line) and phonetic (dashed line) targets (b), to illustrate the correspondence of each factor with the temporal locus of activity. Factor labels (in single quotes) were chosen to reflect both the time course of the factor loadings (a) and the polarity of the associated ERP components (b).

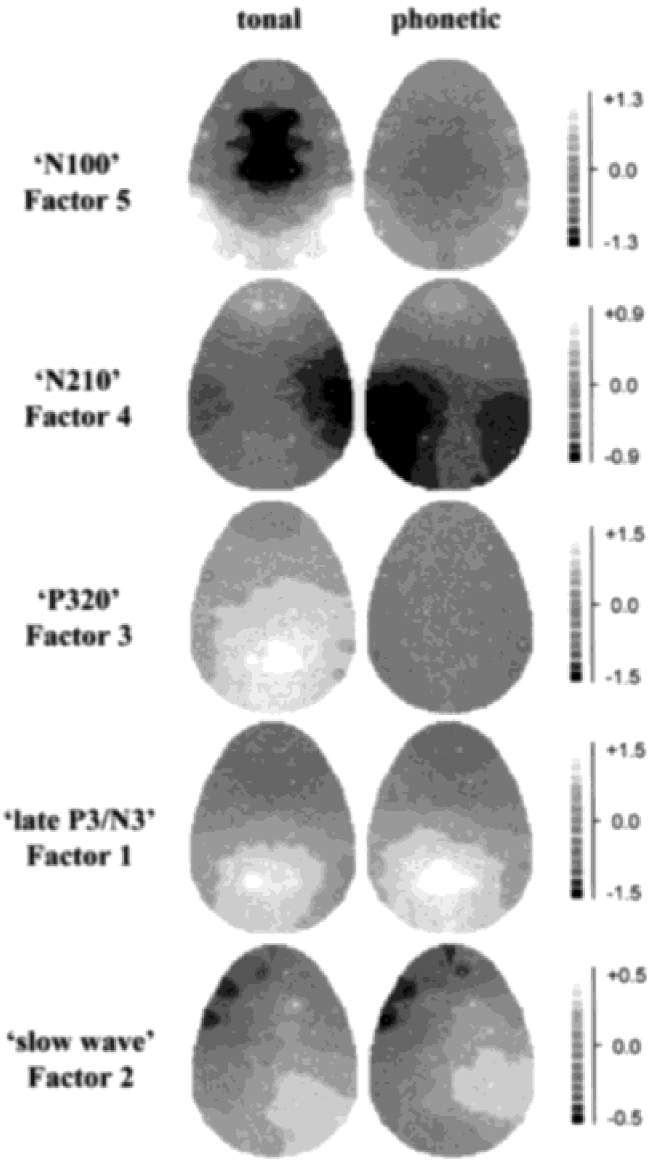

Figure 4. Topographic mappings of principal components analysis (PCA) factor amplitudes for tonal (left) and phonetic (right) target stimuli. Maps were calculated from the factor scores for 26 lateral electrodes averaged across task, response hand, and gender. Scores represent the degree of association of each region with each factor. The sign of the factor scores reflects the polarity of the underlying event-related potential (ERP) component (positive scores are associated with positive ERP components and vice versa).

roughly corresponds to the duration of the respective ERP components as a proportion of the total recording epoch (interval −100 to 1,000 ms), taking into account that not all ERP components are present at all sites in all conditions. As factor loadings tend to occupy distinctive triangle-shaped windows with only slight overlap between components (see Figure 3), they describe contributions of ERP components more efficiently than conventional window averages. In both approaches, component amplitude must be compatible with common knowledge about ERP components and clearly evident in the observed data. Unlike time windows, which are chosen to reflect ERP waveform peaks, Varimax rotated, orthogonal PCA factors detect time windows representing the variance source in the data (Chapman & McCrary, 1995). Accordingly, if the extracted factors are meaningful, PCA factors are the preferable methodological approach.

Findings for PCA Factor Scores

Results of the repeated measures ANOVA performed on the factor scores for each factor revealed significant condition main effects for 'N210', $F(1,22) = 94.98$, $p < .001$, 'P320', $F(1,22) = 29.72$, $p < .001$, and 'late P3/N3', $F(1,22) = 8.95$, $p < .01$, and several significant higher order interactions involving condition, confirming that N2, early P3, and late P3/N3 were present mainly for targets (see Figures 1 and 2). Although condition main effects were not found for factors 'N100' and 'slow wave', there was a significant three-way Task × Condition × Site interaction for 'N100', $F(12,264) = 4.47$, $p < .01$, $\epsilon = .2317$, and a significant four-way Response Hand × Hemisphere × Condition × Site interaction for 'slow wave', $F(12,264) = 2.97$, $p < .05$, $\epsilon = .4049$. For all factors, significant site main effects and several higher order interactions involving site were indicative of the distinctive topography for each factor (see Figure 4).

To evaluate these effects, repeated measures ANOVA were performed on the factor scores for targets only. Table 1 lists the results of these analyses for all effects at a significance level of $p < .05$. However, to reduce the likelihood of Type I errors, site main effects and interactions including site were evaluated at a more stringent significance level ($p < .01$), unless they were explicitly hypothesized (i.e., effects involving a Task × Hemisphere interaction). This decision was further supported by a power analysis that revealed sufficient power (.80) to detect medium to large effects including site at a $p = .01$ significance level, but for all other effects, a $p = .05$ significance level was needed to establish the same conventional power (Cohen, 1988, 1992). Effect size measures (η^2) given in Table 1 correspond to large effects (see Cohen, 1988).

Factor 'N100'. A significant site main effect and a significant Task × Site interaction were observed for factor 'N100' (see Table 1). Simple task main effects at each recording site revealed that 'N100' amplitude was larger (i.e., more negative factor scores) for the tonal compared with the phonetic task at Fp1/2, F7/8, F3/4, FC5/6, and C3/4, and 'N100' amplitude was smaller (i.e., more positive factor scores) for the tonal compared with the phonetic task at TP9/10, P9/10, P7/8, and O1/2, for all simple task main effects, $F(1,22) > 19.3$, $p < .001$. Overall, 'N100' amplitude was most prominent over frontocentral regions, and less evident for the phonetic task at these locations (see Figure 4), which is compatible with an N1 difference seen in Figure 3b.

Factor 'N210'. Besides a significant site main effect, deriving from a lateral-temporal topography typical of N2 for an auditory task (Hillyard & Picton, 1987; see Figure 4), there were significant interactions of Task × Site, Task × Hemisphere, and Task × Hemisphere × Site (see Table 1). Simple task main effects at each recording site revealed 'N210' amplitude to be more negative for the phonetic task at sites P9/10, $F(1,22) = 4.43$, $p < .05$, P7/8, $F(1,22) = 5.31$, $p < .05$, P3/4, $F(1,22) = 9.38$, $p < .01$, and 01/2, $F(1,22) = 10.39$, $p < .01$. The Task × Hemisphere effects originate from the differential regional asymmetry of 'N210' amplitude across tasks, as can be easily seen from Figure 4. For the tonal task, 'N210' amplitude was mainly evident at lateral-temporal regions, particularly over the right hemisphere. For the phonetic task, 'N210' amplitude covered a broader area including lateral-temporal and lateral parietal regions, and this broad coverage was particularly evident over the left hemisphere. These observations were supported by simple interaction effects of Task × Hemisphere, calculated for homologous pairs of electrodes over the two hemispheres, which proved to be strongest at sites FC5/6, $F(1,22) = 31.88$, T7/8, $F(1,22) = 16.93$, P9/10, $F(1,22) = 18.10$, TP9/10, $F(1,22) = 15.46$, and P7/8, $F(1,22) = 15.02$, each $p < .001$, but this interaction was also present in the same direction at sites FT9/10, $F(1,22) = 13.42$, O1/2, $F(1,22) = 12.59$, CP5/6, $F(1,22) = 11.76$, F7/8, $F(1,22) = 9.91$, C3/4, $F(1,22) = 9.10$, F3/4, $F(1,22) = 8.20$, each $p < .01$, and at P3/4, $F(1,22) = 4.55$, $p < .05$. Furthermore, a simple task main effect at left hemisphere, $F(1,22) = 7.16$, $p < .05$, indicated a larger 'N210' amplitude for the phonetic compared with the tonal task over the left hemisphere, and a trend for a simple hemisphere main effect for the tonal task, $F(1,22) = 3.42$, $p < .10$, suggested a larger 'N210' amplitude over right than left hemisphere for the tonal task.

Factor 'P320'. The tonal task was the main contributor to factor 'P320' (see Figure 4), which was reflected in a significant task main effect and a significant Task × Site interaction (see Table 1). Simple task main effects at each recording site revealed that 'P320' amplitude was significantly more positive for the tonal compared with the phonetic task at all sites except Fp1/2, particularly at posterior and lateral sites (i.e., simple task main effects at P3/4, P7/8, P9/10, O1/2, CP5/6, TP9/10, T7/8, and FT9/10, each $F(1,22) > 28.9$, each $p < .0001$). For the tonal task, factor 'P320' displayed a distinct P3-like topography, which was responsible for these effects (see Figure 4). In addition, a significant Task × Hemisphere interaction stemmed primarily from greater

Table 1. *Summary of F Ratios (and ϵ Corrections) From Repeated Measures ANOVA Performed on PCA Factor Scores for Target Stimuli*

		Factor				
Variable	*df*	'N100'	'N210'	'P320'	'Late P3/N3'	'Slow wave'
TASK	1, 22			29.28***		
HEMI	1, 22				17.77***	5.51*
SITE	12, 264	105.93*** (0.1840)	11.09***	8.12*** (0.1796)	48.51*** (0.2558)	3.96** (0.3042)
TASK × HEMI	1, 22		19.35***	6.09*		
TASK × HEMI	12, 264	57.10*** (0.1783)	6.72*** (0.2203)	15.28*** (0.2103)		
TASK × HEMI × SITE	12, 264		4.38** (0.3585)			
HAND	1, 22			7.77*		
HEMI × HAND	1, 22				4.41*	
SITE × HAND	12, 264			3.65* (0.1796)		
TASK × HEMI × HAND	1, 22		13.96**			
TASK × SITE × HAND	12, 264				5.34** (0.2829)	
HEMI × SITE × HAND	12, 264				7.36*** (0.3670)	
TASK × HEMI × SITE × HAND	12, 264		3.07* (0.3585)			

Note: TASK = nonverbal/verbal task; HEMI = hemisphere; SITE = electrode site; HAND = response hand. Only F ratios with $p < .05$ are reported. Effect sizes (partial eta squared) for significant effects ($p < .05$) range from $\eta^2 = .12$ to $\eta^2 = .83$.
$^*p < .05$. $^{**}p < .01$. $^{***}p < .001$.

right-hemispheric positivity in the tonal task (see Figure 4), although low amplitude asymmetries in the opposite direction for the phonetic task contributed to this effect. Simple effects computed for the Task × Hemisphere interaction at each electrode site were most substantial at C3/4, $F(1,22) = 12.52$, and CP5/6, $F(1,22) = 10.87$, each $p < .01$, but were also present at sites P3/4, $F(1,22) = 6.72$, TP9/10, $F(1,22) = 6.51$, P7/8, $F(1,22) = 5.74$, P9/10, $F(1,22) = 5.49$, and FT9/10, $F(1,22) = 4.35$, each $p < .05$.

Factor 'late P3/N3'. Significant topographic effects (site and hemisphere; see Table 1) were observed for 'late P3/N3'. This factor was most positive over medial-parietal areas and extended asymmetrically toward the left hemisphere, particularly for the phonetic task (see Figure 4). Although no significant Task × Hemisphere interaction was found, the simple main effect hemisphere was significant for the phonetic task, $F(1,22) = 17.20$, $p < .001$, but not for the tonal task, $F(1,22) = 3.02$, $p < .10$.

Factor 'slow wave'. Analyses for factor 'slow wave' also revealed significant topographic effects (site and hemisphere; see Table 1). 'Slow wave' amplitude was more positive over right posterior regions, and more negative over left lateral-frontal locations (see Figure 4). However, the interaction Hemisphere × Site did not reach significance.

Findings for Response Hand

Grand average ERP waveforms for left and right hand responses to target stimuli averaged across task are shown in Figure 5. Late components (i.e., N2, P3, and N3) varied in amplitude at different electrode locations with response hand. Along the midline and the adjacent medial sites, P3 amplitude was larger and peaked earlier for left than right responses. Moreover, the N3 wave was more prominent with left responses. In contrast, N2 amplitude was larger but delayed along the midline for right as compared with left responses. All of these components were markedly affected by a contralateral, response-related negativity that was particularly prominent at frontocentral sites (see Figure 5).

Factor 'N210'. Table 1 indicates that response hand interacted with several of the above-reported effects. For factor 'N210', significant Task × Hemisphere × Response Hand and Task × Hemisphere × Site × Response Hand interactions were found. As shown in Figure 6, response hand interacted with hemisphere mainly for the tonal task by enhancing 'N210' amplitude over the contralat-

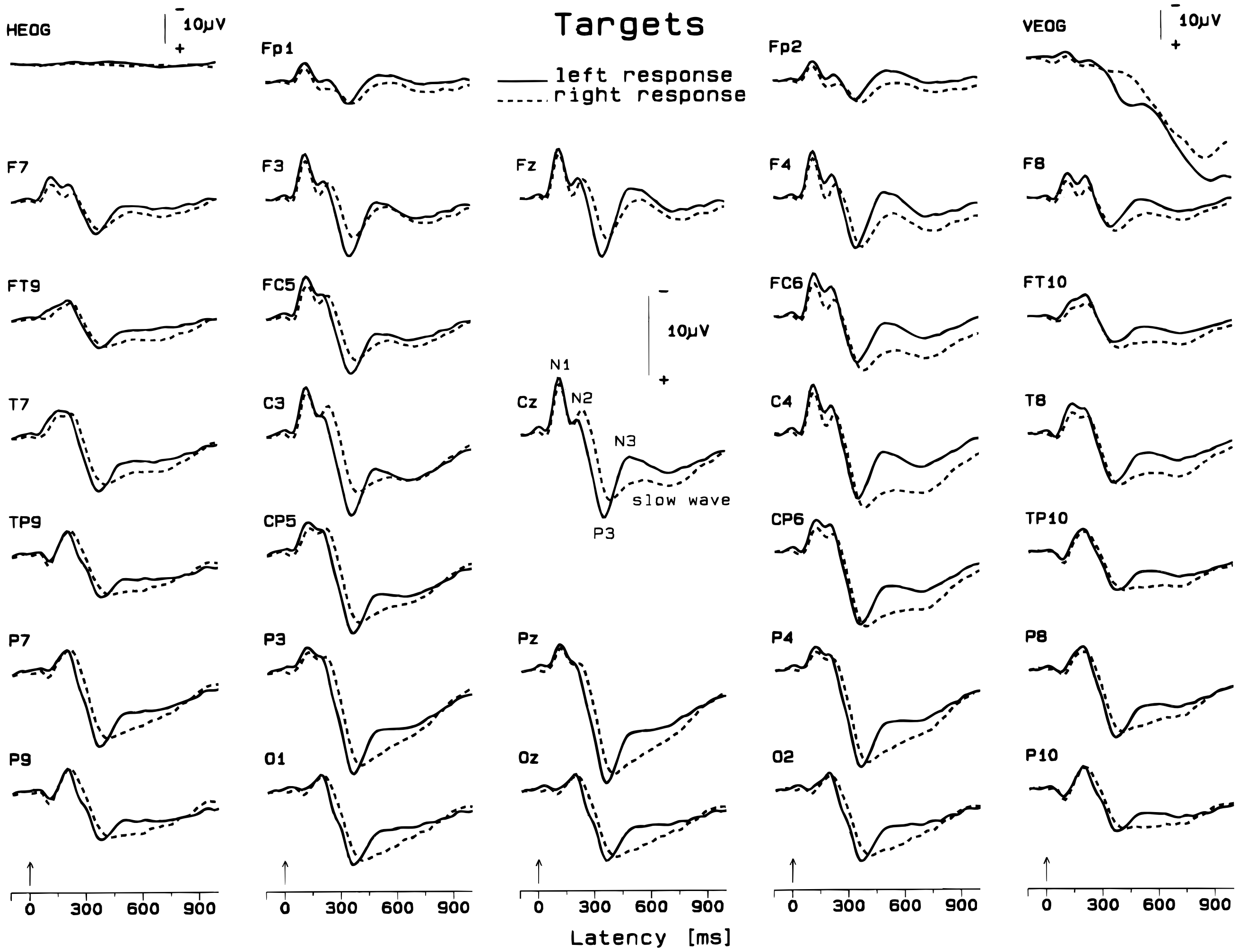

Figure 5. Grand average event-related potentials for target stimuli for left (solid line) and right (dashed line) hand responders ($n = 13$ each) for all recording sites, averaged across task and gender. Component indications and channel scalings are as in Figure 1.

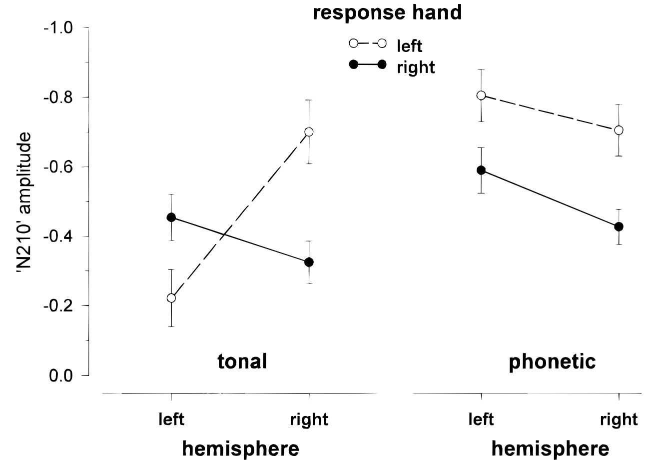

Figure 6. Mean 'N210' amplitudes (and SEM) for tonal (left chart) and phonetic (right chart) target stimuli, plotted as a function of left and right hemisphere, and left (dashed line) and right (solid line) response hand. The scale was inverted to reflect the polarity of the underlying negative event-related potentials (ERP) component N2.

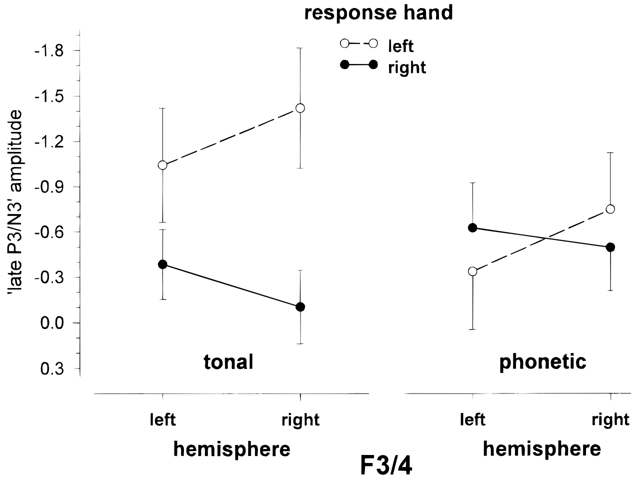

Figure 7. Mean 'late P3/N3' amplitudes (and SEM) at medial-frontal sites (F3/4) for tonal (left chart) and phonetic (right chart) target stimuli, plotted as a function of left and right hemisphere, and left (dashed line) and right (solid line) response hand. The scale was inverted to reflect the polarity of the underlying negative event-related potentials (ERP) component N3 at these sites.

eral hemisphere, whereas for the phonetic task 'N210' amplitude was larger over both hemispheres for left hand responses. Simple effects for the Task × Hemisphere × Response Hand interaction calculated for each electrode location were most robust at FC5/6, $F(1,22) = 21.30$, and C3/4, $F(1,22) = 24.34$, each $p < .001$. Overall, the target ERP waveform included a contralateral, response-related negativity, particularly over frontocentral brain regions, which was superimposed on components associated with cognitive processing. Therefore, frontocentral asymmetries seen for the tonal task were more influenced by response hand than the posterior, parietal asymmetries seen for the phonetic task. However, when averaged across response hand, 'N210' amplitudes were more negative over the right hemisphere for the tonal task, and more negative over the left hemisphere for the phonetic task.

Factor 'P320'. A response hand main effect was found for factor 'P320' (see Table 1). Overall, 'P320' amplitude was larger for left than for right hand responses. However, this effect was also most robust at frontocentral sites (simple main effects response hand at F3/4, $F(1,22) = 9.65$, and C3/4, $F(1,22) = 9.48$, each $p < .01$).

Factor 'late P3/N3'. Response hand also had a major impact on 'late P3/N3', as confirmed by significant Task × Site × Response Hand and Hemisphere × Site × Response Hand interactions. To localize these effects, simple effects for the two-way interactions of Task × Response Hand and Hemisphere × Response Hand were calculated at each site. For both interactions, simple interaction effects were only significant at medial frontocentral sites, that is, where N3 was prominent. For the Task × Response Hand interaction, simple effects were significant at F3/4, $F(1,22) = 9.57$, $p < .01$, and at Fp1/2, $F(1,22) = 5.93$, FC5/6, $F(1,22) = 5.34$, and C3/4, $F(1,22) = 7.08$, each $p < .05$; for the Hemisphere × Response Hand interaction, simple effects were significant at F3/4, $F(1,22) = 50.65$, $p < .0001$, and at FC5/6, $F(1,22) = 14.78$, and C3/4, $F(1,22) = 22.02$, both $p < .001$. Figure 7 displays the means of 'late P3/N3' amplitude at F3/4, where both simple interaction effects were most robust (comparable effects were observed at the other significant sites). As is clear from Figure 7, response hand enhanced the negativity of 'late P3/N3' at medial-frontal sites over the contralateral hemisphere for both tasks, and an additional task-related influence of response hand was evident with greater negativity for left hand responses in the tonal task. Paralleling the findings for 'N210' amplitude, response hand interfered more with the observed fronto-central asymmetries of the tonal task rather than with parietal asymmetries found for the phonetic task.

Findings for N2-P3 Amplitude

Effects of primary interest, that is, different asymmetries for tonal and phonetic tasks, were limited to factors representing N2 and P3. Because it was hypothesized that these components jointly reflected endogenous ERP activity, differences in factor scores representing N2 and P3 were calculated for target stimuli (analogous to N2-P3 peak-to-peak differences). Because P3 was represented by both factors 'P320' and 'late P3/N3', but to a different degree depending on task and response hand, the factor with greater positivity at medial-parietal sites (i.e., P3/4) was used. These 'N2-P3' factor scores were submitted to the same repeated measures ANOVA as described above.

This analysis revealed a significant site main effect, $F(12,264) = 69.94$, $p < .0001$, $\epsilon = .2114$, resulting from an increase in 'N2-P3' amplitude from anterior to posterior sites, and several significant interactions, Task × Hemisphere, $F(1,22) = 19.01$, $p < .001$, Task × Site, $F(12,264) = 4.24$, $p < .01$, $\epsilon = .2363$, and Task × Hemisphere × Site, $F(12,264) = 6.25$, $p < .001$, $\epsilon = .3864$. Mean 'N2-P3' amplitude topographies for both tasks are mapped in Figure 8a. Largest 'N2-P3' amplitudes were seen over parietal regions, but over opposite hemispheric sites for each task (see Figure 8a). The Task × Hemisphere interaction was present at all sites except Fp1/2, as indicated by significant simple effects, with F values ranging from $F(1,22) = 8.11$, $p < .01$, at O1/2, to $F(1,22) = 23.47$, $p < .001$, at FC5/6. The topography of the Task × Hemisphere interaction is depicted in Figure 8b, which

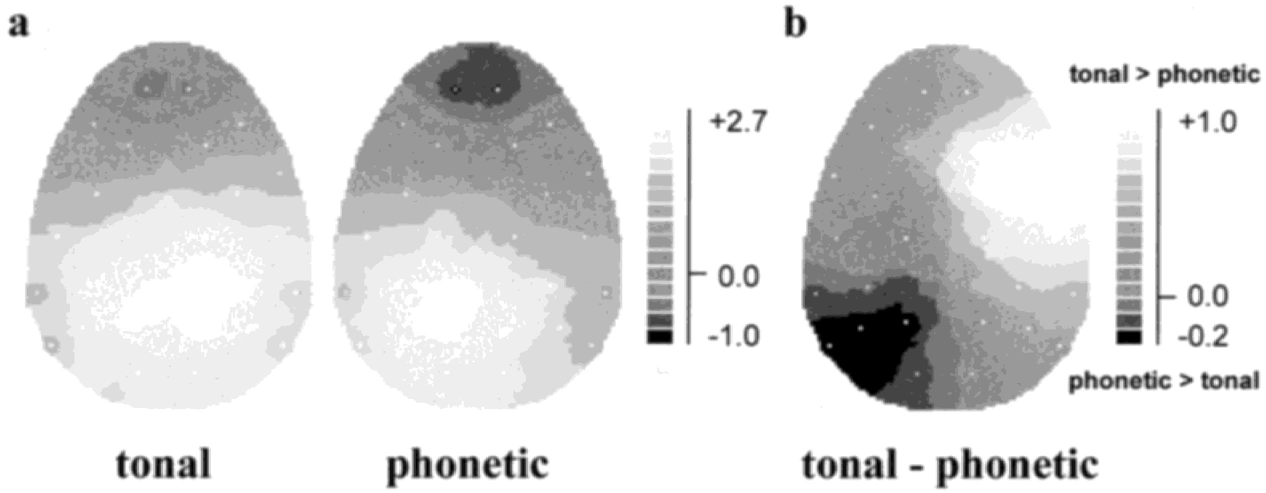

Figure 8. Topographies of 'N2/P3' amplitude (differences of principal components analysis [PCA] factor scores). Maps were calculated for (a) tonal and phonetic target stimuli (averaged across gender and response hand), and (b) the corresponding difference map for nonverbal-minus-verbal target stimuli. Note that the unbalanced difference map results from a larger N2/P3 amplitude for the tonal task.

maps the difference between 'N2-P3' amplitude for tonal and phonetic target stimuli. For this task difference, all locations over the right hemisphere were more positive than their homologous counterparts over the left hemispheric. This hemispheric difference, however, was also clearly modulated by task-specific regional effects. Over frontocentral regions, 'N2-P3' amplitude was particularly larger over the right hemisphere for the tonal task, whereas over temporal-parietal areas, 'N2-P3' amplitude was larger over the left hemisphere for the phonetic task.

Preservation of Effects after Vector Scaling

Interpreting significant interactions in ERP studies involving electrode location can be ambiguous because they may result from differences in source strength from the same source or sources (McCarthy & Wood, 1985). Therefore, significant interactions involving task, hemisphere, and site were also evaluated after scaling the amplitudes for each task by the vector amplitude measured across electrodes (hemisphere and site) in each participant. For each factor, all effects reported in Table 1 involving a Task × Hemisphere interaction were preserved (except for the interaction Task × Hemisphere × Site × Response Hand for factor 'N210', which became insignificant after ϵ correction). Moreover, this finding was also true for 'N2-P3' amplitude, in which the interactions Task × Hemisphere, $F(1,22) = 14.02$, $p < .01$, and Task × Hemisphere × Site, $F(12,264) = 4.09$, $p < .01$, $\epsilon = .2991$, were maintained after scaling.

Supplementary Findings for N2 and P3

Window amplitude measurements. The applicability of PCA methodology in the analysis of ERPs is enhanced when it can be shown that the extracted factors reflect and clarify the conventionally defined component structure of the ERP, without distortion due to misallocated variance from overlapping components, outlying cases, or temporal "jitter" (Friedman, Vaughan, & Erlenmeyer-Kimling, 1981; Kayser et al., 1997; Vaughan, Ritter, & Simson, 1983; see also Wood & McCarthy, 1984). Although these problems are inherent in any technique for component identification (Chapman & McCrary, 1995; Möcks & Verleger, 1986), we corroborated prominent PCA findings by analyzing relevant ERP components with other techniques of ERP measurement. N2 and P3 were defined as the mean voltage area within distinctive latency windows of 180–270 and 280–480 ms, respectively, and submitted to repeated measures ANOVA as described above. Results of the time window analyses were in accordance with the PCA results, although effect sizes were smaller. Most importantly, the Task × Hemisphere interaction was significant for N2, $F(1,22) = 7.07$, $p < .05$, for P3, $F(1,22) = 4.45$, $p < .05$, and for N2-P3 amplitude, $F(1,22) = 12.38$, $p < .01$, and the Task × Hemisphere × Site interaction was significant for N2-P3 amplitude, $F(12,264) = 3.69$, $p < .01$, $\epsilon = .3520$, and suggested for N2, $F(12,264) = 1.98$, $p < .10$, $\epsilon = .4851$.

After vector scaling the window amplitudes, the Task × Hemisphere interaction was still significant for N2-P3 amplitude, $F(1,22) = 10.07$, $p < .01$. However, for the individual ERP components that led to this effect, this interaction was not supported after vector scaling. This finding indicates that, although the topography of N2-P3 amplitude is independent of the overall amplitude in these windows, the topographies of the individual ERP components are influenced by their overall amplitude measured within these windows. This contrasts with the findings for the comparably scaled PCA factors for the individual ERP components. Nonetheless, effects including response hand were consistent after scaling of the window amplitudes, for instance, revealing a Task × Hemisphere × Response Hand interaction for N2, $F(1,22) = 9.25$, $p < .01$, and Hemisphere × Site × Response Hand interactions for N2, $F(12,264) = 4.73$, $p < .01$, $\epsilon = .3130$, P3, $F(12,264) = 4.87$, $p < .01$, $\epsilon = .2238$, and N2-P3 amplitude, $F(12,264) = 3.80$, $p < .01$, $\epsilon = .38373$.

These findings, based on conventional ERP amplitude measures, are supportive of the PCA findings. However, the potency and advantage of the PCA approach was apparent for our data in at least two respects. First, the PCA was able to disentangle temporally and spatially overlapping ERP components, which were distinctively affected by experimental manipulations, and second, by detecting optimized, nonrectangular time windows, statistical power was enhanced.

Peak latencies. N2 and P3 peak latencies were also measured at the lateral electrode locations where each component was most prominent. A significant site main effect for P3, $F(5,110) = 12.02$, $p < .001$, $\epsilon = .5911$, confirmed an increase in P3 latency from frontocentral (at FC5/6, $M = 373.9$ ms, $SD = 45.2$) to lateral-parietal sites (at P7/8, $M = 396.4$ ms, $SD = 49.8$); for N2, a significant site main effect, $F(6,132) = 3.08$, $p < .05$, $\epsilon = .4395$, manifested the opposite relation, that is, a decrease in N2 latency from frontocentral (at C3/4, $M = 211.3$ ms, $SD = 24.8$) to lateral-parietal sites (at P7/8, $M = 203.2$ ms, $SD = 25.5$).

Significant response hand main effects for both N2, $F(1,22) = 14.62$, $p < .001$, and P3, $F(1,22) = 14.46$, $p < .001$, indicated shorter latencies for left than right hand responses (mean latency difference was 18.7 ms for N2, and 48.4 ms for P3; see Figure 5). For N2, hemisphere interacted significantly with response hand, $F(1,22) = 5.16$, $p < .05$, with slightly increased N2 latencies over the contralateral hemisphere (mean latency lags between hemispheres were 4.8 ms and 2.9 ms for left and right hand responses, respectively).

A task influence on N2 and P3 latencies was also found. For P3, a significant task main effect, $F(1,22) = 22.93$, $p < .001$, indicated shorter latencies for tonal ($M = 372.2$ ms, $SD = 45.2$) than phonetic ($M = 401.1$ ms, $SD = 48.7$) target stimuli. Unlike response hand differences in P3 latency, these task-related deviations in P3 latency were paralleled by task differences seen for response latency. For N2, a significant Task × Site interaction, $F(6,132) = 9.64$, $p < .001$, $\epsilon = .4076$, derived from longer N2 latencies for the phonetic than tonal task at lateral-parietal sites (TP9/10, P7/8, P9/10). A significant Task × Hemisphere interaction was also observed for N2, $F(1,22) = 4.84$, $p < .05$, which derived from slightly shorter right hemispheric N2 latencies for the tonal task (left hemisphere, $M = 205.4$ ms, $SD = 24.3$; right hemisphere, $M = 202.9$, $SD = 23.8$), and vice versa for the phonetic task (left hemisphere, $M = 207.0$, $SD = 25.4$; right hemisphere, $M = 211.4$, $SD = 26.1$).

To sum up, ERP component latencies differed across tasks, which appears to reflect differences in task difficulty. N2 and P3 were more sharply defined in both amplitude and latency for the tonal compared with the phonetic task.

Discussion

To assess the basis for hemispheric asymmetries of endogenous ERP components previously observed in simple oddball tasks using nonverbal stimuli (Alexander et al., 1995, 1996; Bruder et al., 1998), we recorded ERP activity from a 30 electrode montage during tonal and phonetic oddball tasks in a within-subjects design. Despite a high accuracy level for both tasks, slightly longer response times indicated higher difficulty level for the phonetic task, which was associated with smaller P3 amplitudes and longer P3 latencies (e.g., Picton, 1992). Increased task demands and different stimulus characteristics may also account for the smaller N1 amplitude in the phonetic task (e.g., Hillyard & Picton, 1987; Näätänen, 1992; Näätänen & Picton, 1987). Nonetheless, the component structure was very similar for both tasks. Most importantly, task-related asymmetries were found for the endogenous ERP components N2 and P3, but not for the exogenous N1 component. Asymmetries for these components revealed, as predicted, a double dissociation: N2 and P3 amplitudes were larger over the right hemisphere for the tonal task but larger over the left hemisphere for the phonetic task. However, the effects were most prominent for N2 and for N2-P3 amplitude, suggesting that hemispheric asymmetries linked to phonetic and tonal processing arise at an early stage of stimulus categorization about 200 ms after stimulus onset, and continue into a later stage of stimulus evaluation, that is, in the region of P3. These findings are in close correspondence to those reported in other studies for auditory tonal (e.g., Alexander et al., 1996; Bruder et al., 1998; Giard et al., 1990; Tenke et al., 1993) and linguistic stimuli (e.g., Ahonniska et al., 1993; van de Vijver et al., 1984). Moreover, the results are also consistent with those of ERP studies using visual nonverbal and verbal tasks (e.g., Alexander et al., 1995; Gevins et al., 1995), supporting the view that these effects originate from modality-independent, higher-order cognitive processes.

Asymmetries in brain morphology are well known (e.g., see reviews by Galaburda, LeMay, Kemper, & Geschwind, 1978; Witelson & Kigar, 1988), which may result in volume-conducted ERP asymmetries at the scalp (Alexander et al., 1995, 1996; Ford et al., 1994a). By using a within-subjects design, we were able to exclude the possibility that structural effects alone accounted for the observed ERP asymmetry effects, because a different asymmetry pattern emerged for phonetic and tonal tasks. In contrast, together with other authors, we argue that structural asymmetries are indeed related to cognitive processing (Ford et al., 1994a; Witelson & Kigar, 1988), ultimately resulting in different ERP topographies for the tonal and phonetic oddball task.

An open question is the extent to which the different endogenous ERP asymmetry for phonetic as compared to tonal stimuli may be due to different stimulus characteristics, independent of their linguistic features. For instance, it is possible that rapid frequency transitions of consonants may contribute to the left hemisphere advantage seen for these stimuli (e.g., Schwartz & Tallal, 1980). Other phonetic dimensions, such as voicing, are evidently also associated with different laterality patterns (see Simos et al., 1997). Although the study did not address the issues of linguistic versus nonlinguistic contributions to these ERP asymmetries, it findings do indicate that asymmetries of endogenous ERPs previously reported for standard oddball tasks are different for typical tonal and phonetic stimuli. Moreover, the direction of the ERP asymmetries, that is, greater N2-P3 amplitude over right hemisphere sites for tones, but over left hemisphere sites for consonant-vowel syllables, are consistent with expectations based on prior dichotic listening studies (Berlin et al., 1973; Bruder, 1991; Sidtis, 1981; Speaks et al., 1982).

Task-Related ERP Topographies

Right-greater-than-left hemispheric differences of N2 amplitude in the tonal task were most substantial at frontocentral sites, whereas the asymmetry of early P3 amplitude was most prominent at parietal-central sites. Evidence from positron emission tomography (PET) studies (Holcomb et al., 1996; Zatorre, Evans, Meyer, & Gjedde, 1992) and EEG findings (Auzou et al., 1995) suggest strongly that both the right prefrontal cortex and the right temporal lobe are involved in a network for maintaining tonal information in auditory working memory and for pitch discrimination. This neurophysiological evidence is corroborated by a left-ear advantage (LEA) typically found in dichotic listening studies using the Complex Tone Test (Sidtis, 1981, 1982; Tenke at al., 1993), and neurological evidence from patients with unilateral brain damage (Sidtis & Volpe, 1988) or unilateral temporal lobe removal (Zatorre, 1988). Moreover, the LEA for complex tones is highly correlated with a hemispheric ERP asymmetry of P3 at parietal and occipital sites, that is, participants with a strong LEA show greater positive amplitudes in the P3 time region over the right hemisphere (Tenke at al., 1993). Although it is still unclear which, if any, of the cognitive processes that have been linked to the P300 wave underlie this asymmetry (e.g., Picton, 1992), a parsimonious interpretation of our findings would be that the right-lateralized frontocentral N2-P3 complex reflects working memory and pitch discrimination processes required for the detection of target tones in the oddball paradigm.

For the tonal task, the right-lateralized early P3 was followed by a later parietal P3-like positivity. This late P3, however, tended to shift to the left parietal region, which replicates the findings of Alexander et al. (1995) who observed a reversal of right frontocentral P3 amplitude superiorities at parietal locations. Alexander et al. speculated that this parietal P3 asymmetry is associated with a localized decision process controlling the response. As late P3-like positivity was clearly linked to a response-related medial-anterior negativity, that is, as reflected in the late P3/N3 factor, the supposition of Alexander et al. is consistent with our data.

For the phonetic task, left-greater-than-right hemispheric differences of N2 were most substantial at lateral temporal-parietal sites covering cortical regions traditionally associated with language perception. Furthermore, the late P3/N3 factor was generally more positive over the left hemisphere, with greater positivity most evident at left medial-parietal sites. Clinical evidence from stimulation mapping and ERPs recorded directly from the human cortex suggests that language functions are organized around the sylvian fissure of the language-dominant (left) hemisphere, with the center of this region involved in decoding of phonemes (e.g., reviewed by Mateer & Cameron, 1989). Zatorre et al. (1992) reported in the above-mentioned PET study that passive listening to speech sounds activated the superior temporal gyrus bilaterally, whereas phonetic discrimination selectively activated areas in the left hemisphere (i.e., parts of Broca's area and the superior parietal region). Magnetoencephalography (MEG) measures of healthy adults performing a visual word recognition task (Salmelin, Service, Kiesilä, Uutela, & Salonen, 1996) provide evidence for a strong activation of the left inferior temporal-occipital cortex (up to 200 ms after stimulus onset) and the left temporal lobe (from 200 to 400 ms). In a series of experiments using computer-modified consonant-vowel syllables ranging between /ba/ and /da/, the N2-P3 complex was found to reflect the phonemic categorization of speech stimuli accurately (Maiste, Wiens, Hunt, Scherg, & Picton, 1995). Moreover, using whole-head magnetic recordings during phoneme perception, Näätänen et al. (1997) have recently located native language-specific mismatch negativities in the auditory cortex of the left hemisphere. It is therefore possible that our N2 findings for both phonetic and tonal stimuli include an asymmetric MMN contribution (see also Aaltonen et al., 1993; Alho et al., 1996; Giard et al., 1990; Näätänen, 1990), but the present paradigm can not distinguish between these overlapping ERP negativities. However, given this line of evidence, we conclude that the left-lateralized temporal-parietal N2-P3 complex observed in this study reflects mental processes required for the discrimination of consonant-vowel syllables.

Several authors have suggested that multiple generators of different neuroanatomical origin contribute to the P3 component, which is assumed to constitute at least two basic subcomponents: a parietal P3b, and an earlier P3a with a more frontal distribution (Johnson, 1993; Molnár, 1994; Picton, 1992). Lesion studies suggest that the prefrontal cortex modulates the amplitudes of N2 and P3, which are assumed to be generated in parietal or temporal regions (e.g., reviewed by Knight, 1990). Latencies and topographies observed for early and late P3 in the tonal task suggest a similarity to these classical P3 subcomponents. The early P3 component, however, appeared to be absent in the phonetic task. If the P3a is indeed related to the fundamental process required in the oddball paradigm, as supposed by Alexander et al. (1995, 1996), and if early P3 resembles P3a, why is there no clear evidence for a phonetic early P3? At first glance, one could assume that early P3 is linked to inherent stimulus characteristics (phonetic/tonal) rather than to the oddball task itself, so that early P3 is linked to regional cortical activity associated with stimulus- or task-specific demands. Perhaps a more likely, but not necessarily exclusive of the former alternative, is that early P3 is delayed in the more difficult phonetic task and is masked by the late P3. Finally, as discussed in the following section, the phonetic early P3 may be masked as a result of an additional experimental manipulation, such as response hand. In any case, our findings strongly suggest that a right-lateralized P3 may reflect fundamental asymmetries for P3 generation, as assumed by Alexander et al. (1996), only for tonal stimuli or other stimuli involving early right-hemispheric processes, but this assumption does clearly not hold for the processing of phonetic stimuli.

Response-Related Modulations of Task-Related ERP Topographies

Voluntary, unilateral movements are typically paralleled by several negative premovement potentials over frontocentral regions of the contralateral hemisphere (Kutas & Donchin, 1980; Neshige et al., 1988; Singh & Knight, 1990). These movement-related potentials (MRPs) are believed to index motor preparatory processes, and are presumably generated by the primary sensorimotor cortex, supplementary, premotor, and prefrontal cortex (Singh & Knight, 1990). Responding to targets with either the left or right hand had a major impact on ERP waveforms of our right-handed sample, primarily affecting late ERP components (N2, P3, N3). However, these findings are not easily explained by equal response-related negativities over contralateral scalp regions.

Intuitively, left-hand responding might appear to be the more demanding condition for right-handers, as compared with their highly overlearned right-hand movements. However, no performance or response latency differences were found between the two response hand groups. But P3 was clearly enhanced in amplitude and shorter in latency for left versus right responses, leading to the conclusion that right-handed individuals compensated for the left response handicap by increasing their effort (cf. Sirevaag, Kramer, Coles, & Donchin, 1989). At the same time, N2 amplitude was reduced for left responses, which might index the same electrophysiological process, an effort-related increased positivity. In addition, the frontal N3 deflection, which occurred at about the same time as the response (i.e., around 480 ms), was enhanced for left responders. The actual motor potential (MP) is preceded by a positive deflection approximately 100 ms before a movement (e.g., see Hillyard & Picton, 1987), which occurred in this study at about 440 ms for the tonal task and at about 485 ms for the phonetic task. If this premotion positivity and the negative motor potential were indeed relatively enhanced for left responses, the observed waveforms could be explained by superimposed but independent processes deriving from the manual response. Furthermore, such an overlap would differentially affect the phonetic and tonal task because of the different response latencies across tasks. These ERP differences would thereby reflect the dissimilar performance challenges linked to the two response hands (cf. Picton, 1992).

The main differences between response hands were dominated by the opposite asymmetries arising from a response-related negativity over the contralateral hemisphere, particularly over frontocentral scalp regions (Kutas & Donchin, 1980; Neshige et al., 1988; Singh & Knight, 1990), beginning as early as 160 ms poststimulus onset. As a consequence, these distinct, asymmetric response-related processes must differentially affect the task-related topographies seen for late ERP components (N2, P3, and N3). Because of the frontocentral origin of the response-related asymmetries, response hand interacted mainly with the tonal task, that is, at right frontocentral sites that appeared to be primarily involved in detecting complex tone targets. For this reason, late ERP components were primarily modulated by response-related negativities over frontocentral regions, and not necessarily over regions where the component amplitudes were maximal. It follows, accordingly, that the more posterior asymmetries observed for the phonetic task were less affected by response-related asymmetries. One reason why the N2-P3 difference was found to be effective in disentangling task-related, topographic effects could be the capacity of a difference measure to eliminate superimposed negativities that overlay both components.

The early P3 was markedly affected by response hand, that is, either reduced with right hand responding or enhanced with left hand responding. To further investigate why there was only vague evidence for an early P3 presence in the phonetic task, separate PCAs were calculated for each response hand, each task, and each of the four combinations of response hand and task. Time course of loadings and topographies of factor scores extracted in these PCAs were compared with the original overall PCA. The extracted factors of the separate PCAs were comparable to the originally extracted factors, and they accurately and concisely described response hand and task differences also evident in the averaged ERP waveforms for all combinations. An early P3 factor was extracted in all PCAs, but was markedly reduced in amplitude in the phonetic as compared with the tonal task in the PCA for right-hand responses. It is not unreasonable to assume that in right-handers the programming of a motor response is indeed supplied by a left-hemispheric network involving frontal supplementary and premotor areas, whereas the actual response execution is initiated by the contralateral primary motor cortex (cf. the close relationship of apraxia and left-hemisphere lesions, e.g., reviewed by De Renzi, 1989). Given these considerations, we propose tentatively that the early P3 in the phonetic task was substantially masked for right-hand responses. Although the exact mechanism remains unclear, another study including a silent counting procedure that requires no overt response might elucidate these issues.

Conclusions

Task-related ERP asymmetries were found for endogenous ERP components, that is, N2 and P3. These distinct, asymmetric ERP topographies presumably reflect differential involvement of cortical structures in identification of complex tones (right frontotemporal) or phonemes (left parieto-temporal), which is consistent with the view that cognitive task operations depend on a network of regionalized, functionally specific subprocessors (cf. Gevins et al., 1995). The findings of this study provide more direct evidence of lateralized brain regions that may contribute to different behavioral ear advantages found in dichotic listening studies using tonal or phonetic stimuli.

The distinct, task-specific asymmetries interact with response hand in an unbalanced fashion. Firstly, the contralateral motor-related negativities arising from the left and right hand responses are unequal in amplitude, and secondly, they differentially affect the ERP topographies associated with phonetic and tonal tasks. It would be difficult, therefore, to conclude anything from the absence of an asymmetry if all responses were made by one hand, because a motor- or response-related potential may contaminate the findings. Thus, a task-related asymmetry effect could easily be overlooked, if the effect was attenuated or eliminated by the superposition of a response-related effect of comparable amplitude. More attention should be given in future studies to controlling or assessing the influence of behavioral responses on late, cognitive ERP components.

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