

Handedness and P300 from Auditory Stimuli

Joel E. Alexander

Western Oregon State College

and

John Polich

The Scripps Research Institute

The P3(00) event-related potential (ERP) was elicited in 20 left- and 20 right-handed normal young adult male subjects using a simple auditory stimulus discrimination task. P3 amplitude from the target stimuli was larger at anterior electrode sites for left- compared to right-handed subjects. P3 latency from the standard stimuli was shorter for left- compared to right-handers. The N1, P2, and N2 components generally demonstrated similar handedness effects. The relationship of ERP amplitude and handedness to anatomical variables and cognitive factors is discussed. © 1997 Academic Press

Hemispheric information processing differences have been demonstrated by using behavioral techniques for auditory, visual, and tactile stimuli (Hellice, 1993; Ivry & Leiby, 1993; O'Boyle, van Wyhe-Lawler, & Miller, 1987; Polich, 1993), as well as with electroencephalographic (EEG) measures (Alexander & Sufka, 1993; Alexander, O'Boyle, & Benbow, 1996; Davidson, Chapman, Chapman, & Henriques, 1990; Gevins et al., 1979) in a wide vari-

Collaborative studies on the Genetics of Alcoholism (H. Begleiter, SUNY HSCB, Principle Investigator; T. Reich, Washington University, Co-Principle Investigator) includes six different centers where data collection takes place. The six sites and Principle Investigator and Co-Investigators are: Indiana University (J. Nurnberger, Jr., P. M. Conneally), University of Iowa (R. Crowe, S. Kuperman), University of California at San Diego and The Scripps Research Institute (M. Schuckit, F. E. Bloom), University of Connecticut (V. Hesselbrock), State University of New, Health Sciences Center at Brooklyn (H. Begleiter, B. Porjesz), and Washington University in St. Louis (T. Reich, C. R. Cloninger). This national collaborative study is supported by the National Institute on Alcohol Abuse and Alcoholism (NIAAA) by U.S.P.H.S. Grants NIAAA U10AA08401–08. The first author was supported by NIAAA Training Grant AA07456-10. This paper is publication NP9001 from The Scripps Research Institute.

Correspondence and reprint requests should be addressed to J. Polich, Department of Neuropharmacology TPC-10, The Scripps Research Institute, 10550 North Torrey Pines Road, La Jolla, CA 92037; E-mail: polich@scripps.edu.

ety of task situations. In addition, despite a general impression that the P3(00) cognitive event-related potential (ERP) is of equal amplitude about the midline (Donchin, Kutas, & McCarthy, 1977), similar hemispheric asymmetries have been observed when task conditions that encourage differential cerebral processing are employed (Kok & Rooyackers, 1986; Schweinberger & Sommer, 1991; Tenke, Bruder, Towey, Leite, & Sidits, 1993). Moreover, several reports even have found P3 amplitude from normal young adult subjects is greater over the right compared to that over the left cerebral hemisphere in the absence of a specific laterality task when a simple stimulus discrimination paradigm is used to elicit the ERPs (Bruyant, Garcia-Larrea, & Mauguiere, 1993; Holinger et al., 1992; Karniski & Blair, 1989; Naumann et al., 1992). These findings suggest that the P3 component may be innately lateralized because of fundamental neurophysiological differences between the cerebral hemispheres (Alexander et al., 1995, 1996).

A major factor that has not been examined in these studies is subject hand preference even though this variable may be of some importance for ERP laterality effects, since handedness is considered to be a behavioral manifestation of individual differences in hemispheric cerebral asymmetry (Halpern, 1992). The relationship of handedness to cerebral lateralization is complex (Braun et al., 1994; Bryden & Steenhuis, 1991; Hardyck & Petrinovich, 1977; McKeever, 1991; Sergent, 1990), but the consistent historical evidence for a 90% preponderance of right-handed preference (Coren & Porac, 1977) and fairly clear indications of genetic determination (Annett, 1985; Carter-Saltzman, 1980) strongly imply that preferential human hand use stems from neuroanatomical causes. In support of this proposition, several neuroanatomy and brain imaging studies have found weaker cerebral size asymmetries for left- compared to right-handed subjects (e.g., Galaburda, LeMay, Kemper, & Geschwind, 1977; LeMay, 1977), although consistent handedness or familial sinistrality effects are not always obtained (cf. Chui & Damasio, 1980; Koff, Naeser, Pieniadz, Foundas, & Levine, 1986). Of importance in this context are observations that corpus callosal size is related directly to handedness preference: Left-handed males have larger callosal areas than right-handed males (Dennenberg, Kertesz, & Cowell, 1991; Habib et al., 1991; Witelson, 1985). Even though there is some debate as to whether these anatomical differences occur primarily at the anterior or posterior sections of the corpus callosum and whether subject sex interacts with callosal size and handedness (cf. Driesen & Raz, 1995; Steinmetz et al., 1992; Weis, Weber, Wenger, & Kimbacher, 1988; Witelson, 1989, 1992), these findings indicate that the neural basis for hand preference is a major factor underlying neurobehavioral (e.g., Christman, 1989; Gordon & Kravetz, 1991; Hines, Chiu, McAdams, Bentler, & Lipcamon, 1992; Polich & Morgan, 1994; Yazgan, Wexler, Kinsbourne, Peterson, & Leckman, 1995) or electrophysiological laterality effects (e.g., Barrett & Rugg, 1989; Kutas, Van Patten, & Beson, 1988; Rugg, 1985).

Given this background and because P3 amplitude has been found to be asymmetric in amplitude across the hemispheres for right-handers, it is not unreasonable to suppose that subject handedness may affect this ERP component. Indeed, since the anatomical origins of subject handedness can contribute to cognitive activity (McKeever, 1991; Polich & Morgan, 1994; Witelson, 1992), handedness also could affect the neural operations underlying P3 generation. Several studies have suggested that multiple generators are engaged when the P3 component is produced (Johnson, 1993; Knight, 1990), with additional findings implying that activation of frontal cortical areas occurs in conjunction with temporal-parietal sources (Courchesne, Hillyard, & Galambos, 1975; Knight, Scabini, Woods, & Clayworth, 1989). This view is consistent with positron-emission tomography results that indicate frontal lobe activity reflects initial attentional mechanisms that are necessary for the stimulus discrimination operations that elicit the P3 (Pardo, Fox, & Raichle, 1991; Posner, 1992). Assuming that interhemispheric communication occurs as these processes are activated (Hellige, 1993; Sergent, 1990), it is plausible that the P3 ERP would be larger and perhaps occur earlier over the frontal recording areas in individuals whose corpus callosal connections are larger than in individuals whose callosal connections are not as prominent. Such handedness effects could occur because information transmission from one hemisphere to the other might be facilitated if callosal connections were larger so that component amplitude and latencies at the midline (and other sites) would be affected. The present study was designed to test this hypothesis by determining whether the P3 component from a simple auditory discrimination task is different in left- compared to right-handed males.

METHOD

Subjects. A total of 20 left- and 20 right-handed, normal young adult males ($M = 22.6$, $SD = 1.8$ years) served as subjects. Handedness was evaluated by a six-item handedness questionnaire (Annett, 1985), with additional items that assessed familial sinistrality. Left-handedness was defined as having left-hand preferences for a minimum of four of the six tasks ($M = 5.6$, $SD = .6$); right-handedness was defined as showing only right (i.e., no left-hand) preferences for all questions ($M = .0$, $SD = .0$). The mean number of left-handed family members reported by the left-handed subjects was 1.4 ($SD = .68$, mode = 1); the mean number of left-handed family members reported by the right-handed subjects was .0. Hence, the sinistral sample was strongly left-handed. All subjects reported an absence of psychiatric or neurologic problems, were screened for alcohol/drug use, and received pecuniary remuneration.

Recording conditions and procedure. EEG activity was recorded monopolarly using an 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 Ω or less. Electroocular (EOG) activity was measured with one electrode placed at the outer canthus of the left eye for horizontal eye movement and a second electrode placed on the forehead to monitor vertical eye movements. The filter bandpass was .02–50 Hz (3 dB down, 6 dB octave/slope). 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 exceeded $\pm 73.3 \mu\text{V}$ 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 .125. Subjects were instructed to press a key pad with their forefinger whenever a target tone was detected and to refrain from responding to the standard. Response hand was counterbalanced across subjects in both handedness groups. Stimulus presentation ended when the first 25 target and 75 standard artifact-free stimuli were acquired.

RESULTS

All analyses of variance employed Greenhouse–Geisser corrections to the degrees of freedom for the repeated measures factors with at least three levels. Only probability values for the corrected df are reported. Post-hoc mean comparisons were performed using the Newman–Keuls procedure.

Task Performance

Task performance was nearly perfect for both groups, with the total number of errors (misses and false alarms) for left-handers at .3% and right-handers at .4%. Mean response time for the target stimuli was for left-handers 412 ms (SD = 52.7) and right-handers 428 ms (SD = 51.1), with no reliable difference found ($F < 1$, $p > .45$). Hence, both groups performed the task with virtually no error and comparable response times.

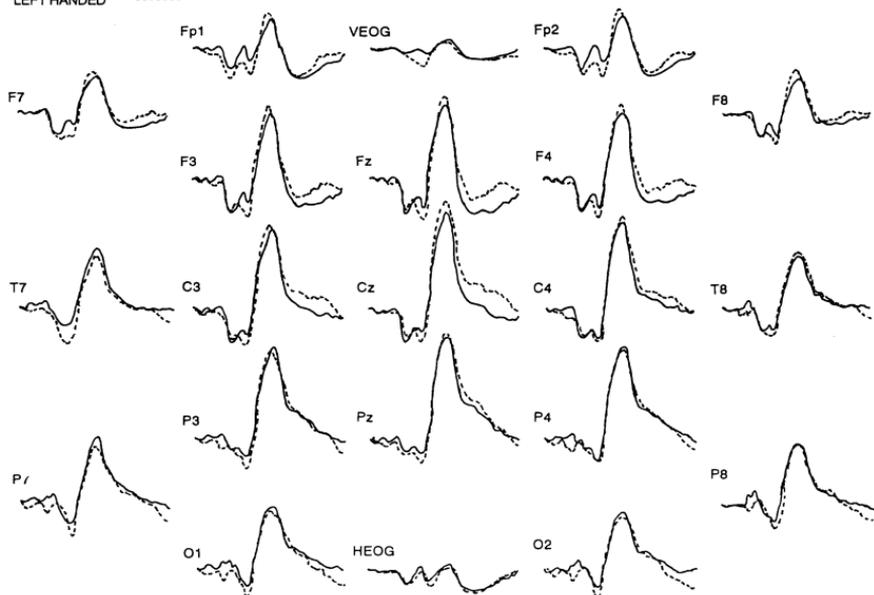
Component Measurement and Analyses

Waveforms were assessed visually and individually for each subject to identify amplitudes and latencies of the N1, P2, N2, and P3 components at each electrode site by locating the most positive or negative component within the latency windows of 100–200, 150–250, 200–300, and 250–450 ms, respectively. Amplitude was measured at the peak of the component relative to the mean of the prestimulus baseline, with peak latency defined as the time of maximum positive or negative amplitude within the latency window. Two points should be noted about this approach: (1) These procedures facilitated the measurement of all components from both the target and standard stimuli, even when the potentials were not morphologically robust (e.g., P3 from the standard tones). (2) This method produces individual component measurements that are unrelated to each other—an assertion that has been verified empirically (Polich, 1992), since each potential is thought to reflect a different set of information processing events. The grand average ERP waveforms for the target and standard stimuli at each electrode position are illustrated in Fig. 1. The mean amplitude/latency values for the P3 component as a function of lateral electrode position and stimulus type are presented in Fig. 2.

Although response hand was counterbalanced across subjects, analysis of this variable revealed no influence on the effects reported below, and it will

TARGET

RIGHT HANDED ———
LEFT HANDED - - - - -



STANDARD

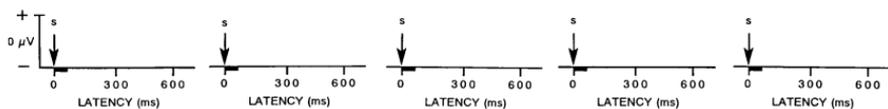
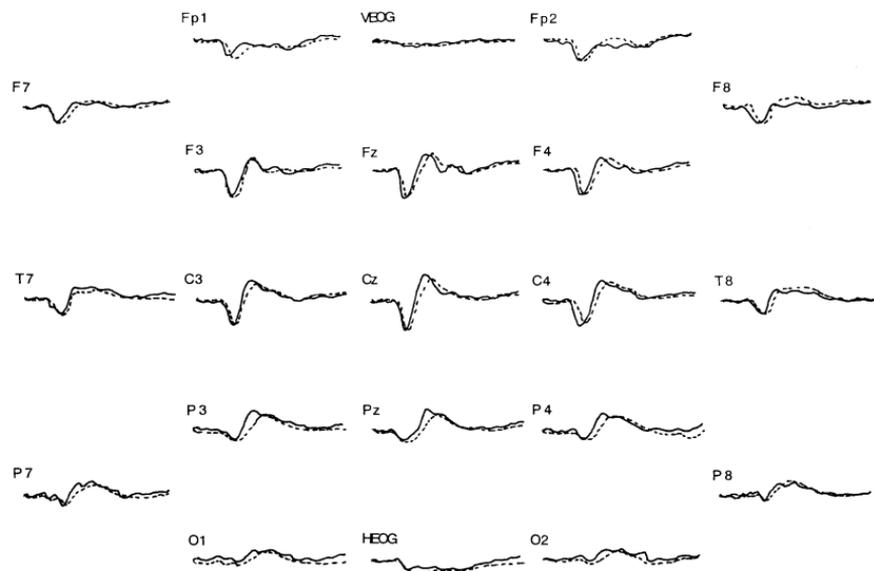


FIG. 1. Grand average event-related potentials from the target and standard stimuli for left- and right-handed subjects ($N = 20$ /handedness group).

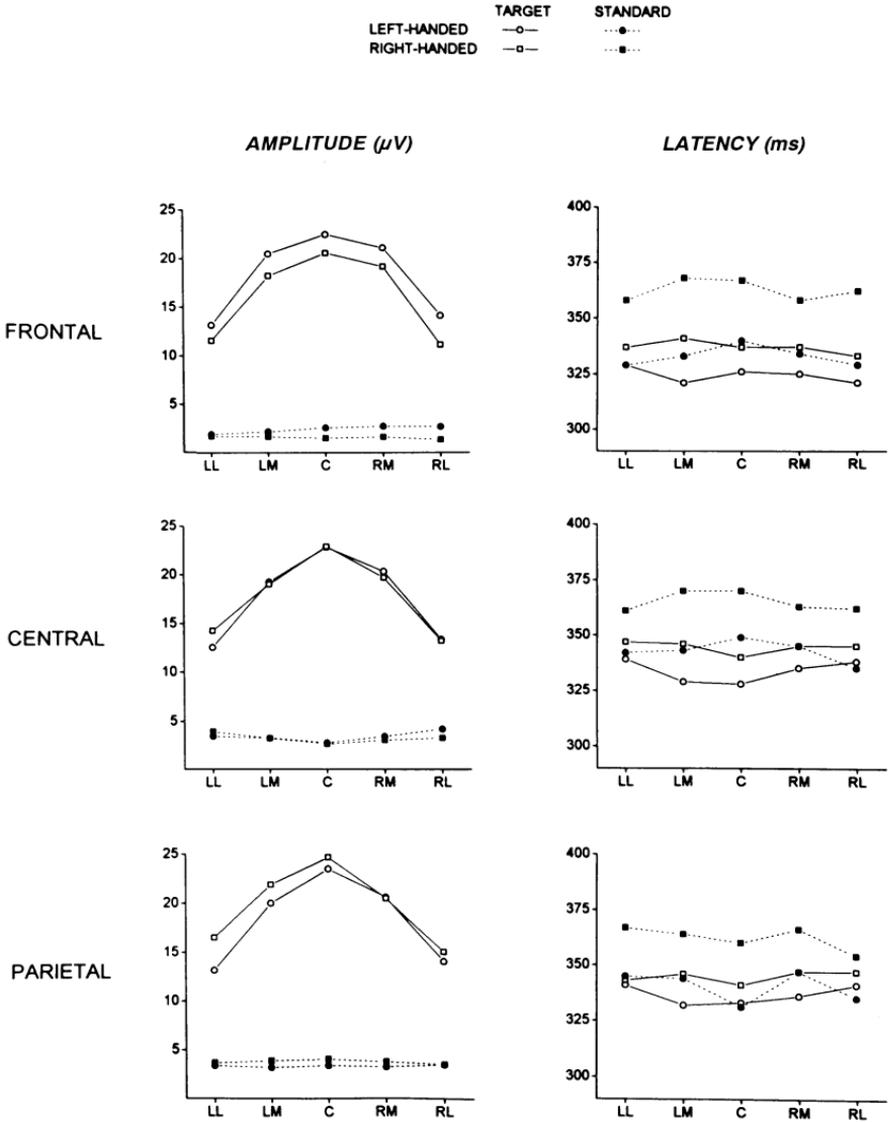


FIG. 2. Mean P3 amplitude and latency from the target and standard stimuli for left- and right-handed subjects as a function of lateral and anterior-to-posterior electrode sites (LL, left lateral; LM, left medial; C, central; RM, right medial; RL, right lateral).

not be considered further. Preliminary analyses indicated no reliable handedness effects from the Fp1/2 and O1/2 electrode sites, and these will not be considered further. All other statistical analyses used the anterior-to-posterior (frontal, central, parietal), lateral (F7/8, T7/8, P7/8), medial (F3/4, C3/4, P3/4), and central (Fz, Cz, Pz) electrode locations. Separate three-factor (handedness group \times anterior-to-posterior electrode \times lateral electrode location)

analyses of variance were performed on the amplitude and latency data obtained from each of the stimulus types for each component. Because the anterior-to-posterior and lateral electrode factors produced main effects in the typical directions for each component, these variables will receive comment only if they yielded statistically reliable interactions with subject handedness.

P3 Component

Target stimulus P3 amplitude was larger for left-handers across the anterior locations compared to right-handers who demonstrated larger component amplitudes at the posterior locations, as indicated by a significant interaction between the handedness group and anterior-to-posterior electrode factors, $F(2, 76) = 5.3, p < .02$. The reliability of this effect is supported by the observation that 17 of 20 left-handed subjects demonstrated this amplitude pattern; the 3 other subjects generally evinced frontal amplitudes midway between or similar to the right-handed subjects. In addition, P3 latency from the standard stimuli was shorter for left- compared to right-handers, $F(1, 38) = 9.6, p < .01$. Further, the degree to which the handedness contributed to P3 amplitude in the absence of any overall differences between the left- and right-handed subjects was assessed by normalizing all values into a percentage based on the Pz electrode site measures (cf. Johnson, 1993). Analysis of these data produced the same outcome for P3 amplitude from the target stimuli, with a somewhat stronger effect obtained ($p < .01$).

N1, P2, and N2 Components

Analyses of the N1, P2, and N2 components were conducted in the same fashion (normalizing transformations for these components has not been demonstrated and will not be considered here). N1 amplitude did not differ between left- and right-handed subjects. N1 latency from the standard stimuli was shorter for left- compared to right-handed subjects, $F(1, 38) = 4.5, p < .05$, most notably at lateral electrode locations, $F(4, 152) = 8.4, p < .001$ —an observation confirmed by post-hoc assessments ($p < .001$). P2 amplitude from the standard stimuli was smaller for the left- compared to right-handers, more so at the central and over the left hemisphere to yield a complex interaction between handedness group and lateral location factors, $F(4, 152) = 4.3, p < .005$. Although P2 latency from the standard stimuli was shorter for the left- compared to the right-handed group, $F(1, 38) = 4.8, p < .05$, inspection of the individual data points revealed that this outcome occurred because of the influence of a few left-handed subjects who produced very short latencies. N2 amplitude did not produce any reliable handedness effects. N2 latency was shorter at anterior locations for left- compared to right-handers for the target stimulus, $F(2, 76) = 3.5, p < .05$. Post-hoc analysis indicated that this difference originated primarily from the ante-

rior electrodes ($p < .01$). Overall, the N1, P2, and N2 components tended to mimic the handedness effects observed for the P3, with left-handed subjects producing larger amplitudes and shorter latencies compared to right handed subjects. Although P2 amplitude from the standard stimuli was smaller for the left- relative to right-handed subjects, this result stemmed from an interaction between handedness group and both the anterior-to-posterior as well as the lateral electrode locations. Thus, with this one exception, the significant ERP effects were larger amplitudes and shorter in latencies for the left-relative to the right-handed subjects.

DISCUSSION

P3 amplitude from the target stimuli was reliably larger for left- compared to right-handed subjects at the anterior electrode positions, with right-handed subjects demonstrating larger amplitudes than left-handed subjects at the posterior electrode positions. These outcomes were obtained even when overall handedness group effects were adjusted with normalizing procedures. P3 latency from the standard stimuli also was shorter for left- compared to right-handed subjects. The N1, P2, and N2 components generally produced results similar to those observed for the P3.

The source of handedness effects on ERPs is not known. It may be that brain morphology, skull thickness, or cranial differences between handedness groups contributed to the P3 effects, since these factors can affect ERP amplitude (e.g., Daniel, Myslobodsky, Ingraham, Coppola, & Weinberger, 1989). Variation in the underlying neural mass could then influence electrophysiological measures by redirecting current flow through the skull, such that larger amplitudes are recorded over locations containing more cellular volume and/or having thinner skull widths (cf. Donchin, Karis, Bashore, Coles, & Gratton, 1986). Although a plausible explanation, measurable cranial irregularities (e.g., plagiocephaly) occur only in about 10% of the population (Binnie, Dekkerm, Smit, & Van der Linden, 1982) and yield slight and apparently unstable relationships between skull thickness and occipital EEG alpha asymmetry (Chui & Damasio, 1980; Myslobodsky et al., 1989). Since the P3 handedness effects occurred primarily between the frontal and parietal locations, and because it is difficult to associate cranial structural differences to the latency effects, it is likely that the present findings are unrelated to skull and brain morphology variation.

Given the previously reported explicit anatomical differences between left- and right-handed individuals with respect to corpus callosal size (Denenberg et al., 1991; Driesen & Raz, 1995; Habib et al., 1991; Witelson, 1985, 1989), it is not unreasonable to suppose that ERP measures might be influenced by variation in callosal mass between the strongly left- and right-handed male subjects employed in the present study (cf. Steinmetz et al., 1992; Weis et al., 1988; Witelson, 1992). If the size of the callosal connection

does contribute to communication efficiency between the hemispheres, variation in P3 values between handedness and, therefore, callosal groups may be reflecting related differences in information processing capability. Although an intriguing possibility, the exact nature of these ERP/handedness differences is still unclear because they could originate from either (1) a difference in neural processing efficiency related to callosal size—i.e., larger amplitudes and shorter latencies with larger callosal cross-sections, or (2) real variation in cognitive function in terms of where, when, and how P3 attentional/memory operations are performed. However, assuming that task processing is communicated via the corpus callosum, discriminating the target from a standard stimulus could initiate frontal lobe engagement, because such a process requires the consistent application of attentional focus (Pardo et al., 1991; Posner, 1992). In this view, left- and right-handed subjects may differ with respect to how the output of fundamental discrimination processes are propagated through the cortical areas involved in P3 generation. The generally similar handedness findings for the preceding sensory ERPs also support this conclusion, as do the indications of hemispheric amplitude asymmetry found for both groups at the frontal electrode sites (cf. Alexander et al., 1995, 1996).

A major theory of the P3 posits that this ERP component reflects a developing representation within short-term memory (Donchin & Coles, 1988; Donchin et al., 1986). This hypothesis is supported by findings from human lesion studies suggesting that multiple neural generators are involved in P3 production (Johnson, 1993; Knight et al., 1989; Yamaguchi & Knight, 1990). In addition, a strong alerting stimulus will elicit an earlier P3a subcomponent that is generally largest over a frontal/central electrode sites (cf. Courchesne et al., 1975; Katayama & Polich, 1997; Squires, Squires, & Hillyard, 1975) and indicates initial signal evaluation (Ford et al., 1994; Knight, 1990), with subsequent attentional capacity and memory processes indexed by the central/parietal or canonical P3b (Knight et al., 1989; Picton, 1992; Polich & Squire, 1993). Because the obtained P3 amplitude handedness results were the most reliable for the target stimulus, directed attention may contribute specifically to these handedness effects. Thus, the frontal–parietal P3 differences observed between the left- and right-handed subjects could reflect subject group neurocognitive variation for the processes activated during oddball task performance.

REFERENCES

- Alexander, J., & Sufka, K. 1993. Cerebral lateralization in homosexual males: A preliminary EEG investigation. *International Journal of Psychophysiology*, **15**, 269–274.
- Alexander, J., O'Boyle, M. W., & Benbow, C. P. 1996. Developmental advanced EEG alpha power in gifted male and female adolescents. *International Journal of Psychophysiology*, **23**, 25–31.
- Alexander, J., Bauer, L., Kuperman, S., Rohrbaugh, J., Morzorati, S., O'Connor, S., Porjesz,

- B., Begleiter, H., & Polich, J. 1995. P300 hemispheric amplitude asymmetries from a visual oddball task. *Psychophysiology*, **32**, 467–475.
- Alexander, J., Bauer, L., Kuperman, S., Rohrbaugh, J., Morzorati, S., O'Connor, S., Porjesz, B., Begleiter, H., & Polich, J. 1996. Hemispheric differences for P300 amplitude from an auditory oddball task. *International Journal of Psychophysiology*, **21**, 189–196.
- Annett, M. 1967. The binomial distribution of right, mixed and left handedness. *Quarterly Journal of Experimental Psychology*, **19**, 327–333.
- Annett, M. 1985. *Left, right, hand and brain: The right shift theory*. Hillsdale, NJ: Erlbaum.
- Barrett, S. P., & Rugg, M. D. 1989. Asymmetries in event-related potentials during rhyme-matching: Conformation of the null effects of handedness. *Neuropsychologia*, **27**, 539–548.
- Binnie, C. D., Dekkerm, E., Smit, A., & Van der Linden, G. 1982. Practical considerations in the positioning of EEG electrodes. *Electroencephalography and Clinical Neurophysiology*, **53**, 453–458.
- Braun, C. M. J., Sapin-Leduc, A., Picard, C., Bonnenfant, E., Achim, A., & Daigneault, S. 1994. Zadel's model of interhemispheric dynamics: Empirical tests, a critical appraisal, and a proposed revision. *Brain and Cognition*, **24**, 57–86.
- Bruyant, P., Garcia-Larrea, L., & Mauguiere, F. 1993. Target side scalp topography of the somatosensory P300. *Electroencephalography and Clinical Neurophysiology*, **88**, 468–477.
- Bryden, M. P., & Steenhuis, R. E. 1991. Issues in the assessment of handedness. In F. L. Kitterle (Ed.), *Cerebral laterality: Theory and research*. Hillsdale, NJ: Erlbaum. Pp. 35–51.
- Carter-Saltzman, L. 1980. Biological and sociological effects on handedness: Comparison between biological and adoptive families. *Science*, **209**, 1263–1265.
- Christman, S. 1989. Temporal integration of form as a function of subject handedness and retinal locus of presentation. *Neuropsychologia*, **28**, 361–374.
- Chui, H. C., & Damasio, A. R. 1980. Human cerebral asymmetries evaluated by computed tomography. *Journal of Neurology, Neurosurgery, and Psychiatry*, **43**, 873–878.
- Coren, S., & Porac, C. 1977. Fifty centuries of right-handedness: The historical record. *Science*, **198**, 631–632.
- Courchesne, E., Hillyard, S. A., & Galambos, R. 1975. Stimulus novelty, task relevance, and the visual evoked potential in man. *Electroencephalography and Clinical Neurophysiology*, **39**, 131–143.
- Daniel, D. G., Myslobodsky, M. S., Ingraham, L. J., Coppola, R., & Weinberger, D. R. 1989. The relationship of occipital skull asymmetry to brain parenchymal measures in schizophrenia. *Schizophrenia Research*, **2**, 465–472.
- Davidson, R. J., Chapman, J. P., Chapman, L. J., & Henriques, J. B. 1990. Asymmetrical brain electrical activity discriminates between psychometrically-matched verbal and spatial cognitive tasks. *Psychophysiology*, **27**, 528–543.
- Dennenberg, V., Kertesz, A., & Cowell, P. 1991. A factor analysis of the human's corpus callosum. *Brain Research*, **548**, 126–132.
- Donchin, E., & Coles, M. G. H. 1988. Is the P300 component a manifestation of context updating? *Behavioral and Brain Science*, **11**, 357–374.
- Donchin, E., Karis, D., Bashore, T. R., Coles, M. G. H., & Gratton, G. 1986. Cognitive psychophysiology and human information processing. In M. G. H. Coles, E. Donchin, & S. W. Porges (Eds.), *Psychophysiology: Systems, processes, and applications*. New York: Guilford Press. Pp. 244–267.
- Donchin, E., Kutas, M., & McCarthy G. 1977. Electro cortical indices of hemispheric utilization. In S. Harnad, R. Doty, L. Goldstein, J. Jaynes, and G. Krauthamer (Eds.), *Lateralization in the nervous system*. New York: Academic Press. Pp. 339–384.
- Driesen, N. R., & Raz, N. 1995. The influence of sex, age, and handedness on corpus callosum morphology: A meta-analysis. *Psychobiology*, **23**, 240–247.
- Ford, J. M., Sullivan, E., Marsh, L., White, P., Lim, K., & Pfefferbaum, A. 1994. The relation-

- ship between P300 amplitude and regional gray matter volumes depends on the attentional system engaged. *Electroencephalography and Clinical Neurophysiology*, **90**, 214–228.
- Galaburda, A., LeMay, M., Kemper, T., & Geschwind, N. 1977. Right-left asymmetries in the brain. *Science*, **199**, 852–856.
- Gevens, A. S., Zeitlin, G., Doyle, J., Yingling, C., Schaffer, R., Callaway, E., & Yeager, C. 1979. Electroencephalogram correlates of higher cortical functions. *Science*, **203**, 665–668.
- Gordon, H., & Kravetz, S. 1991. The influence of gender, handedness, and performance level on specialized cognitive functioning. *Brain and Cognition*, **15**, 37–61.
- Habib, M., Gayraud, D., Oliva, A., Regis, J., Salamon, G., & Khalil, R. 1991. Effects of handedness and sex on the morphology of the corpus callosum: A study with brain magnetic resonance imaging. *Brain and Cognition*, **16**, 41–61.
- Halpern, D. F. 1992. *Sex differences in cognitive abilities*. Hillsdale, NJ: Earlbaum.
- Hardyck, C., & Petrinovich, L. 1977. Left-handedness. *Psychological Bulletin*, **84**, 385–404.
- Hellige, J. 1993. Unity of thought and action: Varieties of interaction between the left and right cerebral hemispheres. *Current Directions in Psychological Science*, **2**, 21–25.
- Hines, M., Chiu, L., McAdams, L., Bentler, P., & Lipcamon, J. 1992. Cognition and the corpus callosum: verbal fluency, visuo spatial ability, and language lateralization related to midsagittal surface areas of callosal subregions. *Behavioral Neuroscience*, **106**, 3–14.
- Holinger, D., Faux, S., Shenton, M., Sokol, N., Seidman, L., Green, A., & McCarley, R. 1992. Reversed temporal region asymmetries of P300 topography in left and right-handed schizophrenic subjects. *Electroencephalography and Clinical Neurophysiology*, **84**, 532–537.
- Ivry R. B., & Leiby, P. 1993. Hemispheric differences in auditory perception are similar to those found in visual perception. *Psychological Science*, **4**, 41–45.
- Johnson, R. 1993. On the neural generators of the P300 component of the event-related potential. *Psychophysiology*, **30**, 90–97.
- Karniski, W., & Blair, R. C. 1989. Topographical and temporal stability of the P300. *Electroencephalography and Clinical Neurophysiology*, **72**, 373–383.
- Katayama, J.-I., & Polich, J. 1997. Stimulus context determines P3a and P3b. *Psychophysiology*, in press.
- Knight, R. 1990. Neural mechanisms of event-related potentials from human lesion studies. In J. Rohrbaugh, R. Parasuraman, & R. Johnson (Eds.), *Event-related brain potentials: Basic issues and applications*. New York: Oxford. Pp. 3–18.
- Knight, R., Scabini, D., Woods, D., & Clayworth, C. 1989. Contributions of temporal-parietal junction to the human auditory P3. *Brain Research*, **502**, 109–116.
- Koff, E., Naeser, M., Pieniadz, J., Foundas, A., & Levine, H. 1986. Computed tomographic scan hemispheric asymmetries in right- and left-handed male and female subjects. *Archives of Neurology*, **43**, 487–491.
- Kok, A., & Rooyackers, J. 1986. ERPs to laterally presented pictures and words in a semantic categorization task. *Psychophysiology*, **23**, 672–683.
- Kutas, M., Van Patten, C., & Besson, M. 1988. Event-related potential asymmetries during the reading of sentences. *Electroencephalography and Clinical Neurophysiology*, **69**, 218–233.
- LeMay, M. 1977. Asymmetries of the skull and handedness: Phrenology revisited. *Journal of Neurological Science*, **32**, 243–253.
- McKeever, W. F. 1991. Handedness, language laterality, and spatial ability. In F. L. Kitterle (Ed.), *Cerebral laterality: Theory and research*. Hillsdale, NJ: Erlbaum. Pp. 53–70.
- Myslobodsky, M., Coppola, R., Bar-Ziv, J., Karson, C., Daniel, D., & Weinberger, D. R. 1989. EEG asymmetries may be affected by cranial and brain parenchymal asymmetries. *Brain Topography*, **1**, 221–228.
- Myslobodsky, M., Coppola, R., & Weinberg, D. 1991. EEG laterality in the era of structural brain imaging. *Brain Topography*, **3**, 381–390.
- Naumann, E., Huber, C., Maier, S., Plihal, W., Wustmans, A., Diedrich, O., & 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. *Electroencephalography and Clinical Neurophysiology*, **83**, 254–264.
- O'Boyle, M. W., van Wyhe-Lawler, F., & Miller, D. A. 1987. Recognition of letters traced in the right and left palms: Evidence for a process-oriented tactile asymmetry. *Brain and Cognition*, **6**, 474–494.
- Pardo, J. V., Fox, P., & Raichle, M. 1991. Localization of a human system for sustained attention by positron emission tomography. *Nature*, **349**, 61–64.
- Pfefferbaum, A., & Rosenbloom, M. 1989. Skull thickness influences P3 amplitude. *Psychopharmacology Bulletin*, **23**, 493–496.
- Picton, T. W. 1992. The P300 wave of the human event-related potential. *Journal of Clinical Neurophysiology*, **9**, 456–479.
- Polich, J. 1992. On the correlation between P300 amplitude and latency. *Bulletin of the Psychonomic Society*, **30**, 5–8.
- Polich, J. 1993. Hemispheric differences for feature migrations. *Acta Psychologica*, **83**, 179–201.
- Polich, J., & Morgan, C. 1994. Handedness and hemispheric differences for feature perturbations. *Brain and Cognition*, **25**, 220–234.
- Polich, J., & Squire, L. R. 1993. P300 from amnesic patients with bilateral hippocampal lesions. *Electroencephalography and Clinical Neurophysiology*, **86**, 408–417.
- Posner, M. I. 1992. Attention as a cognitive and neural system. *Current Directions in Psychological Science*, **1**, 11–14.
- Rugg, M. D. 1985. The effects of handedness on event-related potentials in a rhyme-matching task. *Neuropsychologia*, **23**, 765–775.
- Schweinberger, S. R., & Sommer, W. 1991. Contributions of stimulus encoding and memory search to right hemisphere superiority in face recognition: Electrophysiological evidence. *Neuropsychologia*, **29**, 389–413.
- Sergent, J. 1990. Furtive incursions into bicameral minds: Integrative and coordinating role of subcortical structures. *Brain*, **113**, 537–568.
- Simpson, D., & David, D. 1986. Craniosynostosis. In H. Hofman & F. Epstein (Eds.), *Disorders of the developing nervous system: Diagnosis and treatment*. Boston: Blackwell. P. 323.
- Squires, N., Squires, K., & Hillyard, S. 1975. Two varieties of long-latency positive waves evoked by unpredictable auditory stimuli in man. *Electroencephalography and Clinical Neurophysiology*, **38**, 387–401.
- Steinmetz, H., Jancke, L., Kleinschmidt, A., Schlaug, G., Volkman, J., & Huang, Y. 1992. Sex but no hand differences in the isthmus of the corpus callosum. *Neurology*, **42**, 749–752.
- Tenke, G. E., Bruder, G., Towey, J., Leite, P., & Sidtis, J. 1993. Correspondence between brain ERP and behavioral asymmetries in a dichotic complex tone test. *Psychophysiology*, **30**, 62–70.
- Weis, S., Weber, G., Wenger, E., & Kimbacher, M. 1988. The human corpus callosum and the controversy about a sexual dimorphism. *Psychobiology*, **16**, 411–415.
- Witelson, S. F. 1985. The brain connection: The corpus callosum is larger in left-handers. *Science*, **229**, 665–668.
- Witelson, S. F. 1989. Hand and sex differences in the isthmus and genu of the human corpus callosum. *Brain*, **112**, 799–835.
- Witelson, S. F. 1992. Cognitive neuroanatomy: A new era. *Neurology*, **42**, 709–713.
- Yazgan, Y., Wexler, B., Kinsbourne, M., Peterson, B., & Leckman, J. 1995. Functional significance of individual variations in callosal area. *Neuropsychologia*, **33**, 769–779.
- Yamaguchi, S., & Knight, R. 1990. Gating of somatosensory input by human prefrontal cortex. *Brain Research*, **521**, 281–288.