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Short Communication

## Hemispheric differences for P300 amplitude from an auditory oddball task

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### Abstract

The P3(00) event-related potential (ERP) was elicited in 80 normal, right-handed male subjects using a simple auditory stimulus discrimination task, with electroencephalographic (EEG) activity recorded at 19 electrodes. P300 amplitude was larger over the right compared to left hemisphere electrode sites primarily at anterior-medial locations (F3/4, C3/4) for both target and standard stimuli. The N100, P200, and N200 components also demonstrated several similar, albeit less robust, hemispheric asymmetries. No hemispheric effects for P300 latency were observed, with few consistent latency findings for any of the other components obtained. The results suggest that the discrimination process underlying P300 generation may originate with right frontal activation.

**Keywords:** P300; Event-related potential (ERP); Hemispheric differences; Auditory stimulus

When an auditory 'oddball' paradigm is used to elicit the P3(00) event-related brain potential (ERP), subjects are required to discriminate between two stimuli that vary on some dimension by responding to a designated target stimulus. The P300 often is measured at the central (Fz, Cz, Pz) electrode sites with lateral electrodes typically not assessed, since

the midline scalp distribution provides substantial information about the attentional and mnemonic processes thought to contribute to P300 generation (Donchin et al., 1986; Donchin and Coles, 1988; Johnson, 1993; Picton, 1992). However, relatively little is known about its possible hemispheric differences asymmetries, perhaps because of the typically small ERP amplitude hemispheric asymmetries observed (e.g., Brown et al., 1985; Molfese et al., 1975; Neville, 1980), which may originate from inadequate numbers or placement of electrodes and

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the often small, inhomogenous samples employed in ERP studies that have reported laterality effects (Donchin et al., 1977). Although cognitive hemispheric differences are observed readily using behavioral techniques for auditory (Kimura, 1993; Ivry and Leiby, 1993), visual (Sergent, 1991; Hellige, 1993; Polich, 1993a), and tactile (O'Boyle et al., 1987; Reitan et al., 1992) stimuli, hemispheric asymmetries for late endogenous components such as the P300 and N4(00) have been found primarily with verbal tasks in the visual modality (e.g., Friedman et al., 1975; Kutas and Hillyard, 1982; Kutas and Van Petten, 1988). Thus, lateralization of the P300 and other cognitive ERPs has been observed for some tasks, but not in all modalities.

Several recent studies that utilized multiple scalp electrodes have suggested that hemispheric amplitude differences for the P300 ERP from an auditory oddball paradigm may exist, such that P300 amplitude from the right hemisphere is larger than that from the left hemisphere (cf. Karniski and Blair, 1989; Holinger et al., 1992; Naumann et al., 1992). However, these effects seem to occur primarily at the anterior and central locations, which is somewhat surprising given that the P300 is usually largest over parietal areas (Johnson, 1989; Polich, 1989) – at least for young adult subjects (cf. Friedman et al., 1993; Vesco et al., 1993). Moreover, although P300 hemispheric asymmetries have been reported they are not completely consistent in their strength or location. The sources of these discrepancies are unclear but are likely related to the nonhomogeneous samples that are compromised by a lack of control over variables that can affect laterality differences (e.g., left/right handedness, male/female subjects, etc.), the relatively small samples are typically employed (e.g.,  $n = 10\text{--}20$ ), and the use of linked ears or mastoids as a reference (this method does not appear to affect asymmetry magnitudes appreciably, but it has caused some controversy in this area; cf. Andino et al., 1990; Faux et al., 1990; Nunez, 1981; Senulis and Davidson, 1989). When taken together, previous studies suggest a possible P300 hemispheric difference for nonlateralized stimulus presentations and simple discrimination tasks, but the nature of these effects is uncertain.

The present study was designed to determine in a comprehensive fashion whether the P300 component

from an auditory oddball task is hemispherically asymmetric. If laterality differences for the P300 and other components can be demonstrated, such asymmetries may help disentangle the possible influences of neuroanatomical factors on ERP morphology (Ford et al., 1994; Myslobodsky et al., 1989; Pfefferbaum and Rosenbloom, 1989). Furthermore, these data also may be helpful in the evaluation of ERP scalp distribution changes that occur with normal aging and clinical disorders (Holinger et al., 1992; Pfefferbaum et al., 1989; Ford and Pfefferbaum, 1991; Polich, 1993b; Polich and Luckritz, 1995).

A total of 80 young adult right-handed males (mean = 22.6, SD = 1.8 years) served as subjects for pecuniary remuneration, with several laboratories using the same equipment and methods contributing to the data set (cf. Alexander et al., 1994). Males were used exclusively to maximize the likelihood of obtaining cognitive based hemispheric differences (Halpern, 1992). Based on responses to a comprehensive survey, all subjects reported an absence of psychiatric or neurologic problems and were screened for alcohol and drug use. Handedness was evaluated by a self-report questionnaire, derived from standard assessment methods (Bryden, 1977), that assessed use of dominant hand, foot, and eye use on a variety of tasks in addition to experimenter observation of writing, with all subjects reported being strongly right-handed.

EEG activity was recorded monopolarly using an ECI electrode-cap at 19 electrode sites (FP1/2, F3/4, C3/4, P3/4, F7/8, T7/8, P7/8, O1/2, Fz, Cz, Pz) referred to the nose, with a forehead ground and impedances at 5 k $\Omega$  or less. Electro-ocular (EOG) activity was assessed with two channels referenced to the nose. One electrode was placed at the outer canthus of the left eye to measure vertical eye movement and the second electrode was located on the forehead to monitor horizontal eye movement. The filter bandpass was 0.02–50 Hz (3 dB down, 6 dB octave/slope) and the EEG was digitized at 3.9 ms/point for 1500 ms, with a 187 ms prestimulus baseline. ERP data were averaged on-line, with the same computer also used to control the stimulus presentation and artifact rejection. Trials on which the EEG or EOG exceed +73.3  $\mu\text{V}$  were rejected automatically.

ERPs were elicited with 400 auditory binaurally

presented stimuli consisting of 600 Hz (standard) and 1600 Hz (target) tones presented at 60 dB SPL (10 ms r/f, 60 ms plateau). The interstimulus interval was 1.5 s and the target tone occurred randomly with a probability of 0.125. Subjects were instructed to press a key pad with their forefinger whenever a target tone was detected and to refrain from responding when the standard tone was presented. Response hand was counterbalanced across subjects. Stimulus presentation was concluded when 25 target and 75 standard artifact-free stimuli were acquired.

All analyses of variance employed Greenhouse-Geisser corrections to adjust for violations of the sphericity assumption inherent in repeated measures designs. Only probability values from corrected df are reported here. Task performance was virtually perfect with fewer than 2% of the target trials rejected and/or misperceived across subjects. Mean response time (RT) to the target stimulus taken over all subjects was 379 ms. Waveforms for both target and standard stimuli were analyzed visually by iden-

tifying amplitudes and latencies of the N100, P200, N200, and P300 components at each electrode site by locating the most negative or positive component within the latency windows of 75–125, 100–200, 125–275, and 250–450 ms, respectively. Amplitude was measured relative to the prestimulus baseline, with peak latency defined as the time point of maximum positive or negative amplitude within the latency window.

Results for the midline electrode sites (Fz, Cz, Pz) have been reported elsewhere as part of a large-scale study on inter-laboratory reliability and will not be considered further (Alexander et al., 1994). To assess within-hemisphere effects the left lateral (F7, T7, P7), left medial (F3, T3, P3), right medial (F4, T4, P4), and right lateral (F8, T8, P8) electrode locations were analyzed (preliminary evaluation indicated that the Fp1/2 and O1/2 electrode sites yielded no hemispheric effects). Additional analyses of peak latency found no reliable P3 hemispheric results and only a few inconsistent effects for the

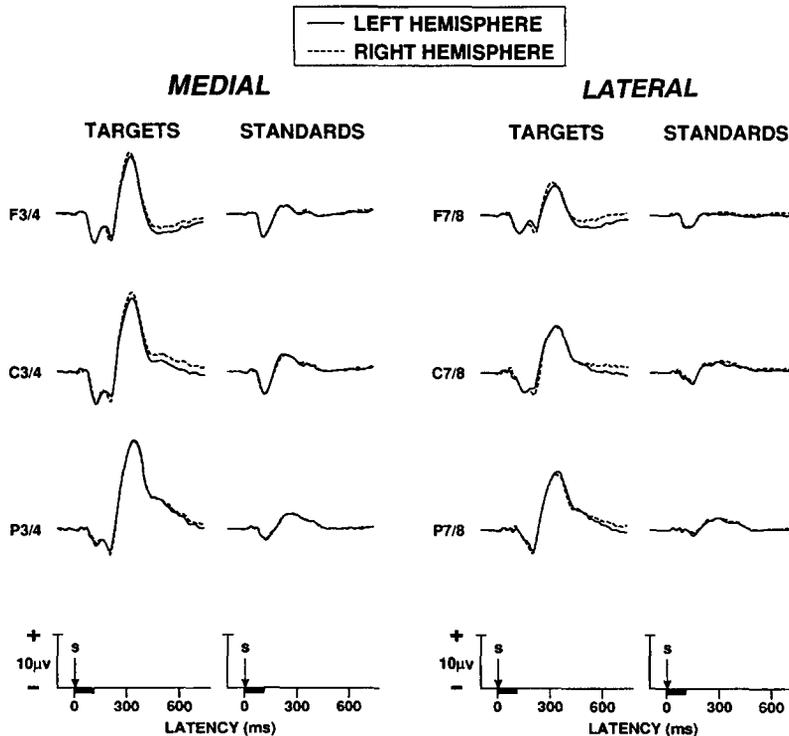


Fig. 1. Grand average event-related potentials from the target and standard stimuli for the medial and lateral electrodes for the frontal, central, and parietal recording sites ( $N = 80$ ).

other components. Because virtually all of the latency data demonstrated no hemispheric asymmetry of apparent consequence, analyses of these data are not reported. Finally, the anterior-to-posterior amplitude changes stemming from the electrode factor were highly significant for all components, and the statistical outcomes for the main effects of this factor were not reported, although any interactions with hemispheric factors were specified. Statistical analyses were performed on the amplitude data such that the same anterior-to-posterior locations (frontal, central, parietal) were employed for both the *medial* (F3/4, C3/4, P3/4) and *lateral* (F7/8, T7/8, P7/8) electrode sites. The grand average ERP waveforms for the target and standard stimuli at each anterior-to-posterior electrode position for the medial and lateral sites are presented in Fig. 1. Note that P300 amplitudes are larger for the right frontal-central compared to the left sided recording locations.

The mean P300 amplitudes for each hemisphere and medial/lateral location from the target and standard stimuli as a function of electrode position are presented in Fig. 2. Appreciable differences between

the hemispheric electrode sites were observed in addition to the typical increase in P300 amplitude from the frontal to parietal electrode sites. A three-factor (hemisphere  $\times$  medial/lateral location  $\times$  electrode) analysis of variance was performed on the P300 amplitude data from each electrode for the target and standard stimuli separately. For *target* stimuli, P300 amplitude was larger overall for the right hemisphere compared to left hemisphere locations,  $F(1,79) = 6.6$ ,  $p < 0.02$ . This hemispheric asymmetry was produced primarily by the medial locations as indicated by a two-way interaction between medial/lateral location and electrode,  $F(1,79) = 7.0$ ,  $p < 0.02$ . Hemispheric differences in P300 amplitude favoring the right hemisphere also were larger for the medial compared to lateral locations over the frontal and central relative to parietal electrode sites and produced a three-way interaction between these factors,  $F(1,158) = 16.8$ ,  $p < 0.001$ . For *standard* stimuli P300 amplitude also was larger over the right hemisphere compared to the left hemisphere locations,  $F(1,79) = 17.7$ ,  $p < 0.001$ . In contrast to the target stimuli effects, the standard stimuli

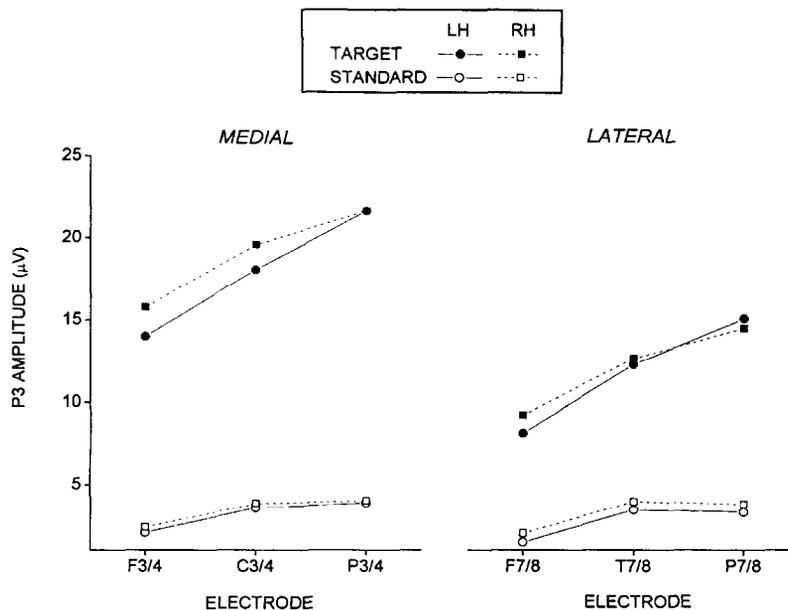


Fig. 2. Mean P3 amplitude from the target and standard stimuli at medial and lateral locations as a function of anterior-to-posterior electrode sites.

demonstrated stronger hemispheric asymmetries for the lateral rather than medial locations,  $F(1,79) = 10.5$ ,  $p < 0.002$ . However, both the target and standard stimuli produced highly similar patterns of P300 hemispheric asymmetry.

To assess the relative strengths of the P300 amplitude hemispheric differences, two-factor (hemisphere  $\times$  electrode) analyses of variance were performed on the data from the medial and lateral locations separately. P300 amplitude from *target* stimuli recorded at medial locations was larger over the right hemisphere,  $F(1,79) = 12.4$ ,  $p < 0.001$ . P300 amplitude asymmetry was greater at the frontal compared to parietal electrode sites to yield a significant interaction between the hemisphere and electrode factors,  $F(1,158) = 13.2$ ,  $p < 0.001$ . P300 amplitude recorded at lateral recording sites evinced no hemispheric differences, but an interaction between hemisphere and electrode similar to that observed for the target stimuli was found,  $F(1,158) = 6.5$ ,  $p < 0.01$ . For *standard* stimuli P300 amplitude was greater over the right hemisphere for both medial,  $F(1,79) = 9.4$ ,  $p < 0.01$ , and lateral,  $F(1,79) = 19.8$ ,  $p < 0.001$ , locations.

The N100, P200, and N200 components are illustrated in Fig. 1. Preliminary three-factor (hemisphere  $\times$  medial/lateral location  $\times$  electrode) analyses of variance applied to these data revealed a number of interactions between the hemisphere and medial/lateral location factors. To simplify presentation, only the statistically reliable effects from the two-factor (hemisphere  $\times$  electrode) analyses for each medial/lateral location for both target and standard stimuli are described.

*N1 amplitude* from the target stimuli at medial locations was larger over the left compared to right hemisphere locations,  $F(1,79) = 4.2$ ,  $p < 0.05$ , with this asymmetry greater at the posterior compared to anterior electrodes,  $F(1,158) = 6.4$ ,  $p < 0.01$ . *N1 amplitude* from the standard stimuli was larger over the left compared to right hemisphere primarily for the central and parietal electrode sites to produce an interaction between the hemisphere and electrode factors,  $F(1,158) = 3.4$ ,  $p < 0.05$ . *P2 amplitude* from the standard stimuli at medial locations was larger over the left compared to right hemisphere,  $F(1,79) = 7.8$ ,  $p < 0.01$ . This effect was stronger primarily at the central and posterior electrode loca-

tions to yield an interaction between the hemisphere and electrode factors,  $F(1,158) = 5.0$ ,  $p < 0.02$ . No significant effects were found for the target stimuli. *N2 amplitude* from the target stimuli at lateral locations was larger over the right compared to left hemisphere,  $F(1,79) = 4.9$ ,  $p < 0.05$ . *N2 amplitude* from the standard stimuli at the medial locations was larger over the right compared to left hemisphere,  $F(1,79) = 4.0$ ,  $p < 0.05$ .

P300 amplitude from an auditory oddball paradigm was found to be consistently larger over the right hemisphere frontal and central electrode sites for both target and standard stimuli waveforms. Since this right hemisphere amplitude asymmetry was observed for both stimulus categories, these lateralized P300 amplitude effects are not likely originating from differences in task response requirements. The magnitude of the P300 hemispheric amplitude asymmetry was about 1–2  $\mu\text{V}$  and was statistically very robust for the large sample of right-handed male subjects employed in the present study, since over 70% of the subjects exhibited this right-hemisphere asymmetry. When taken together with previous studies (Karniski and Blair, 1989; Holinger et al., 1992; Naumann et al., 1992), it is reasonable to assume that these amplitude asymmetries are reflecting fundamental hemispheric differences for P300 generation. The amplitude asymmetries observed for the N100, P200, and N200 components were generally weaker and more variable compared to the P300 component. These effects may reflect the orientation of the specific neural generators for each of these components (Picton et al., 1974; Polich and Starr, 1983), although their relationship to the stronger asymmetries observed for the P300 component is uncertain.

The sources of these ERP asymmetries are not known. It could be argued that structural differences in brain morphology, skull thickness, and cranial irregularities contribute to the P300 hemispheric amplitude variations observed, since it is known that such factors can affect ERP amplitude. For example, plagiocephaly or the underlying brain configuration associated with lateralized cranial deformities consists of a counterclockwise torque in which the left occipital pole flattens and the right frontal locations are larger and often protrude forward (Simpson and David, 1986; Daniel et al., 1989). The resulting

hemispheric difference in neural mass may therefore produce electrophysiological asymmetries by redirecting current flow through the skull, such that larger amplitudes are recorded over locations that contain more cellular volume and/or have thinner skull widths (cf. Ford et al., 1994; Pfefferbaum and Rosenbloom, 1989). Although a plausible explanation, measurable plagiocephaly occurs only in about 10% of the population (Binnie et al., 1982). Further, only a slight and apparently unstable relationship between skull thickness and occipital EEG alpha asymmetry has been reported (Myslobodsky et al., 1991), with strong indications that plagiocephaly affects the occipital recording sites more than the symmetrical, central, parietal, and temporal recording locations (Chui and Damasio, 1980; Myslobodsky et al., 1989). Thus, the lateralized effects found for P300 amplitude at the frontal and central locations are most likely unrelated to structural differences in skull and brain morphology.

Alternatively, it is possible to speculate that fundamental differences in the cognitive processing used to discriminate the target and standard stimuli would contribute to the larger P300 amplitudes from the right hemisphere. Although the theoretical interpretation of the P300 is debated, the most prominent view posits that this ERP component reflects a developing representation within short-term memory (Donchin et al., 1986; Donchin and Coles, 1988). This hypothesis dovetails nicely with the results of human ERP lesion studies, which have suggested that multiple neural generators — most likely originating from portions of temporal-parietal cortex — are involved in P300 production (Johnson, 1989; Knight et al., 1989; Yamaguchi and Knight, 1990). Further, very surprising or alerting stimuli will produce a P3a subcomponent that is of maximum amplitude over a frontal/central electrode sites and occurs before the parietal P3b elicited with an oddball paradigm (cf. Squires et al., 1975; Courchesne et al., 1975; Polich, 1988). The P3a appears to originate from the frontal lobe, reflects initial signal evaluation, and readily habituates (Roth, 1973; Ford et al., 1976; Knight, 1984). When the stimulus is subsequently processed in memory, the central/parietal canonical P3b is generated (Knight, 1990; Polich and Squire, 1993), so that both empirical and theoretical reasons indicate that at least two different ERPs comprise 'the

P300' component, and that these different subcomponents have distinct neuroanatomical generators (Johnson, 1993; Picton, 1992).

If this portrait of the neural and theoretical mechanisms for P300 generation is approximately correct, the right hemisphere amplitude superiorities observed in the present study could stem in part from neural activity related to the processing of the incoming signal in a manner similar to effects observed using positron emission tomography (Posner and Petersen, 1990). Discriminating the target from the standard stimulus may initiate right frontal engagement, because it requires the consistent application of attentional focus — a major attribute of frontal lobe function (Pardo et al., 1991; Posner, 1992). The larger right compared to left P300 amplitudes for the target stimuli relative to the smaller asymmetry observed for the standard stimuli support this view. The reason for the diminution of these effects at the parietal locations is not clear, but may stem from localized decision processes that govern response production. In addition, because the P300 is the largest of the ERP components elicited in this task situation, its asymmetric generation might also contribute to the laterality effects obtained for the other components. When taken in concert with the possible contribution of the functional asymmetries outlined above, the P300 hemispheric differences observed for the auditory oddball paradigm in the present study may be reflecting attention allocation during the early phases of stimulus processing. Thus, P300 amplitude asymmetries may be a relatively more precise manifestation of context updating processes than are midline recordings because the this component is initiated in the right frontal lobe areas.

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## References

- Alexander, J., Polich, J., Bloom, F.E., Bauer, L., Kuperman, S., Rohrbaugh, J., O'Conner, S.J., Porjesz, B. and Begleiter, H. (1994) P300 from an auditory oddball task: Inter-laboratory consistency. *Int. J. Psychophysiol.*, 1994, 17: 35–46.
- Andino, S.L., Marqui, R., Sosa, P., Lirio, R., Machado, C., Diaz, G., Rodriguez, P., and Torez, C. (1990) Brain electrical field measurements unaffected by linked earlobe reference. *Electroenceph. Clin. Neurophysiol.* 75: 155–160.
- Binnie, C.D., Dekkerm, E., Smit, A., and Van der Linden, G. (1982) Practical considerations in the positioning of EEG electrodes. *Electroenceph. Clin. Neurophysiol.* 53: 453–458.
- Brown, W., Marsh, J. and Ponsford, R. (1985) Hemispheric differences in event-related brain potentials. In: D.F. Benson and E. Zaidel (Eds.), *The Dual Brain: Hemispheric Specialization in Humans*. Karger, Basel.
- Bryden, M.P. (1977) Measuring handedness with questionnaires. *Neuropsychologia* 15: 617–624.
- Chui, H.C., and Damasio, A.R. (1980) Human cerebral asymmetries evaluated by computed tomography. *J. Neurol. Neurosurg. Psychiatry* 43: 873–878.
- Courchesne, E., Hillyard, S. and Galambos, R. (1975) Stimulus novelty, task relevance, and the visual evoked potential in man. *Electroenceph. Clin. Neurophysiol.* 39: 131–43.
- Daniel, D.G., Myslobodsky, M.S., Ingraham, L.J., Coppola, R., and Weinberger, D.R. (1989) The relationship of occipital skull asymmetry to brain parenchymal measures in schizophrenia. *Schizophrenia Res.* 2: 465–472.
- Donchin, E. and Coles, M.G.H. (1988) Is the P300 component a manifestation of context updating? *Behav. Brain Sci.* 11: 357–374.
- Donchin, E., Karis, D., Bashore, T.R., Coles, M.G.H. and Gratton, G. (1986) Cognitive psychophysiology and human information processing. In M.G.H. Coles, E. Donchin and S.W. Porges (Eds.), *Psychophysiology: Systems, Processes, and Applications*. New York: The Guilford Press, 1986, pp. 244–267.
- Donchin, E., Kutas, M. and McCarthy G. (1977) Electrocortical indices of hemispheric utilization. In S. Hamad, R. Doty, L. Goldstein, J. Jaynes and G. Krauthamer (Eds.), *Lateralization in the Nervous System*. New York: Academic Press, pp. 339–384.
- Ford, J. and Pfefferbaum, A. (1991) Event-related potentials and eyeblink responses in automatic and controlled processing: Effects of age. *Electroenceph. Clin. Neurophysiol.* 78: 361–377.
- Ford, J., Roth, W.T. and Kopell, B. (1976) Auditory evoked potentials to unpredictable shifts in pitch. *Psychophysiology* 13: 32–39.
- Ford, J.M., Sullivan, E., Marsh, L., White, P., Lim, K., and Pfefferbaum, A. (1994) The relationship between P300 amplitude and regional gray matter volumes depends on the attentional system engaged. *Electroenceph. Clin. Neurophysiol.* 90: 214–228.
- Friedman, D., Simpson, G. and Hamberger, M. (1993) Age-related changes in scalp topography to novel and target stimuli. *Psychophysiology* 30: 393–396.
- Friedman, D., Simson, R., Ritter, W. and Rapin, I. (1975) Cortical evoked potentials elicited by real speech words and human sounds. *Electroenceph. Clin. Neurophysiol.* 38: 13–19.
- Faux, S., F., Shenton, M., McCarley, R., Nestor, P., Marcy, B., and Ludwig, A. (1990) Preservation of P300 event-related potential topographic asymmetries in schizophrenia with use of either linked-ear or nose reference sites. *Electroenceph. Clin. Neurophysiol.* 75: 378–391.
- Halpern, D.F. (1992) *Sex differences in cognitive abilities*. Hillsdale, NJ: Lawrence Erlbaum Associates.
- Hellige, J. (1993) Unity of thought and action: Varieties of interaction between the left and right cerebral hemispheres. *Cur. Dir. Psychol. Sci.* 2: 21–25.
- Holinger, D., Faux, S., Shenton, M., Sokol, N., Seidman, L., Green, A. and McCarley, R. (1992) Reversed temporal region asymmetries of P300 topography in left and right-handed schizophrenic subjects. *Electroenceph. Clin. Neurophysiol.* 84: 532–537.
- Ivry, R.B. and Leiby, P. (1993) Hemispheric differences in auditory perception are similar to those found in visual perception. *Psychol. Sci.* 4: 41–45.
- Johnson, R. (1989) Developmental evidence for modality-dependent P300 generators: A normative study. *Psychophysiology* 26: 651–667.
- Johnson, R. (1993) On the neural generators of the P300 component of the event-related potential. *Psychophysiology* 30: 90–97.
- Karniski, W. and Blair, R.C. (1989) Topographical and temporal stability of the P300. *Electroenceph. Clin. Neurophysiol.* 72: 373–383.
- Kimura, D. (1993) *Neuromotor mechanisms in human communication*. New York: Oxford University.
- Knight, R. (1984) Decreased response to novel stimuli after prefrontal lesions in man. *Electroenceph. Clin. Neurophysiol.* 59: 9–20.
- Knight, R. (1990) Neural mechanisms of event-related potentials from human lesion studies. In: J. Rohrbaugh, R. Parasuraman and R. Johnson (Eds.), *Event-Related Brain Potentials: Basic Issues and Applications*. New York: Oxford University Press, pp. 3–18.

- Knight, R.T., Scabini, D., Woods, D. and Clayworth, C. (1989) Contributions of temporal-parietal junctions to the human auditory P3. *Brain Res.* 502: 109–116.
- Kutas, M. and Hillyard, S. (1982) Lateral distribution of event-related potentials during sentence processing. *Neuropsychologia* 20: 579–590.
- Kutas, M. and Van Petten, C. (1988) Event-related brain potential studies of language. In: P.A. Ackles, R. Jennings and M.G.H. Coles (Eds.), *Advances in Psychophysiology*, Vol. 3. Greenwich, CT: JAI Press, pp. 139–187.
- Molfese, D., Freeman, R. and Palmero D. (1975) The ontogeny of lateralization for speech and nonspeech stimuli. *Brain Lang.* 2: 356–368.
- Myslobodsky, M., Coppola, R., Bar-Ziv, J., Karson, C., Daniel, D. and Weinberger, D.R. (1989) EEG asymmetries may be affected by cranial and brain parenchymal asymmetries. *Brain Topogr.* 1: 221–228.
- Myslobodsky, M., Coppola, R., and Weinberg, D. (1991) EEG laterality in the era of structural brain imaging. *Brain Topogr.* 3: 381–390.
- Naumann, E., Huber, C., Maier, S., Plihal, W., Wustmans, A., Diedrich, O. and Bartussek, D. (1992) The scalp topography of P300 in the visual and auditory modalities: A comparison of three normalization methods and the control of statistical type II error. *Electroenceph. Clin. Neurophysiol.* 83: 254–264.
- Neville, H. Event-related potentials in neuropsychological studies of language. *Brain Lang.*, 1980, 11: 300–318.
- Nunez, P. (1981) *Electrical Fields of the Brain*. New York: Oxford University Press.
- O'Boyle, M.W., van Wyhe-Lawler, F. and Miller, D.A. (1987) Recognition of letters traced in the right and left palms: Evidence for a process-oriented tactile asymmetry. *Brain Cog.* 6: 474–494.
- Pardo, J.V., Fox, P. and Raichle, M. (1991) Localization of a human system for sustained attention by positron emission tomography. *Nature* 349: 61–64.
- Pfefferbaum, A. and Rosenbloom, M. (1989) Skull thickness influences P3 amplitude. *Psychopharmacol. Bull.* 23: 493–496.
- Pfefferbaum, A., Ford, J.M., White, P. and Roth, W. T. (1989) P3 in schizophrenia is affected by stimulus modality, response requirements, medication status, and negative symptoms. *Electroenceph. Clin. Neurophysiol.* 46: 1035–1044.
- Picton, T.W. (1992) The P300 wave of the human event-related potential. *J. Clin. Neurophysiol.* 9: 456–479.
- Picton, T.W., Hillyard, S.A. and Galambos, R. (1974) Human auditory evoked potentials I. Evaluation of components. *Electroenceph. Clin. Neurophysiol.* 74 36: 179–190.
- Polich, J. (1988) Bifurcated P300 peaks: P3a and P3b revisited? *J. Clin. Neurophysiol.* 5: 287–294.
- Polich, J. (1989) P300 from a passive paradigm. *Electroenceph. Clin. Neurophysiol.* 74: 312–320.
- Polich, J. (1993a) P300 in clinical applications: Meaning, method, and measurement. In: E. Niedermeyer and F. Lopes da Silva (Eds.), *Electroencephalography: Basic Principles, Clinical Applications, and Related Fields*, 3rd Ed. Williams and Williams, Baltimore, MD, pp. 1005–1018.
- Polich, J. (1993b) Hemispheric differences for feature migrations. *Acta Psychologica* 83: 179–201.
- Polich, J. and Luckritz, J.Y. (1995) EEG and ERPs in young and elderly subjects. In: G. Karmos, M. Molnar, V. Csepe, I. Czizler and J.E. Desmedt (Eds.), *The State of the Art in Event-Related Potential Research*. Amsterdam, Elsevier, pp. 358–368.
- Polich, J. and Starr, A. (1983) Middle, late- and long-latency auditory evoked potentials. In E. J. Moore (Ed.), *Bases of Auditory Brain Stem Evoked Responses*. New York: Grune and Stratton, pp. 345–361.
- Polich, J. and Squire, L.R. (1993) P300 from amnesic patients with bilateral hippocampal lesions. *Electroenceph. Clin. Neurophysiol.*, 86: 408–417.
- Posner, M.I. (1992) Attention as a cognitive and neural system. *Curr. Dir. Psychol. Sci.* 1: 11–14.
- Posner, M.I. and Petersen, S.E. (1990) The attention system of the human brain. *Annu. Rev. Neurosci.* 13: 25–42.
- Reitan, R.M., Wolfson, D. and Hom, J. (1992) Left cerebral dominance for bilateral simultaneous sensory stimulation. *J. Clin. Psychol.* 48: 760–766.
- Roth, T.W. (1973) Auditory evoked responses to unpredictable stimuli. *Psychophysiology* 10: 125–138.
- Senulis, J.A., and Davidson, R.J. (1989) The effect of linking ears on the hemispheric asymmetry of EEG. *Psychophysiology*, 26 (Suppl.), S55 (abstract)
- Sergent, J. (1991) Judgments of relative position and distance on representations of spatial relations. *J. Exp. Psychol.: Hum. Percep. Perform.* 17: 762–780.
- Simpson, D., and David, D. (1986) Craniosynostosis. In: H. Hofman and F. Epstein (Eds.), *Disorders of the Developing Nervous System: Diagnosis and Treatment*. Boston: Blackwell, p. 323.
- Squires, N., Squires, K. and Hillyard, S. (1975) Two varieties of long-latency positive waves evoked by unpredictable auditory stimuli in man. *Electroenceph. Clin. Neurophysiol.* 38: 387–401.
- Vesco, K., Bone, R., Ryan, J. and Polich, J. (1993) P300 in young and elderly subjects: Auditory frequency and intensity effects. *Electroenceph. Clin. Neurophysiol.* 88: 302–308.
- Yamaguchi, S. and Knight, R.T. (1990) Gating of somatosensory input by human prefrontal cortex. *Brain Res.* 521: 281–288.