Response- and Stimulus-Related ERP Asymmetries in a Tonal Oddball Task: A Laplacian Analysis

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Summary: Previous studies have found greater P3 amplitude over right than left hemisphere sites in a tonal oddball task with a reaction time (RT) response. This asymmetry had a central topography, and interacted with response hand. Identification of the processes underlying these asymmetries requires the use of additional methods for separating response- and stimulus-related contributions. We applied local Hjorth and spherical spline algorithms to compute surface Laplacian topographies of ERP data recorded from 30 scalp electrodes in a pooled sample of 46 right-handed healthy adults. For both methods, the current sources underlying the late positive complex were largest at medial parietal regions, but were asymmetric at central and frontocentral sites. Although a frontocentral sink contralateral to the response hand contributed to the asymmetry of the classic P3 peak, the source asymmetry was most robust after the sink had resolved. The late source was largest at electrode C4 for right hand responses, and was further enhanced in subjects showing a dichotic left ear advantage, but was unrelated to response speed. We conclude that the right hemisphere source reflects an interaction of response-related asymmetries with right hemisphere processes responsible for pitch discrimination.

Key words: Current source density; Event-related potentials; P300 (P3); Hemispheric asymmetry; Reaction time (RT); Pitch discrimination.

Introduction

Hemispheric asymmetries of late event-related potential (ERP) components have been reported in a number of paradigms. In cognitively demanding tasks, such as dichotic listening tasks (Neville 1974; Tenke et al. 1993a; van de Vijver et al. 1984; Woods et al. 1984), these asymmetries have been shown to be related to hemispheric specialization for verbal or nonverbal task demands. More recently, hemispheric asymmetries have also been reported in a simpler task, the classic oddball, for both visual (Alexander et al. 1995) and auditory (Alexander et al. 1996; Bruder et al. in press; Kayser et al. in press) modalities.

In two independent studies using complex tones in an oddball task, we reported a larger P3 component over the right than the left hemisphere in healthy adults (Bruder et al. in press; Kayser et al. in press). In both, the asymmetries had a central topography, and interacted with response hand. The asymmetries previously reported for a tonal dichotic task, in which a delayed response was used, had a more posterior distribution (Tenke et al. 1993a). Although these findings could indicate that the same right hemisphere regions are differentially involved in pitch perception and the generation of P3 in both oddball and dichotic tasks, the apparent difference in component topography in the two paradigms precludes the presumption of a common generator (Johnson 1993). As such, the origin and significance of the asymmetry in the oddball task could only be addressed using specialized topographic techniques.

A surface Laplacian is a 2-dimensional adaptation of the Current Source Density (CSD) technique (Nunez 1981). Formally, it is based on simplifications of Poisson's equation relating the field potential at any point in a conductive medium to their underlying current generators (e.g., Mitzdorf 1985), so that a local generator of an extracellular negativity (current sink) corresponds to local neuronal depolarization, while a local generator of a positivity (current source) corresponds to repolarization or hyperpolarization. CSD provides a concise, reference-free method for describing and simplifying an ERP topography, although the anatomical and physiological organization of putative generator regions must be carefully evaluated before attributing a physiological or functional correlate to a CSD component.

This paper examines the asymmetry of the late

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positive complex in a nonverbal auditory oddball task using CSD techniques. Healthy, right-handed subjects were pooled across our two previous studies (Bruder et al. in press; Kayser et al. in press) to produce a sufficiently large sample (N=46) to better characterize this asymmetry and its interaction with response hand. Since estimates of the surface Laplacian are dependent on both the computational algorithm and specific recording montage, we examined these asymmetries using two distinct methods: the local Hjorth (Hjorth 1980) and the spherical spline (Perrin et al. 1989). In addition to examining topographic differences related to response hand, the combined sample allowed important subgroupings of subjects to further explore the nature of these hemispheric differences of the late positive complex. Groupings based on individual perceptual asymmetry for tonal stimuli (dichotic Complex Tone Test; Sidtis 1981) were used to differentiate perceptual from response-related asymmetries (see Tenke et al. 1993a). Groupings based on response speed, operationalized by reaction time (RT), were examined to evaluate the contribution of time-locked, response-related asymmetries (e.g., motor or readiness potentials).

Methods

Subjects

Subjects were 46 normal paid volunteers (22 females, 24 males), aged 21-60 years (mean=34.8, sd=10.4), who had been screened for neurological impairment, psychopathology and substance abuse. All subjects were given an audiometric screening, and had less than a 10 dB difference between ears and a hearing loss no greater than 30 dB at 500, 1000 and 2000 hz. All subjects were right handed, as indicated by a positive laterality quotient (LQ>0) on the Edinburgh Inventory (Oldfield 1971). Degree of handedness was unrelated to ERP asymmetries or their interactions with response hand, as indicated by analyses using handedness LQ as a grouping factor.

Oddball Task

A series of binaural complex tones (250 msec square waves, linearly tapered over first and last 10%) was used, with fundamental frequencies corresponding to the major notes of the octave from middle C to C5 (264-528 Hz). Tones were presented in six blocks of 50 trials, with ISIs of 1750 ms. Nontargets (80%) and targets (20%) for each block were distinct tones with different fundamental frequencies. Subjects were instructed to respond as quickly as possible by pressing a button to the rare tone. Response hand was balanced across subjects (22 left hand; 24 right hand).

Behavioral Asymmetry for Complex Tones

Each subject was also tested on the dichotic Complex Tone Test (Sidtis 1981; Tenke et al. 1993a), in which a different complex tone is presented simultaneously to each ear. Subjects indicate whether or not a subsequent binaurally presented probe tone matched either tone of the dichotic pair by pressing a response button after a delay period. The properties of the binaural stimuli were as described for the oddball task. Subjects were presented with six, 28-trial blocks, and responded with the same hand used in the oddball task. While the Complex Tone Test typically yields a mean left ear advantage in normal adults, there are considerable individual differences. Based on a laterality quotient (LQ) computed for each subject, LQ= 100(R-L)/(R+L), subjects were classified according to the presence of a left ear advantage (LQ<0, n=26; 15 left, 11 right responders) or a right ear advantage (LQ>=0, n=20; 7 left, 13 right responders) to examine the relationship between perceptual asymmetry in this task and ERP asymmetry in the oddball task. Ear advantage did not significantly interact with response hand (continuity corrected chi squared=1.51, p=.22).

Response Speed

As an additional approach to disentangling motor-related asymmetries, subjects were grouped according to their mean RT latencies. Subjects with RTs below the median (418 ms) were classified as fast responders (11 left, 12 right hand). The remaining subjects were classified as slow responders (11 left, 12 right hand).

ERP Recordings

ERP were recorded from four midline (Fz; Cz; Pz; Oz) and 13 lateral pairs of electrodes (FP1/2; F7/8; F3/4; FT9/10; FC5/6; T7/8; C3/4; TP9/10; CP5/6; P9/10; P7/8; P3/4; O1/2) at 10K gain, .01-30 Hz bandpass, using an electrode cap (Electro-Cap International, Inc.) with a nose reference. Special care was taken during placement of the cap to assure the symmetry and placement of the cap relative to Cz, as well as the locations of the lateral electrodes. Horizontal and vertical EOGs were recorded differentially from outer canthi and immediately above and below the right eye, respectively, for eye movement rejection and blink correction (Semlitsch et al. 1986).

Local Hjorth Laplacian Analysis

The local Laplacian was estimated using the Hjorth algorithm (Hjorth 1980):

$$H(i,N) = P_i - \frac{\sum_{j=1}^{N} P_j / d_{(i-j)}}{\sum_{j=1}^{N} (1 / d_{(i-j)})} \qquad (1)$$

For a montage that is adequately dense and symmetric, the Hjorth algorithm estimates the second spatial derivative **H** from the potential at a given electrode **i** and the linear potential gradient to each electrode **j** of **N** neighboring electrodes, weighted according to the inverse distance between them, $\mathbf{d}_{(i-j)}$. Equation 1 is computationally identical to the 3-point estimate used in intracranial recordings (Freeman and Nicholson 1975; Schroeder et al. 1995; Tenke et al. 1993b).

An estimate of a surface Laplacian is independent of recording reference, but it is not independent of the specific recording montage. Although often computed over a complete montage, Hjorth estimates deviate from a true second derivative as the surrounding electrodes deviate from symmetry (e.g., near the edges of a montage, or when a montage is unevenly sampled). Additionally, when a large number of electrodes are used in the estimate, the localized potential measure of interest may be biased by contributions from distant gradients. Smoothing and interpolation methods improve the fidelity of estimates of distributed generators, but they also attenuate (spatially low-pass) sharply localized contributions, and are still subject to misallocation of sources and sinks when the generator is undersampled (Tenke et al. 1993b). This degradation of the CSD may, at times, lead to a topography that more closely resembles that of average reference topography, rather than a true CSD.

In the present application, spatial symmetry and sampling constraints were imposed to increase the comparability of the estimates at each electrode. For each estimate, the **N** neighbors were selected on the basis of symmetry, rather than distance alone. For most electrodes, a computational simplification was used in place of measured distances between electrode placements, as shown in figure 1. Traditional 10/20 sites (F3, Fz, F4; C3, Cz, C4; P3, Pz, P4) were represented as being spaced equidistantly along a rectangular grid. Hjorth Laplacian estimates were computed from the four equidistant, symmetric neighbors on this grid (shown by bold lines figure 1). Estimates at the two interpolated electrodes (FC5/6; CP5/6) and T7/8 were likewise computed from four symmetric neighbors (light lines in figure 1). Estimates for FP1/2, FT9/10, TP9/10 and P9/10 were set to zero, since second derivatives are undefined at the edges of the montage. For the remaining electrodes, which were at or near the edges of the montage (light dots in figure 1), sufficient two-dimensional sampling and radial symmetry existed to allow the calculation of meaningful estimates with the present montage. Direct measurements from a representative cap placement were made for distances between these electrodes. It should be emphasized that the rectangular model produced nearly identical estimates to those obtained using measured distances at all sites, and that the hemispheric symmetry of the estimates was unaffected.

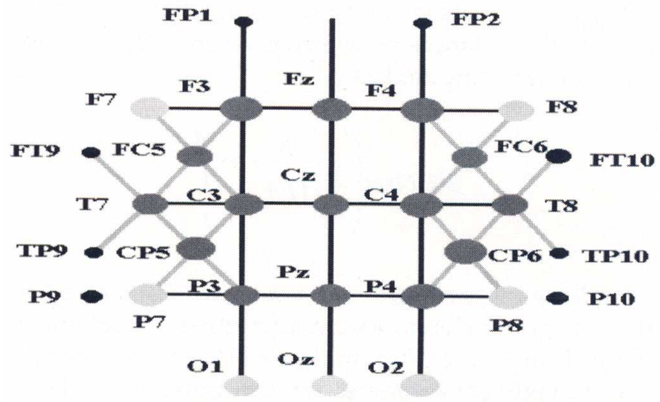

Figure 1. Electrode montage and the electrodes used to compute the local Hjorth Laplacian. The montage is simplified as a rectangular grid consisting of three equidistant sagittal lines (FP1 to O1; FPz to Oz; FP2 to O2) and three equidistant coronal lines (F7 to F8; T7 to T8; P7 to P8), with interpolated electrodes positioned along diagonals on the grid. Electrodes computed using a symmetric, 4-neighbor algorithm are indicated as dark gray dots. The neighbors used in the computation are the four symmetric, equidistant neighbors, e.g., for C3, the neighbors are F3, Cz, P3, T7; for FC5, the neighbors are F7, F3, C3, T7. FPz was estimated as the mean of FP1 and FP2. Electrodes that were not computed (small black dots) were the most lateral electrodes, FP1 and FP2, since the spatial second derivative is not defined along one dimension for these electrodes. Although the six lateral pairs of symmetric estimates (dark gray dots; excluding Fz, Cz, Pz, Oz) were the only ones used for statistical analyses, seven additional electrodes (light gray dots) were used for maps. These additional electrodes were computed using 3-5 neighbors (for F7, neighbors were FT9, FC5 and FP1; for P7, neighbors were P9, O1, P3, CP5 and TP9; for O1, neighbors were P3, P9, P10; for Oz, neighbors were Pz, P9, P10; right hemisphere uses homologous electrodes), and linear distances directly measured from representative electrode placements.

Since the local Hjorth measure is affected only by relative distances within its computational range (the **N** neighbors), comparisons between estimates from different differentiation grids requires an additional scale factor, **S(i,N)**, which is proportional to the inverse square of the grid size (Freeman and Nicholson 1975). In conformity with the distances expressed in equation 1, these scale factors were computed as:

$$S(i,N)=\left(\frac{N}{\sum_{j=1}^{N}(1/d_{(i-j)})}\right)^2 \qquad (2)$$

Using the main grid as a reference, scale factors for the 4-neighbor electrodes equaled either 1 (bold lines in figure 1) or 2 (light lines in figure 1) . The remaining (3 and 5 neighbor) estimates were empirically scaled to match the grid coordinates before applying equation 2.

Comparison with Spherical Spline Laplacian maps

The application of CSD methods to highly localized field potential gradients allows the description of physiologically relevant patterns of current generation, even when the spatial sampling density of the recording electrodes is marginal (Tenke et al. 1993b). However, computational noise increases as spatial resolution improves. Various smoothing methods (both planar and spherical) reduce computational noise, but conversely are suboptimal for detecting highly localized physiological variations. For this reason, spherical spline Laplacians were interpolated without additional smoothing (λ=0). Weighting functions were tabled (interpolated over 2000 points with 50 iterations; m=4 as recommended by Perrin et al. 1989). For each subject, Laplacian waveforms were retained at each of the recording electrode sites for each condition (target/nontarget), and subjected to the same statistical analyses as the local Hjorth waveforms.

Laplacian maps were computed from average ERP waveforms and displayed using a radial projection, with the edges stretched to 95° (down from Cz). The extreme lateral electrodes (FT9/10, TP9/10 and P9/10) were not displayed, to avoid overinterpretation at the edges of the montage (i.e., "current closure" artifacts produced by the spherical spline Laplacian algorithm), and to facilitate comparisons to the local Hjorth maps (Hjorth estimates undefined and set to zero at these electrodes). Localized effects were only interpreted if they were in close proximity to actual recording sites.

Component Identification and Statistical Methods

The component structure of the average ERP waveforms of the combined sample was as previously reported (Bruder et al. in press; Kayser et al. in press). The P3 component peaked at 350 ms, had a parietal maximum, and was noticeably asymmetric, with greater positivity over the right than the left hemisphere. The asymmetry was greatest at medial central electrodes (C4>C3) when the subject responded with the right hand. In our previous dichotic study (Tenke et al. 1993a), the late positive complex was characterized by both early and late subcomponents. Inspection of the Hjorth waveforms in the present study revealed sources corresponding to these subcomponents. The separation of these subcomponents was further supported by a Principal Components Varimax Analysis of the Hjorth asymmetry data.

Laplacian waveforms were averaged over an early positivity window (260-420 ms), a late positivity window (430-700 ms), and a window corresponding to the N2 ERP component (180-250 ms). Window averages of the Laplacian waveforms were computed and submitted to repeated measures ANOVA using the following factors: **condition** (target/nontarget), **hemisphere** (left, right) and **site** (each of the six pairs of lateral electrodes for which symmetric Hjorths were computed: F3/4; FC5/6; C3/4; T7/8; CP5/6; P3/4). Response **hand** (left/right) was used as a grouping factor in all analyses. Since both Laplacian methods indicated prominent asymmetries localizeable to central regions and consistent with previous ERP reports (Bruder et al. in press), subsequent analysis of simple effects focussed on the C3/4 pair. For these analyses, either **ear advantage** (LQ) derived from the dichotic Complex Tone Test, or response speed (mean reaction time; **RT**) was used as a second grouping factor. The results for the two Laplacian methods were generally comparable, including F ratios, effect sizes and significance levels. Only the results obtained for the local Hjorth that reflect hemispheric asymmetries will be detailed, with differences between methods noted in the text. Effect sizes were evaluated from the partial eta squared (η^2) values produced by the ANOVA results. As described by Cohen (1988), η^2 >.059 is a medium effect size (f>.25), while η^2>.138 is a large effect size (f>.40).

Results

Figure 2 shows the local Hjorth Laplacian waveforms for left and right responses to targets. The waveforms show surface sinks corresponding to N1 at electrodes anterior to the supratemporal plane, followed by sinks associated with N2 at medial frontocentral sites. These sinks are, in turn, followed by a broadly distributed posterior source that corresponds to the late positive complex of the ERP. In the Laplacian waveforms, this source is characterized by an early peak, maximal at Pz, and a late peak, most prominent at central sites (C3, C4). The latencies of these peaks match those of the early and late positive windows used to compute time averages.

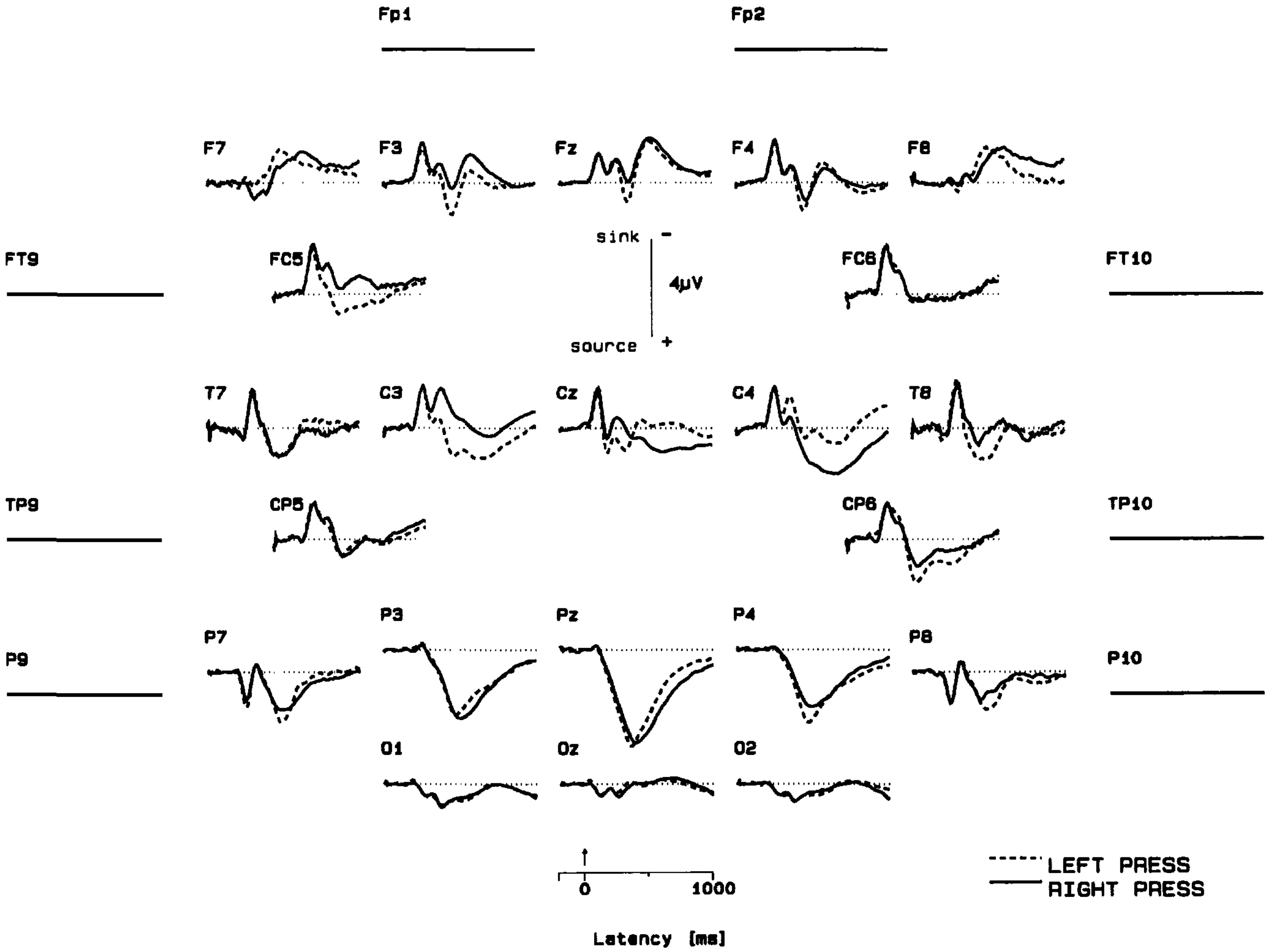

Figure 2. Local Hjorth waveforms for targets in groups of subjects responding with their left (dashed lines) and right (solid lines) hands. Differences between response hand are most prominent over left frontocentral electrodes (F3, FC5) and across the three central electrodes (C3, Cz, C4). Although the units of the scaled Hjorth are proportional to µV/cm^2, the use of a unit scale factor allows its interpretation as µV. Sink is up.

Clear differences in Laplacian topography are evident between response hands, beginning with the rise of N2 and persisting throughout the late positive complex (figure 2). The impact of response hand is twofold: 1) Right hand responses were associated with a larger sink at medial frontocentral sites over the left hemisphere (F3, FC5 and C3) than were left hand responses. The difference between waveforms for the two hands began with N2, and persisted into the latency range of the late positive window. These differences across hands were not paralleled by an inverse difference over homologous right hemisphere sites. 2) For right hand responses, the source at central sites was markedly asymmetric during both positivity windows, being prominent only over the right hemisphere (electrode C4). For left hand responses, the source was intermediate in amplitude, with a small asymmetry in the opposite direction. While N2 asymmetries were statistically significant only in their interaction with response hand (larger sink contralateral to the response hand), an overall asymmetry, with greater source activity over the right than the left hemisphere, was evident during the early positivity window across response hands (table 1A: EP, hemisphere effect). For the late window, a condition x hemisphere interaction also attained significance for the local Hjorth, and approached significance for the spherical spline Laplacian (F[1,44]=2.84, p=.10).

Source asymmetries are evident in the topographic maps shown in figure 3. Maps are shown for both early (figure 3A) and late (figure 3B) positivity windows for the

Table I. Summary of F ratios (ε corrections) [η^2] for repeated measures ANOVAs

A.HAND ANOVA: HEMISPHERIC ASYMMETRIES OF HJORTH AT 12 ELECTRODES

VARIABLE	df	N2	EP	LP
HEM	1,44		4.87* [.100]	
COND X HEM	1,44			5.41* [.110]
HAND X SITE X HEM	5,220	3.72** (.790) [.078]	6.75*** (.677) [.133]	4.79** (.755) [.098]
HAND X COND X HEM	1,44	6.68* [.132]	7.78** [.150]	5.97* [.120]
HAND X COND X SITE X HEM	5,220	3.63* (.688) [.076]	8.26*** (.725) [.158]	4.68** (.585) [.096]

B. HAND X LQ ANOVA: CENTRAL HJORTH ASYMMETRIES (SIMPLE EFFECTS)

VARIABLE	df	N2	EP	LP
HEM	1,42		4.84* [.103]	6.10* [.127]
COND X HEM	1,42			5.75* [.120]
HAND X HEM	1,42	19.10*** [.313]	24.52*** [.369]	28.03*** [.400]
HAND X COND X HEM	1,42	21.67*** [.340]	43.84*** [.511]	40.22*** [.489]
LQ X HAND X COND X HEM	1,42			4.81* [.103]

Note: N2 = N2 window (180-250 ms); EP = early positivity (260-420 ms); LP = late positivity (430-700 ms);
HEM = hemisphere; SITE = electrode site; COND = condition (target/nontarget); HAND = response hand.
LQ = laterality quotient (dichotic ear advantage)
Only hemispheric asymmetries (HEM or HEM interactions) significant at $p<.05$ are shown. *$p<.05$; **$p<.01$; ***$p<.001$

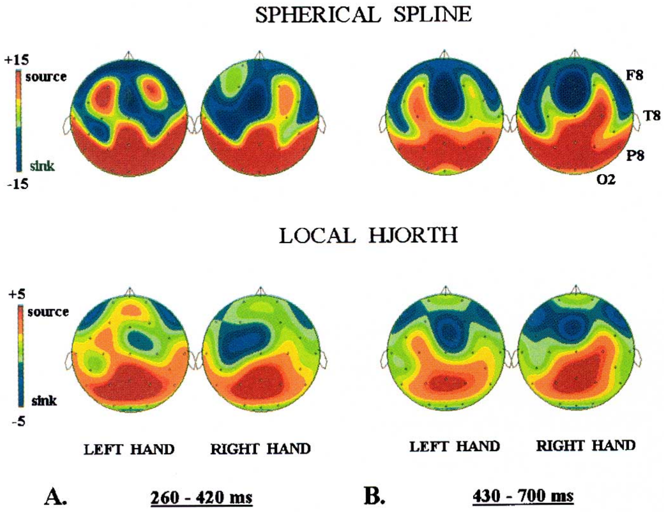

Figure 3. Spherical spline (upper row) and local Hjorth (bottom row) Laplacian maps computed from group mean ERPs to targets during early (A) and late (B) positivity windows. For each window, left responder maps are shown on the left, and right responders on the right. The complementary symmetry of the frontocentral motor-related sink is only evident for the early window. The central source is most robust and topographically distinct during the late window for right responders. Electrode locations as indicated.

spherical spline (top) and the local Hjorth (bottom) Laplacian. The frontocentral sink and central source asymmetries related to response hand (described above) were differentially associated with the two positivity windows. In the early window, the (presumably motor-related) frontocentral sink was distinctly contralateral to the response hand, and of greater amplitude, and more widely distributed for right than for left responses (see figure 3A). The symmetry of the source during the early window was distorted at central sites by this sink. For left hand responses, the overall topography was not inconsistent with an additive superposition of an asymmetric sink and a bilateral, broadly distributed source (figure 3A, left maps). However, for right responders, anterior source activity was only evident at electrodes over the right hemisphere (figure 3A, right maps). Differences in source hemispheric asymmetry between hands were statistically supported by interactions involving hand and hemisphere (table 1A). In contrast to the early window, the current sink in the late window had a more frontal, midline topography (see figure 3B). Both spherical spline and Hjorth maps indicate source activity at frontocentral sites over the right hemi-

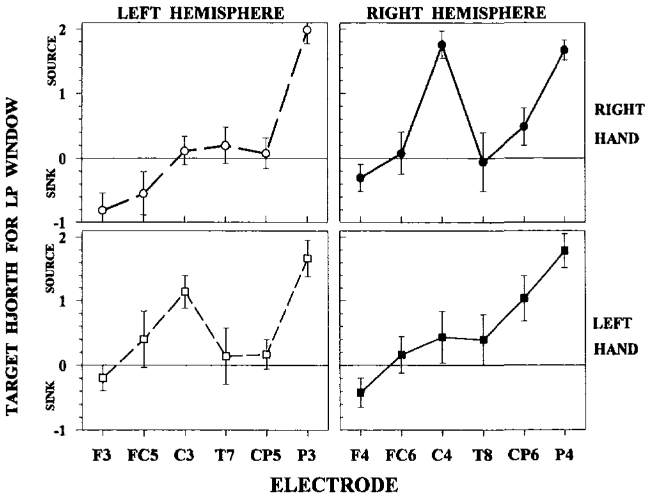

Figure 4. Local Hjorth for targets over the left and right hemispheres during the late positivity window, separated according to response hand (group mean ± standard error). For right responders, the central (C) source over the right hemisphere was most prominent, and topographically distinct from the frontal sink.

sphere for both response hands during the late window. Source activity was bilateral for left responses, although a noticeable asymmetry was also evident (greater over the left). For right responses, the source at central electrode sites was unilateral, localized, and topographically distinct from the frontal sink.

The response-related asymmetries of the local Hjorth Laplacian at the 12 electrodes used in the ANOVAs are illustrated in figure 4 for target waveforms during the late window. The parietal maximum of the sources is evident, as well as the sharp localization of the source asymmetries to central sites (i.e., C3/4 show the most prominent asymmetry). For right responses, an asymmetric sink was restricted to frontal electrode sites (F3 and FC5, but not C3), and was topographically distinct from the prominent source at C4. For left hand responses, the source was bilateral and less asymmetric at central sites (C3 larger than C4). The interactions of response hand with hemisphere and electrode site were statistically well-defined (medium and large effect sizes; see table 1A). Hemispheric asymmetry for the late window, evident across response hands (greater source over the right than the left hemisphere), was most prominent for targets (condition interaction).

In view of the regional specificity (i.e., site interactions) observed for the hand-related asymmetries of the late positivity window, we also examined the simple effects at each level of factor site. An overall hemisphere effect was supported at central (F[1,44]=6.56, p=.014) and centroparietal sites (F[1,44]=5.54, p=.023), as well as their interactions with condition (central: F[1,44]=4.11,p=.049; centroparietal: F[1,44]=4.91, p=.032). Response-related asymmetries were supported at frontal (hand x condition x hemisphere : F[1,44]=6.92, p=.0117), and central sites (hand x hemisphere: F[1,44]=28.99, p<.0001; hand x condition x hemisphere: F[1,44]= 40.99, p<.0001). Thus, only hand-related asymmetries were found at frontal sites, while only hand-independent asymmetries were found at centroparietal sites. Central electrodes showed both asymmetries. Asymmetries for the early window showed a similar distribution of hand-related and hand-independant asymmetries, except that the significant anterior effects were observed at the frontocentral (hand x hemisphere: F[1,44]=8.26, p=.0062), rather than the frontal electrode sites (hand x hemisphere: F[1,44]=2.89, p=.096).

We also examined the relation of a distinct, perceptual asymmetry measure, the ear advantage (LQ) derived from the dichotic Complex Tone Test, on the central source asymmetry in the oddball task (simple effects at C3/4, using ear advantage as a grouping factor). As shown in table 1B, an overall hemispheric asymmetry was observed for the early and late positivities (greater source over the right hemisphere). In addition to these overall asymmetries, a condition-related asymmetry was also evident across hands for the late window. Most importantly, a significant ear advantage x hand x condition x hemisphere interaction was found for the late positivity window, but not the early positivity or N2 window. This interaction largely reflects the difference in hemispheric asymmetry between the two ear advantage groups in subjects responding with their right hand. Subjects with a left ear advantage showed a larger late positivity source over right central regions, while subjects with a right ear advantage did not. A test of simple effects showed a significant interaction for right responders (ear advantage x condition x hemisphere, F[1,42]=5.50, p<.025), but not for left responders (ear advantage x condition x hemisphere, F[1,42]=.75, ns). In contrast to ear advantage, response speed had no effect on the central asymmetry. A repeated measures ANOVA for fast and slow responders (grouping factors: RT group and hand), revealed no interactions with RT grouping. Likewise, groupings based on the handedness LQ were unrelated to ERP hemispheric asymmetry, either directly or interacting with response hand.

Discussion

Surface Laplacian estimates computed using both local Hjorth and spherical spline interpolation methods indicated prominent parietal current sources corresponding to the late positive complex, as well as source asymmetries as far anterior as central and frontocentral regions. While an overall source asymmetry favoring the right hemisphere was evident in averages combined across response hand, the asymmetry interacted strongly with response hand. It was robust at longer latencies, i.e., after the classic P3 peak, when the lateralized, motor-related sink had resolved. The asymmetry was largest at central electrode sites (greater source at C4 than C3) for right hand responses, and was further enhanced in subjects showing a left ear advantage for perceiving dichotic complex tones.

Dissociation of Source from Motor Processes

The superposition of a motor-related frontocentral negativity on the topography of the P3 component has long been recognized. The P3 enhancement during nogo trials of a go/nogo task has likewise been seen as the simple result of removal of this negativity (Simson et al. 1977; Kopp et al. 1996; although see Roberts et al. 1994 for an alternative interpretation). Movement-related negativities are known to be lateralized in tasks requiring responses with only one hand (e.g., Kutas and Donchin 1980). Our results indicate that these motor-related sinks are prominent in a tonal oddball task, but are not sufficient to account for the observed P3 asymmetries.

One argument against a simple motor origin of the asymmetry is its temporal persistence. If the asymmetry was largely produced by the imposition of a contralateral motor potential, it would be expected to be smaller during the late window for subjects with fast responses. We found no support for this interpretation. For right responders, in whom the central asymmetry was most marked, the ERP asymmetry was not reduced in subjects who responded more quickly. Indeed, while an identifiable sink was apparent during the N2 component and during the early positivity window at electrode C3, a robust source was prominent throughout the late window at electrode C4.

Response-related asymmetry of the late positive complex (smaller contralateral to response hand) in an auditory oddball RT task has been reported to develop following a symmetric readiness potential, and to persist throughout the peak of the P3 component (Starr et al. 1995). Our data emphasize the importance of response hand in the late asymmetry, but also indicate a differential involvement of the right hemisphere. In our sample of right handed subjects, we did not find any evidence of an association between the late asymmetry and the strength of hand preference. However, further evaluation of the contribution of handedness to the source asymmetry must await a study in which the degree and direction of handedness is more completely sampled.

Relation of Source Asymmetry and Perceptual Asymmetry

An association between perceptual and ERP asymmetry was previously reported for the dichotic Complex Tone Test (Tenke et al. 1993a), which uses a delayed response, rather than RT paradigm. Subjects with a strong left ear advantage showed greater late positivity over the right hemisphere, while subjects with a right ear advantage or no advantage did not. Thus, a perception-related ERP asymmetry for dichotic tone discrimination was observed, corresponding to a relatively late stage of information processing. In the present study, an asymmetry of source activity at central sites was found to be related to the perceptual asymmetry of subjects for the dichotic Complex Tone Test. Subjects with a left ear (right hemisphere) advantage for perceiving complex tones showed a greater source asymmetry (i.e., larger source over the right than the left hemisphere) than those with a right ear advantage. A parsimonious interpretation is that the behavioral and ERP asymmetries in the dichotic and oddball tasks reflect a common contribution from the right hemisphere related to pitch perception. However, the perception-related and response-related asymmetries are not additive, since the enhanced late source asymmetry in left-ear advantage subjects was evident only when responses were made with the right hand.

Relationship of Source Asymmetry to Putative Generators of the Late Positive Complex

The use of a large sample of subjects and a standard oddball task provides both statistical power and a degree of generalizability to our findings. It should also be noted that all effects reported here reflect medium to large effect sizes. Likewise, the asymmetry measures are unbiased, since the local Hjorth was computed using radially symmetric neighbors at homologous sites over the left and right hemisphere. While our 30-electrode montage does not allow a high resolution description of either the topography of ERP components or the multiple regional generators contributing to them, the degree of localization observed for the source asymmetry at central sites allows us to unambiguously rule out the contributions of putative generators which would produce inconsistent patterns of scalp current flow. A direct contribution to the central asymmetry from deep structures, such as the hippocampus, may safely be excluded. Although the hippocampus is clearly a local generator of P3-related activity (McCarthy et al. 1989; Paller et al. 1992), and may be responsive to self-initiated movements as well (Arezzo et al. 1987), it could not produce the degree of scalp localization observed here.

Of all the regions suggested as generators of the P3 component, possibly the most consistently cited is the temporoparietal region. Temporoparietal damage has been clearly shown to decrease the amplitude of auditory P3 (e.g., Knight et al. 1989). The prominent right central (C4) source that is evident in the Laplacian analysis is not easily ascribed to superficial temporoparietal generators. The radial orientations of these cortical regions would project too far posterior, where they could make substantial contributions to CP6, but not the central region itself. The only temporoparietal location at all likely to project to electrode C4 is on or near the supratemporal plane itself. This possibility has considerable face validity, particularly for overall asymmetries of auditory ERPs that may be present for both targets and nontargets (Bruder et al. in press). It is also consistent with the finding that asymmetries of the late positive complex vary with inherent stimulus characteristics, i.e., the asymmetry of N2/P3 is in the opposite direction for tonal and phonetic oddball tasks (Kayser et al. in press).

Conclusions

Our results indicate that an asymmetric central source, maximal over the right hemisphere, is at least partially responsible for the asymmetry of the late positive complex in a tonal oddball task. At least two distinct processes are involved. The first, dominant contribution is related to response hand, reflected in a maximal source over the right hemisphere for right hand responses. This contribution persists after the apparent resolution of the contralateral response-related sink. The second, modulatory contribution is related to the process of pitch discrimination, and presumably reflects an overall right hemispheric superiority for subjects with a left ear advantage for dichotic pitch discrimination. Further clarification of these interactions requires a within-subject manipulation of response hand, and/or response mode (e.g., silent counting) using a more dense recording montage.

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