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Correspondence between brain ERP and behavioral asymmetries in a dichotic complex tone test

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Abstract

Electrophysiologic correlates of perceptual asymmetry for dichotic pitch discrimination were investigated in 20 normal subjects. Brain event-related potentials (ERPs) elicited by dichotic pairs and binaural probe tones in the Complex Tone Test (Sidtis, 1981) were recorded from homologous scalp locations over left and right hemispheres (F3, F4; C3, C4; P3, P4; O1, O2). Baseline-to-peak amplitudes were measured for N100, P200, and a late positive complex consisting of P350, P550, and slow wave. A left ear advantage (LEA) was evident in 70% of the subjects, and hemispheric asymmetries related to this behavioral asymmetry were found for P350 and P550 amplitudes to probe stimuli. Subjects with a strong LEA had greater amplitudes over the right hemisphere than the left, whereas subjects with little or no LEA showed a nonsignificant trend toward the opposite hemispheric asymmetry. Hemispheric asymmetry of these late ERPs at parietal and occipital sites was highly correlated with behavioral asymmetry. These findings suggest the utility of electrophysiological measures in assessing hemispheric asymmetries for processing complex pitch information.

Descriptors: Event-related potentials, P300 (P3), Dichotic listening, Pitch discrimination, Laterality

The perceptual asymmetries evident during dichotic listening have been used to study differences between the functional organization of auditory areas in the two cerebral hemispheres. A range of verbal materials produce a right ear advantage (REA) in performance on dichotic listening tasks (Bryden, 1988), a behavioral asymmetry consistent with the typical dominance of the left hemisphere for language. The general correspondence between performance in verbal dichotic listening tasks and clinical evidence bearing on the organization of language in the brain has reinforced the belief that perceptual asymmetries during dichotic listening can provide evidence of functional localization.

Although the study of left hemisphere functions can derive significant advantage in both initial design and subsequent interpretation by referring to well-defined language dysfunctions associated with damage to specific neuroanatomic regions, there are no comparably established clinical syndromes to which studies of right hemisphere functions can refer. At various times, both music and emotional prosody have been suggested as right hemisphere analogs to language, but unilateral right hemisphere damage does not consistently produce identifiable syndromes in either of these domains (Brust, 1980; Cancelliere & Kertesz, 1990; Gates & Bradshaw, 1977). Despite the lack of a readily identifiable clinical syndrome associated with auditory processing by the right hemisphere, there is at least one area of auditory function in which the right hemisphere has a demonstrable advantage over the left. Nonverbal dichotic listening studies have demonstrated a left ear advantage (LEA) for the discrimination of the pitch of complex tones (Sidtis, 1980), suggesting a right hemisphere advantage for this task.

Using the Complex Tone Test (Sidtis, 1981), the LEA for pitch discrimination has been shown to be complementary to the REA for speech syllables in normal adults (Sidtis, 1982) and children (Sidtis, Sadler, & Nass, 1987). Moreover, the assumption that the LEA that most normal listeners demonstrate in this task relates to right hemisphere function is supported by findings from patients with unilateral brain damage (Sidtis & Volpe, 1988) and with surgical or pathological disconnection of the two hemispheres (Sidtis, 1988; Sidtis, Sadler, & Nass, 1989). The role of the right hemisphere in pitch processing has also found support in a study of patients after unilateral temporal lobe surgery (Zatorre, 1988) and, in one patient, after a transient ischemic attack (Sidtis & Feldman, 1990).

Although studies that demonstrate selective deficits after focal lesions can establish functional localization, they are less effective at revealing detailed characteristics of the localized

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function because the clearest evidence of localization typically comes from the most severe deficit. Once localization is established, however, psychophysical and electrophysiological techniques can be used with greater confidence in both normal and abnormal subjects to study the function in question in greater detail. To establish the electrophysiological correlates of the LEA for complex pitch perception in normal listeners, the present study recorded brain event-related potentials (ERPs) during performance on the Complex Tone Test. ERPs recorded from homologous sites overlying left and right cerebral hemispheres provide a means of examining both the general relationship between ERP and perceptual asymmetries and the degree to which individual differences in such asymmetries are related to each other.

One advantage of measuring ERPs during the Complex Tone Test is that ERP components are time locked to the tones and may therefore provide evidence concerning the stage of information processing in which behavioral asymmetries arise. The early ERP components, such as N100, are thought to be primarily exogenous because they are dependent on physical stimulus variables. N100 is, however, also modulated by selective attention (Hillyard & Picton, 1979; Näätänen & Picton, 1987) and by physiological arousal (Kerkhof, 1982). Later ERP components, most notably the classical P300 and slow wave, are thought to be primarily endogenous because they are influenced by the salience or significance of the stimulus and by the information processing demands of the task (Donchin, 1979; Ruchkin & Sutton, 1983). By measuring exogenous and endogenous ERP components during the Complex Tone Test, we sought to determine whether behavioral asymmetries in this task are related to early sensory/attentional processes (e.g., as reflected by N100) or to later information processing (e.g., as reflected by P300).

Although a mean LEA of 5–10% has consistently been observed on the Complex Tone Test (Bruder et al., 1989; Sidtis, 1981, 1982), there are considerable individual differences in both the magnitude and direction of perceptual asymmetry. Among right-handed adults, 68% had an LEA, 21% had an REA, and 11% had no ear advantage (Sidtis et al., 1989). In the present study, the relationship between individual differences in perceptual asymmetry and ERP measures of hemispheric asymmetry was investigated by comparing ERPs for two groups of normal adults with different behavioral asymmetries: those with a strong LEA and those with little or no LEA. The hypothesis was that the strong LEA subjects would exhibit greater evidence of ERP asymmetries indicative of right hemisphere dominance for processing complex tones when compared with subjects with little or no LEA. The strength of the relationship between perceptual and ERP asymmetries for individuals was also examined using regression analyses.

Methods

Subjects

ERPs were recorded from 20 subjects (12 women and 8 men) whose ages ranged from 21 to 47 years ($M = 31.8$, $SD = 9.1$). All but one subject was right handed on the Edinburgh Handedness Inventory (Oldfield, 1971). Ten items concerning hand preference for writing, drawing, holding a spoon, and so forth, were used to compute a laterality quotient (*LQ*), where $LQ = 100(R - L)/(R + L)$. A score of 100 equals completely right handed and −100 equals completely left handed. Nineteen of the subjects had handedness *LQ*s in a moderately to strongly right-handed range (44–100). One subject, who reported herself to be right handed, had a handedness *LQ* of −5. Eleven of the subjects had one or more family members who were left handed or ambidextrous. Subjects were screened for hearing loss using standard audiometric procedures. All subjects were required to have less than a 10-dB difference between ears at threshold, and a hearing loss no greater than 25 dB at 500, 1,000, or 2,000 Hz. Two subjects who performed the task at 98% or better for both ears were not included because a valid behavioral asymmetry could not be measured. Subjects were also excluded if a history of psychopathology, substance abuse, or organic brain impairment was present. Subjects were volunteers and were paid $10.00/hr for their participation.

Complex Tone Test

A different complex tone was presented simultaneously to the two ears, followed by a binaurally presented probe tone. The probe tone was either the same as one member of the dichotic pair or different from both. The subject pressed a response button when the probe matched one of the dichotic tones. Each trial was 7.5 s in duration and was signalled by the onset of a fixation light 1 s prior to the initial dichotic pair of complex tones. The dichotic pair was followed 2 s later by the probe tone. The subject was required to respond during a 3-s response period that was signalled by the offset of the fixation light, 1.5 s after the probe tone.

A digitally synthesized version of the Complex Tone Test was generated for this study using the MUSIC-11 (Vercoe, 1979) software package to generate the individual tones, and the WAVED and RANDOM programs in the Barus Laboratory Interactive Speech System BLISS (Mertus, 1984) to edit the tones, verify their durations and spectral composition, and create the dichotic and probe stimuli and sequences. The synthesis and analysis were conducted using a Digital Equipment Corporation Micro PDP-11/83 computer with a Data Translation digital-to-analog converter. All stimuli were synthesized at a 20-kHz sampling rate, and each channel was band-pass filtered (75 Hz to 9.5 kHz) through a pair of Krohn-Hite filters. There were eight complex tones with fundamental frequencies corresponding to the major notes in the octave between middle C (264 Hz) and C5 (528 Hz). Each tone was synthesized using sinusoids at the fundamental frequency and the first three harmonics to approximate a square wave. Tones were 250 ms in duration, with rise and decay times of 25 ms.

Trials were arranged in six 28-trial blocks. In each block, half of the probe stimuli matched a member of the dichotic pair and there were equal numbers of left and right ear matches. Two practice blocks (binaural and dichotic) were also included. Stimuli were presented at 72 dB SPL via a matched pair of TDH-49 earphones. Earphone orientation and response hand were randomized across subjects.

Behavioral Asymmetry

An ear advantage *LQ* was computed for each subject from the percentage of correct responses to probe stimuli that matched right (*R*) or left (*L*) stimuli in the dichotic pair: $LQ = 100(R - L)/(R + L)$. The median ear advantage *LQ* for the 20 subjects was used to divide them into two groups: (a) 10 subjects with a strong LEA greater than the median (S-LEA), and (b) the remaining subjects who had a weak LEA ($n = 4$) or an REA ($n = 6$) (N-LEA). Our rationale for using the median *LQ* to form subgroups with different ear advantages was threefold: (a) it is an objective (unbiased) split that results in two groups with equal sample sizes; (b) the median *LQ* is a relatively stable value (the median for the 20 subjects in this study is essentially the same as that for a larger sample of 92 normal adults); and (c) subjects with a weak LEA (less than the median) are likely to be heterogeneous in the direction of their physiological asymmetry. Combining their data with those for subjects having a S-LEA would increase variability and weaken ERP asymmetry findings for LEA subjects.

ERP Recording

Scalp recordings were made at four lateral pairs of electrodes (F4, F3; C4, C3; P4, P3; O2, O1) and along midline (Fz, Cz, Pz, Oz) using a commercially available electrode cap (Electro Cap International, Inc.). EEGs were recorded with a nose tip reference and a mastoid ground. A nose reference was chosen for this study because it is inherently symmetric and has been used successfully in prior studies (e.g., Vaughan & Ritter, 1970; Vaughan, Ritter, & Simson, 1980). Electrodes at supra- and infraorbital sites surrounding the right eye were used to monitor eyeblinks and vertical eye movements (bipolar), and electrodes at right and left outer canthi monitored horizontal eye movements (bipolar). The cap and reference electrodes were composed of tin, and all other electrodes were standard Beckman Ag/AgCl electrodes. EEG and EOG were recorded from amplifiers with a band pass of 0.032–50 Hz. Gains were set at 10,000 for EEG channels and 5,000 for EOG channels. A PDP 11/34 minicomputer recorded the ERP data (100 Hz sampling rate) and the behavioral responses and stored them on hard disk. Data were acquired over 1,200-ms recording epochs for dichotic pairs and probe stimuli, with a 170-ms prestimulus period.

ERP Analyses

Averaging and artifact removal. Subjects were instructed to inhibit blinks or eye movements whenever the fixation light was on. Trials contaminated by blinks or large amplitude eye movements were excluded from analysis by using a 50-μV RMS rejection criterion for EOG channels. This cutoff level was effective in eliminating blinks and large eye movements during extensive piloting in our recording environment. This criterion led to a mean of 7 ($SD = 10.5$) trials lost from a total of 168 trials; most losses were due to blinks. Smaller eye movements were corrected on a trial-by-trial basis whenever the RMS amplitude of the EOG exceeded the RMS amplitude at Fz. By using this RMS comparison, the correction procedure is less susceptible to overcorrection when eye movement is minimal and the ERP has a frontal distribution.

The correction procedure eliminated EOG contributions to each EEG channel using linear regression procedures (Gratton, Coles, & Donchin, 1983; Verleger, Gasser, & Moecks, 1982). After removal of DC offsets, transfer coefficients between the EOG channels and the EEG channels were computed from the corresponding correlation coefficients. In our implementation, transfer coefficients were computed independently for each trial. No attempt was made to compute coefficients appropriate for blinks, because those trials were already eliminated. After eye movement correction, trials in which EEG RMS amplitude exceeded 50 μV were excluded from analysis.

Averaged ERP waveforms were computed for each subject and across subjects on the basis of electrode site (frontal, central, parietal, occipital), hemisphere (left, right), and condition (different, same right, same left). The ERP waveforms were filtered to an equivalent upper cutoff frequency (−3 dB) of 9 Hz (Ruchkin & Glaser, 1978) to improve the reliability of measurements of the late peaks. Although this filter attenuated N100 by approximately 33%, it did not affect the resolution of relative amplitude differences across conditions, hemispheres, or groups. Although faster activity was markedly reduced, we did not intend to measure components earlier than N100 (e.g., P50). This report presents ERPs recorded at lateral electrodes to dichotic pair and probe stimuli. ERPs to probes are for stimuli that were correctly identified as being the same as a tone in the dichotic pair or as being different (correct rejection).

Baseline-to-peak measurements. Baseline-to-peak amplitudes were measured interactively for the following ERP components for probe stimuli, named for their polarities and characteristic latencies: (a) N100, a negative peak between 80 and 130 ms poststimulus; (b) P200, a positive peak between 170 and 250 ms; (c) P350 and P550, a pair of late positive peaks between 260 and 480 ms and between 430 and 700 ms, respectively; and (d) positive slow wave, computed as the average value between 730 and 1,030 ms. Because the late positive peaks (P350 and P550) were identifiable in the waveforms of each subject, measures of baseline-to-peak amplitudes, rather than averages across time windows, were obtained to maximize the distinction between the overlapping components. The 170-ms prestimulus interval was used as the baseline for amplitude measurements. For the dichotic stimuli, N100, P200, and slow wave were computed as described for probe stimuli. However, the variable incidence and smaller amplitude of the late positive P350 and P550 components for dichotic stimuli required the use of average values within their respective time windows.

Statistical methods. For probe stimuli, the baseline-to-peak amplitudes of each component were subjected to a repeated measures analysis of variance (ANOVA) with the following factors: Group (S-LEA, N-LEA), Electrode (Frontal, Central, Parietal, Occipital), Hemisphere (Right, Left), and Condition (Different, Same Right, Same Left). The same repeated measures ANOVA was conducted for ERP amplitudes for dichotic stimuli, except that no Condition variable was included because this variable has relevance only for the discriminative probe stimuli. Significant interactions involving Electrode or Hemisphere were also evaluated after scaling the amplitudes for each condition by the vector amplitude measured across electrodes in each subject (McCarthy & Wood, 1985). All *F* ratios were evaluated using degrees of freedom computed using the Greenhouse-Geisser epsilon correction (Jennings & Wood, 1976) to counteract heterogeneity of variance–covariance matrices associated with repeated measures. Only findings that reached a .05 significance level are considered in this report.

We also examined correlations between ear advantages and ERP asymmetries as a measure of the strength of the relationship between these continuous variables. For each component, we computed a hemispheric difference (right hemisphere − left hemisphere amplitude) as a measure of physiological asymmetry at each of the lateral pairs of electrodes. We then computed product-moment correlations between these hemispheric differences and ear advantages (*LQ*s) across all subjects. Statistically significant correlations were verified using scaled amplitudes and Spearman rank order correlations.

Results

Behavioral Data

Across all subjects, the mean accuracy for matching probe tones to the dichotic pair was significantly higher ($t = 3.02$; $df = 19$; $p < .01$) for matches to the left ear (86% correct) than the right ear (76% correct). The median ear advantage *LQ* was −5.0 ($M = -7.2$, $SD = 10.9$), with individual scores ranging from −37 to 8. Fourteen subjects (70%) had an LEA, and the remaining six subjects had an REA. When subjects were divided at the median *LQ* score into two groups, the S-LEA group had a mean *LQ* of −14.9 ($SD = 10.1$) and the N-LEA group had a mean *LQ* of 0.6 ($SD = 3.9$). No differences were evident between the S-LEA and N-LEA groups in sex, age, or handedness. There were six women and four men in each group, and there was no difference between the mean age of S-LEA subjects (30.3, $SD = 9.5$) and N-LEA subjects (33.3, $SD = 9.0$). Edinburgh handedness *LQ* means were 74.4 ($SD = 16.4$) for the S-LEA group and 77.3 ($SD = 32.9$) for the N-LEA group. There was a family history of left handedness in seven S-LEA and four N-LEA subjects.

ERP Waveforms to Probe Tones: Overview

Figure 1 shows the average ERP waveforms of the S-LEA and N-LEA groups at electrode sites over each hemisphere for correct judgments to probe tones. N100 and P200 components are most prominent frontocentrally. A late positive complex is also clearly evident, which is small frontally and maximum parietally and consists of peaks at about 350 and 550 ms, followed by a sustained slow wave. Hemispheric differences related to behavioral asymmetry (S-LEA vs. N-LEA) were confined to this late positive complex. S-LEA subjects showed greater amplitude of late positive peaks (P350 and P550) over the right hemisphere than the left, whereas N-LEA subjects exhibited the opposite asymmetry. The difference in asymmetry between S-LEA and N-LEA groups was evident for both same and different judgments (Figure 2).

N100 and P200

ANOVAs of N100 and P200 amplitude showed a main effect of Electrode, which reflects the frontocentral maximum scalp distribution (N100: $F[1.4, 24.2] = 79.23$, $p < .001$; P200: $F[1.6, 28.3] = 6.91$, $p < .01$). N100 exhibited no significant interactions and P200 showed only a Condition × Electrode interaction ($F[2.6, 46.3] = 7.68$, $p < .001$; vector scaled: $F[2.9, 52.6] = 4.41$, $p < .01$). The nature of this interaction is evident in Figure 3a, which shows average waveforms for probe stimuli that were correctly matched to a member of the dichotic pair (same), and for probe stimuli that were correctly rejected (different). The scalp distribution for the different condition shows greater frontal and less posterior P200 amplitude when compared to the distribution for the same condition.

Late Positive Complex

The two late positive peaks and slow wave showed significant electrode effects related to their posterior topography (P350: $F[1.4, 25.0] = 30.96$, $p < .001$; P550: $F[1.3, 22.6] = 34.87$, $p < .001$; slow wave: $F[1.2, 20.9] = 9.46$, $p < .01$). The Condition × Electrode interaction seen for P200 was also present in ANOVAs for P350 ($F[3.0, 54.2] = 18.72$, $p < .001$; vector scaled: $F[2.3, 40.8] = 5.66$, $p < .01$) and P550 ($F[3.2, 57.1] = 16.04$, $p < .001$; vector scaled: $F[2.1, 37.0] = 8.05$, $p < .01$). Although the scalp distributions for P350 and P550 shared a common parietal maximum for all conditions (Figure 3A), there was relatively greater frontal positivity for different than for same conditions.

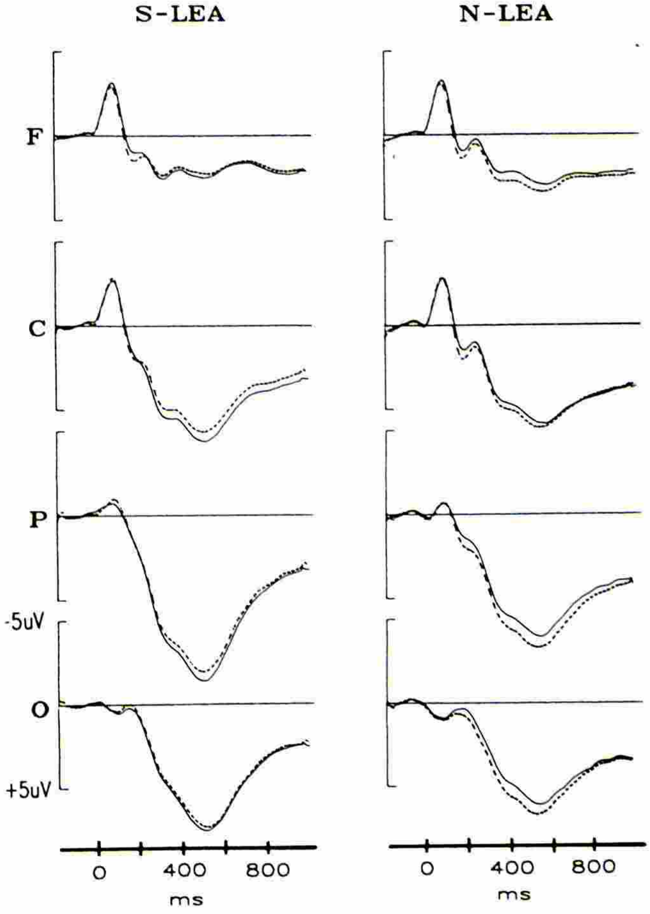

Figure 1. Average waveforms for probe stimuli for S-LEA and N-LEA groups at right hemisphere (solid line) and left hemisphere (dashed line) sites averaged over correct same and different judgments.

The difference between S-LEA and N-LEA groups in hemispheric asymmetry for late positive peaks (Figures 1 and 2) were substantiated by significant Group × Hemisphere interactions in the ANOVAs for both P350 ($F[1, 18] = 6.14$, $p < .05$) and P550 ($F[1, 18] = 11.78$, $p < .01$). These interactions were also present after vector scaling (P350: $F[1, 18] = 5.11$, $p < .05$; P550: $F[1, 18] = 11.18$, $p < .01$). Analysis of simple effects revealed that S-LEA subjects had greater P350 and P550 amplitudes over the right hemisphere than the left (P350: $F[1, 9] = 4.80$, $p = .05$; P550: $F[1, 9] = 19.71$, $p < .01$), but N-LEA subjects showed a nonsignificant asymmetry in the opposite direction (P350: $F[1, 9] = 2.40$, $p = .15$; P550: $F = 3.50$, $p = .09$).

A Hemisphere × Condition × Electrode interaction was found for P350 ($F[3.1, 55.1] = 3.15$, $p < .05$), P550 ($F[2.8, 51.2] = 5.36$, $p < .01$), and slow wave ($F[3.2, 57.6] = 6.63$, $p < .001$). After vector scaling, the interaction remained significant for P550 ($F[3.4, 61.1] = 6.50$, $p < .001$) and slow wave ($F[2.7, 48.2] = 3.67$, $p < .05$) but not for P350. Figure 3B shows difference waveforms obtained by subtracting waveforms for the same from the different conditions at electrode sites over

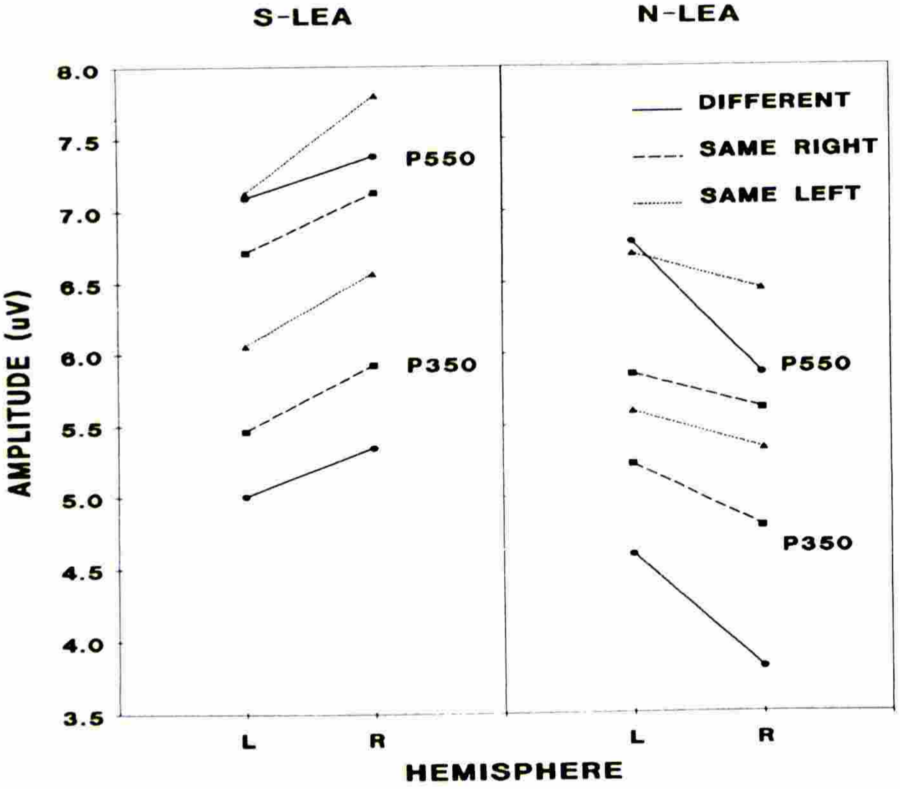

Figure 2. Mean baseline-to-peak amplitude of P350 and P550 over left and right hemisphere for S-LEA and N-LEA groups plotted separately for probe tones that were correctly judged to be different or same (right or left ear match).

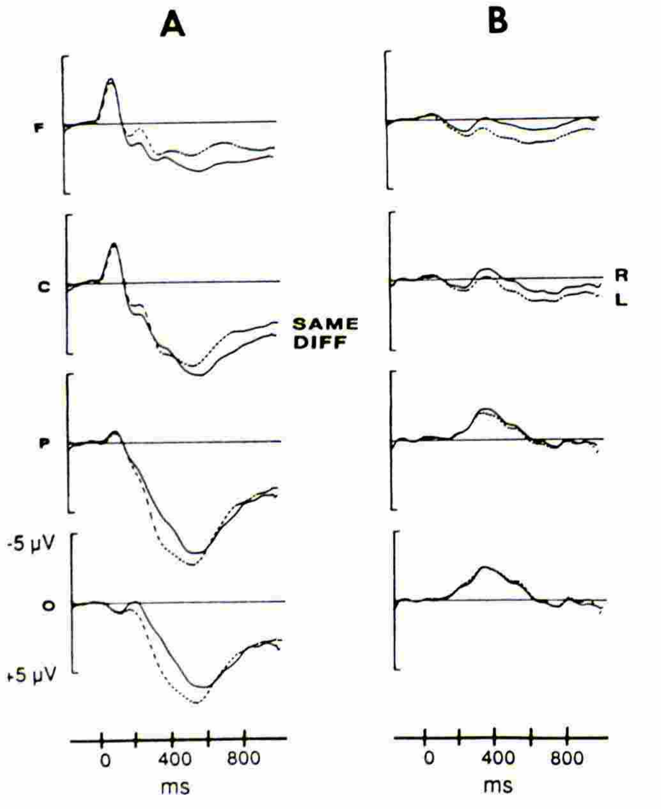

Figure 3. (A) ERP waveforms to probe stimuli for correct different and same judgments (averaged over right and left hemisphere sites). (B) Difference waveforms obtained by subtracting same from different waveforms for right and left hemisphere.

each hemisphere. At frontocentral sites, but not at posterior sites, the amplitude of the late positive P550 and slow wave components was greater for different than same judgments and this effect was larger over the left than the right hemisphere. In contrast, the amplitude of the late positive peaks (P350 and P550) at parietal and occipital sites was less for different than for same judgments. The difference waveforms show that this effect peaked in the region of 350 ms, and was equally present over each hemisphere. The difference in hemispheric asymmetry for same and different conditions, and its dependence on electrode site, is further illustrated in Figure 4. It is apparent that P550 and slow wave at frontocentral sites was greater over the left hemisphere than the right for the different condition, but the opposite hemispheric asymmetry was present for both same conditions.

Correlational Analyses

Table 1 gives the correlations between ear advantage (*LQ*) and ERP asymmetry for each electrode site and condition. Significant correlations between ear advantage and ERP asymmetry were primarily present for P350 and P550 at parietal and occipital sites. The negative correlations indicate that higher accuracy for left than right ear stimuli (negative *LQ*) was associated with larger P350 and P550 amplitude over the right than the left hemisphere. These correlations were equally strong for same and different conditions. Figure 5 shows scatter plots and least squares regressions relating ear advantages and P550 asymmetry (averaged over conditions) for all subjects. The correlations at parietal ($r = -.68$, $p < .01$; Spearman rho $= -.68$) and occipital ($r = -.60$, $p < .01$; Spearman rho $= -.77$) sites were not caused by a few outliers.

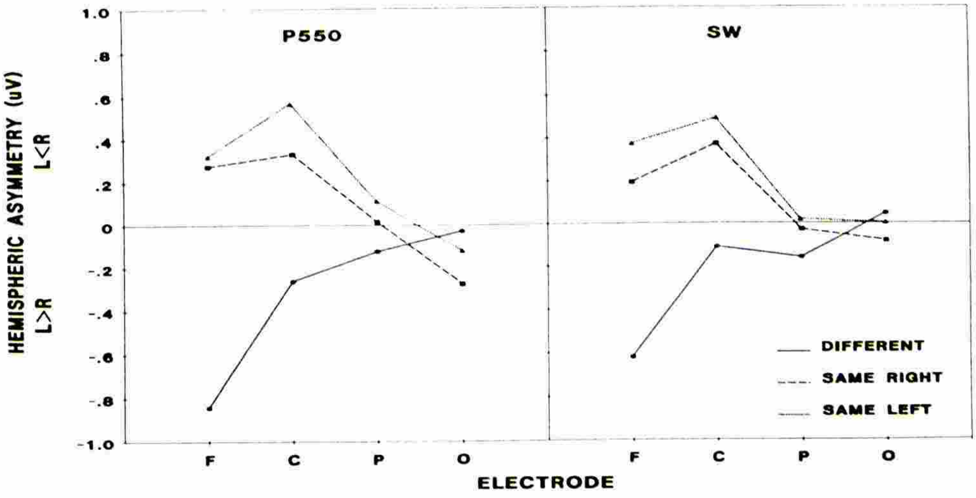

Figure 4. Mean hemispheric asymmetries of P550 and slow wave (SW) as a function of electrode site for probe tones that were correctly judged to be different or same (right or left ear match).

ERP Asymmetry and Handedness

Separate repeated measures ANOVAs of ERPs were conducted using handedness and family history of left handedness as a grouping factor. When subjects were divided at the median Edinburgh handedness *LQ* into two groups, there was no evidence of a difference in ERP asymmetry between these groups; that is, there was no Group × Hemisphere interaction. Likewise, the ERP findings for subjects with no left-handed relatives ($n = 9$) were indistinguishable from those with left-handed relatives ($n = 11$). However, caution is necessary in interpreting these negative results because of the limited range of handedness scores.

Table 1. *Correlations Between Ear Advantage (LQ) and Hemispheric Asymmetry*

ERP component Electrode	Condition Same right	 Same left	 Different
N100			
F	.14	.22	.08
C	.02	−.09	−.28
P	−.07	−.08	−.53*
O	−.57**	−.23	−.39
P200			
F	.27	.35	.23
C	.42	−.11	−.07
P	−.10	−.13	−.26
O	.16	−.34	−.47*
P350			
F	−.22	.05	−.33
C	−.19	−.52*	−.50*
P	−.67**	−.58**	−.65**
O	−.53*	−.55*	−.69**
P550			
F	−.04	−.18	−.11
C	.12	−.29	−.57**
P	−.65**	−.49*	−.64**
O	−.65**	−.61**	−.63**
Slow wave			
F	−.27	−.20	−.15
C	−.20	−.20	−.20
P	−.45*	−.08	−.24
O	−.23	−.39	−.45*

*$p < .05$, **$p < .01$; two-tailed test.

ERP Waveforms to Dichotic Pairs

Figure 6 shows grand mean waveforms for the dichotic stimuli. Although the N100 and P200 components were comparable to those seen for probe stimuli, the late positive components were much smaller in amplitude. Additionally, the waveforms for dichotic stimuli show a sustained frontal negativity following P200. Figure 6 shows no evidence of the behavior-related hemispheric asymmetries observed for late positive peaks to probe stimuli. Repeated measures ANOVAs of average amplitudes showed no evidence of a Group × Hemisphere interaction for P350 ($F[1, 18] = 0.35$, $p > .50$), P550 ($F[1, 18] = 0.50$, $p > .25$), or slow wave ($F[1, 18] = 0.02$, $p > .50$). The expected electrode effect attained significance for N100 ($F[1.5, 27.3] = 88.19$, $p < .001$), P350 ($F[1.3, 23.4] = 20.38$, $p < .001$), P550 ($F[1.2, 22.1] = 39.54$, $p < .001$), and slow wave ($F[1.2, 21.3] = 38.30$, $p < .001$).

Discussion

Our subjects showed a mean LEA of 10% on the Complex Tone Test, 70% of them performing better for left ear than right ear stimuli, which agrees with prior evidence of right hemisphere advantage for this task (Sidtis, 1981; Sidtis et al., 1987). Moreover, individual differences in ear advantage were related to hemispheric asymmetry of late positive ERPs to probe tones. Subjects with a strong LEA had greater late ERP positivities over the right hemisphere than the left, whereas subjects with little or no LEA showed a nonsignificant trend toward the opposite ERP asymmetry. Although dichotomizing subjects based on the median ear advantage was useful in comparing ERPs for S-LEA and N-LEA subjects, regression analyses revealed a continuous relationship between ear advantages for complex tones and asymmetries of late ERP positivities.

It is common to find three late positive ERP components, two positive peaks and a sustained slow wave (Verleger, 1988). Both of the positive peaks in this study (P350 and P550) had parietal maximum scalp distributions typical of the classical P300 component. They also shared the same behavior-related hemispheric asymmetries, although the asymmetry for P550 was some-

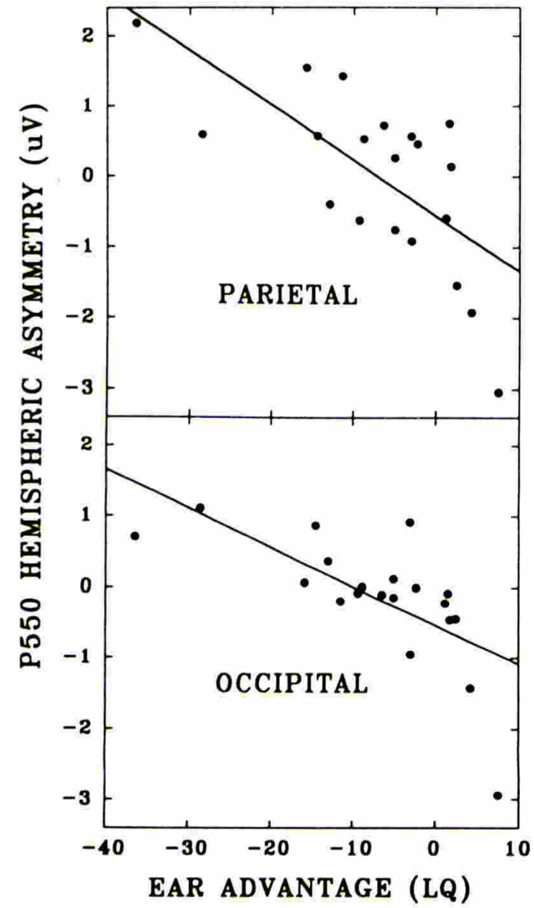

Figure 5. Scatter plot of P550 hemispheric asymmetry versus ear advantage (*LQ*), collapsed across conditions, at parietal and occipital sites.

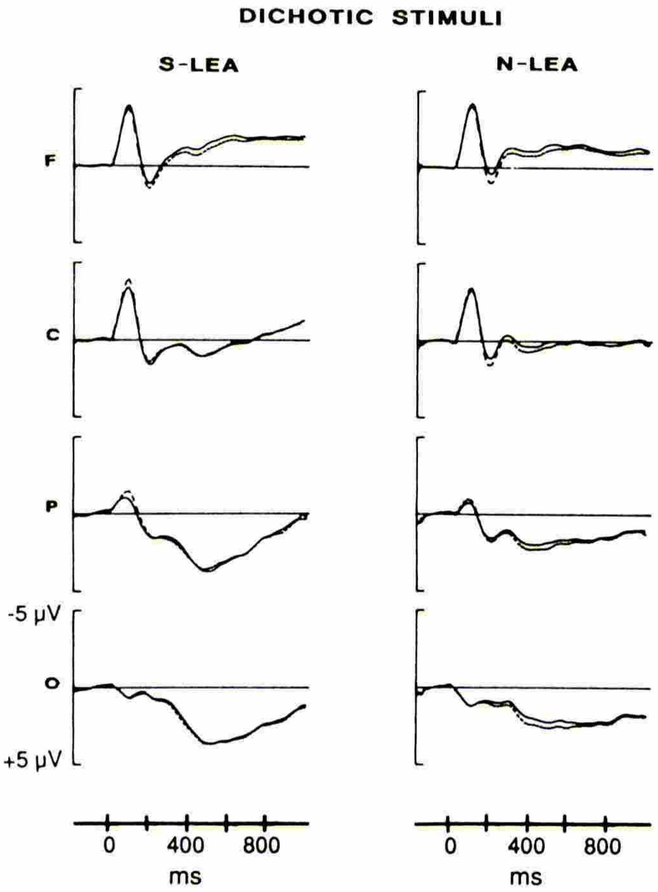

Figure 6. Average waveforms to dichotic stimuli for S-LEA and N-LEA groups at right hemisphere (solid line) and left hemisphere (dashed line) sites.

what stronger. Both peaks may therefore reflect a common process, perhaps representing an initial evaluation and a subsequent reevaluation of stimulus information (Friedman, Vaughan, & Erlenmeyer-Kimling, 1981). Positive slow wave has a scalp distribution similar to that of the late positive peaks. However, slow wave and P300 behave differently in relation to experimental variables (Ruchkin & Sutton, 1983) and display different hemispheric asymmetries (Bruder et al., 1992; Ruchkin, Johnson, Mahaffey, & Sutton, 1988). In the present study, asymmetries of the two late positive peaks during the Complex Tone Test were separable from asymmetries of slow wave; slow wave did not show the behavior-related hemispheric asymmetries.

Hemispheric differences related to behavioral asymmetry were confined to the late positive peaks (P350 and P550), which has implications for understanding the processes that might underlie ear advantages for complex tones. Early sensory or attentional processes, at least those that would be reflected in N100 amplitude, do not appear to be related to ear advantages for complex tones. More likely candidates are stimulus evaluation, short-term memory, and judgmental processes, which are thought to modulate the amplitude of late positive components.

Asymmetries of late ERP components, in particular P300, appear to depend on both the nature of the cognitive processing (e.g., whether it is language or nonlanguage processing) and on the subject's hemispheric dominance for this processing. This observation supports the conclusion that these ERP asymmetries are related to asymmetrically mediated cognitive processes rather than to asymmetric electrode placement or to a fixed structural difference between hemispheres (Donchin, Kutas, & McCarthy, 1977; Rugg, 1983). The S1–S2 (i.e., dichotic probe) nature of the Complex Tone Test provides further evidence that late ERP asymmetries are processing dependent. A behavior-related asymmetry occurred only to probe stimuli, when subjects presumably were evaluating the probe stimulus, comparing it to the short-term memory template of the preceding dichotic pair, and making a judgment. This asymmetry may therefore reflect a hemispheric asymmetry of cognitive processes related to the classification of the probe tone.

Citing evidence that the amplitude of late ERP components, such as P300, reflect the extensiveness of control processes related to task demands, Rugg, Kok, Barrett, and Fischler (1986) suggested that hemispheric asymmetries in the amplitude of late components may reflect differences in "processing effort" or the "amount of resources" in the two hemispheres. Greater late positive amplitude over the right hemisphere in subjects with strong LEA may therefore reflect the greater involvement of this hemisphere in complex tonal processing. A recent brain imaging study (Coffey, Bryden, Schroering, Wilson, & Mathew, 1989) reported similar evidence of hemispheric asymmetries for dichotic pitch perception. Coffey et al. measured regional cerebral blood flow at resting baseline and during a dichotic pitch discrimination task, which yielded an LEA in 75% of right-handed subjects. Ear advantages in this task were associated with increased activity in the contralateral temporal lobe. Subjects with an LEA showed greater activation over right posterior temporal cortex, whereas those with an REA showed activation over the left temporal region. Taken together, the findings of Coffey et al. and the present study provide support for the use of dichotic listening tests as indices of hemispheric asymmetry for complex pitch discrimination.

Prior studies have also found ERP correlates of left hemisphere dominance for language processing in dichotic listening (Neville, 1974; van de Vijver, Kok, Bakker, & Bouma, 1984; Woods, Hillyard, & Hansen, 1984) and divided visual-field tests (Kok, van de Vijver, & Bouma, 1985; Nelson, Collins, & Torres, 1990; Neville, Kutas, & Schmidt, 1982). Neville (1974) recorded ERPs to dichotic digit pairs and found shorter latencies of early ERP components (N100 and P200) from the left hemisphere than the right. Woods et al. (1984) observed greater attention-related negativity over the left hemisphere than the right during selective listening to speech passages. The study by van de Vijver et al. (1984) is particularly relevant here because they related individual differences in ear advantages on a dichotic digit recall task to ERP asymmetries recorded during the task. Subjects with an REA for digit recall showed an asymmetry of sustained positivity during the preresponse period that was strongly correlated with their behavioral asymmetry. In contrast, subjects with an LEA for digit recall showed a smaller, nonsignificant ERP asymmetry. Van de Vijver et al. concluded that the ERP asymmetries represent greater mobilization of resources from the left hemisphere in this verbal dichotic task. Studies measuring late ERP components (P300 or N410) in divided visual-field experiments have found greater amplitude over the left hemisphere than the right in letter matching (Kok et al., 1985) and word identification tasks (Neville et al., 1982). Most recently, Nelson et al. (1990) used a divided visual-field "oddball" task with language and nonlanguage stimuli. P300 amplitude (i.e., maximum positivity between 350 and 750 ms) was larger over the left parietal (P3) than the right parietal (P4) site in right-handed subjects when the language stimulus was presented to the right visual field (i.e., the left hemisphere). This asymmetry was not found for nonlanguage stimuli, for left-handed subjects, or for N200 and slow wave components. Nelson et al. concluded that P300 lateralization in right handers reflects the homogeneity of their hemispheric dominance for language processing.

Behavior-related ERP asymmetries were present for both same judgments (correct matches) and different judgments (correct rejections). However, the ERP data for same and different judgments did differ in some important respects. The scalp distribution for different judgments had greater frontal and less posterior positivity when compared to same judgments. At parietal and occipital sites, the difference in positivity for same and different judgments occurred in the region of 200–600 ms, with a peak at about 350 ms. Similar findings have been reported for S1–S2 face matching (Barrett, Rugg, & Perrett, 1988) and picture matching (Friedman, Putnam, Ritter, Hamberger, & Berman, 1992). As Barrett et al. indicated, it is impossible to tell whether this effect is due to an enhancement of a positive-going potential to same stimuli or to an increase in a negative component to different stimuli. They suggested, however, that this same–different effect is due to larger N400 amplitude to different stimuli and is analogous to N400 findings for verbal stimuli (Kutas & Hillyard, 1983; Rugg, 1984). The same–different effect at frontal and central electrodes is unlike that seen at the more posterior sites. Greater positivity for different than for same judgments at frontocentral sites extended from P200 to the end of the recording epoch (i.e., 1,000 ms). The late positive ERPs, in particular slow wave at frontocentral sites, were differentially lateralized for same and different judgments; they were greater over the left hemisphere for different judgments and greater over the right hemisphere for same judgments. These findings are consistent with the view that same and different judgments are mediated by two distinct processes (Magnani, Mazzucchi, & Parma, 1984; Taylor, 1976).

Hemispheric asymmetry of late cognitive ERPs identified with the classical P300 component was related to perceptual asymmetry for complex pitch perception in normal listeners. The ERP asymmetries reflected the known relationship between ear and hemisphere in dichotic listening studies; better performance for stimuli presented to one ear was accompanied by greater late positive activity over the contralateral hemisphere. The larger effect over the right hemisphere is consistent with the localization established in lesion studies. Further research is needed to clarify the mechanisms that underlie individual differences in ERP and behavioral asymmetries. For example, it is not clear to what extent these differences are due to individual differences in hemispheric specialization or to variations in "characteristic arousal asymmetry" (e.g., Levy, Heller, Banich, & Burton, 1983). Moreover, studies using current-source density and source localization techniques might be of value to further clarify the origins of hemispheric asymmetries of late ERPs.

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