Late Positive Event-Related Potentials after Commissural Section in Humans

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Abstract

■ The lateral distribution of the P300 component of the event-related brain potential (ERP) was studied in five epileptic patients whose corpus callosum had been surgically sectioned and in seven neurologically intact controls. The P300 was elicited in an auditory "oddball" task using high- and low-pitched tones and in a visual oddball task in which target words were presented either to the left or right visual fields, or to both fields simultaneously. Commissurotomy altered the normal pattern of bilaterally symmetrical P300 waves over the left and right hemispheres, but in a different manner for auditory and visual stimuli. The auditory P3 to binaural tones was larger in amplitude over the right than the left hemisphere for the patients. In the visual task, the laterality of the P300 varied with the visual field of the target presentation. Left field targets elicited much larger P300 amplitudes over the right than the left hemisphere, as did bilateral targets. In contrast, right field targets triggered P300 waves of about the same amplitude over the two hemispheres. The overall amplitude of the P300 to simultaneous bilateral targets was less than the sum of the individual P300 amplitudes produced in response to the unilateral right and left field targets. These shifts in P300 laterality argue against the view that the P300 is an index of diffuse arousal or activation that is triggered in both hemispheres simultaneously irrespective of which hemisphere processes the target information. The results further demonstrate that the P300 does not depend for its production on interhemispheric comparisons of information mediated by the corpus callosum, as suggested recently by Knight et al. (1989). ■

INTRODUCTION

Over the last decade, there has been an increasing number of investigations of the neural bases of perceptual and cognitive processing in humans, primarily due to the availability of noninvasive techniques for measuring brain activity. One such technique, the recording of event-related potentials (ERPs) from the scalp, can reveal patterns of brain electrical activity associated with sensory, motor, and cognitive processes. The most widely studied of the "cognitive ERP" components is a late positive wave (variously termed the P3, P3b, P300, or LPC). The P300 is typically elicited by task-relevant stimuli that require a decision from a subject (for reviews see Pritchard 1981; Donchin et al. 1986; Hillyard and Picton 1987). The sensitivity of the P300 to a variety of experimental manipulations has been examined extensively in the so-called "oddball" paradigm, wherein a relevant stimulus (i.e., the oddball or target) is presented infrequently and unexpectedly within a repetitive sequence of other background stimuli (i.e., standards). These standard and target classes may be defined either in terms of simple physical attributes or in terms of higher order conceptual categories. The P300 elicited by target stimuli has a latency that depends on the difficulty or complexity of the target discrimination and an amplitude that varies with the subjective expectancy for target occurrence (reviewed in Donchin and Coles 1988). Additionally, many studies have shown that the P300 is more closely coupled to stimulus evaluation and classification than with subsequent response selection and mobilization processes (e.g., Magliero et al. 1984).

Although many of the factors that influence P300 amplitude (e.g., task relevance, stimulus discriminability, expectancy) have been delineated, there is still a lively controversy concerning its functional significance (Donchin and Coles 1988; Verleger 1988). On the one hand, this ERP has been linked to a number of specific processing events such as delivery of task-relevant information (Sutton et al. 1967), sensory decision making (Smith et al. 1970), orienting and cognitive evaluation (Ritter and Vaughan 1969), and updating of stimulus contexts or representations in memory (Donchin and Coles 1988). On the other hand, it has been argued that the P300 is nothing more than an index of the waxing and waning of a diffuse arousal or activation process during sensory analysis (Karlin 1970; Näätänen 1967, 1975). In this view, the P300 has been equated with the positive-going resolution of the slow, negative shift in the electroencephalogram (termed the contingent negative variation or CNV) that develops during periods of anticipation of significant stimuli.

Along these lines, Desmedt (1980, 1981) has hypothesized that both the CNV and its resolution (identified with the P300 in Desmedt's view) reflect the influence of diffuse, bilateral projections of the midbrain reticular formulation (MRF) on cortical activity. Specifically, the CNV was taken to represent elevated "neuromodulatory" regulation of the telencephalon by the midbrain reticular formation (MRF) during periods of timed expectancy, while the P300 was viewed as a transient reduction in this neuromodulation resulting from inhibition of the MRF by frontal cortex pursuant to the "closure" of a decision—such as that following identification of a target stimulus in a serial detection (oddball) task. Evidence that P300 elicitation is sensitive to the state of ascending mesencephalic projections comes from the findings of Pineda et al. (1989), who showed that bilateral lesions of the locus ceruleus in monkeys greatly reduced the amplitude of a late positive ERP (considered to be a P300 homologue) that was elicited by deviant sounds in a random sequence.

Further evidence for candidate neural generator(s) of the human P300 come from studies in which ERPs were recorded intracranially from epileptic patients performing tasks that are known to produce P300s at the scalp. Such investigations have documented the presence of large endogenous potentials in mesial temporal lobe (MTL) structures that share many of the functional properties of the scalp-recorded P300 (Alain et al. 1989; Halgren et al. 1980, 1986; McCarthy et al. 1989; Stapleton and Halgren 1987; Wood et al. 1984). These depth-recorded potentials exhibit steep voltage gradients and polarity reversals that are indicative of local generator sources in deep MTL structures including the hippocampus and amygdala. Reports that unilateral temporal lobectomy does not affect P300 amplitudes or scalp distributions to the extent that one would expect if the MTL strutures were its sole generators, however, have spurred the continued search for other brain areas that must be involved in its generation (Johnson 1988, 1989; Stapleton et al. 1987; McCarthy et al. 1989). One key piece of evidence comes from the recent finding of Knight et al. (1989) that unilateral cortical lesions at the temporal–parietal junction (a neocortical area spared in the above-mentioned temporal lobectomies) almost completely abolished the P300 to infrequent auditory targets in an oddball paradigm. Determining whether the temporal–parietal junction participates directly in the generation of P300 activity or merely subserves acoustic processing functions preliminary to the generation of P300s to auditory stimuli, however, must await the results of similar experiments using visual and somatosensory stimuli.

The Split-Brain Approach

The neural systems involved in generating the human cognitive ERPs may also be clarified by studying the consequences of sectioning the corpus callosum (i.e., commissurotomy) on the ERPs recorded at the scalp (Gazzaniga and Hillyard 1973; Hillyard 1973; Kutas et al. 1988). For example, Gazzaniga and Hillyard used this approach to show that a signal lateralized to one visual field, thereby warning only the contralateral hemisphere to expect a subsequent imperative stimulus, nonetheless elicited a substantial CNV that was symmetrical over *both* cerebral hemispheres. Since the CNV was observed over the hemisphere that had not been exposed to the warning stimulus, Gazzaniga and Hillyard concluded that the CNV was under the control of a diffuse, bilaterally projecting system originating in the brainstem. Widespread involvement of nonspecific, subcortical projection systems in the genesis of the CNV also was posited by McCallum et al. (1973) on the basis of depth recordings in humans.

We employed a similar approach in the present experiment to examine the lateral distribution of the P300 component in commissurotomized (split brain) patients under conditions wherein a visual "target" stimulus (subject's own first name) was projected to only one hemisphere at a time. Previous studies in normal subjects have noted that P300 components elicited by unilateral target stimuli in all modalities (i.e., visual, auditory, and somatosensory) are either bilaterally symmetrical on the scalp (Desmedt and Robertson 1977; Snyder et al. 1980) or exhibit a slight tendency to be larger in amplitude ipsilateral to the visual field of stimulation (Heinze et al. in press; Hillyard and Munte 1984; Mangun and Hillyard 1990). The present study was designed to assess the consequences of sectioning the corpus callosum on the bilateral distribution of the P300 to unilaterally presented visual targets. As a control experiment, P300s were also recorded to binaurally presented target tones in an oddball paradigm. Since these tones would be detected by both hemispheres simultaneously, we expected the as-

sociated P300 to present with a bilaterally symmetrical distribution at the scalp.

By recording P300 waves from split-brain patients a number of important questions regarding the physiological and psychological properties of this ERP component could be addressed. First, by presenting the stimulus triggering the P300 to only one of the surgically separated cerebral hemispheres at a time, we could determine whether its scalp distribution was lateralized over that hemisphere or whether, like the CNV, the P300 was elicited bilaterally in response to unilateral task-relevant stimuli. A bilaterally distributed P300 in response to unilateral target stimuli would implicate a diffuse subcortical system as opposed to a lateralized cortical source in its generation. A second but closely related question concerns the psychological specificity of the P300; insofar as the P300 was lateralized to the hemisphere that received the target stimulus in split-brain subjects, this would support the view that this ERP is a sign of specific processing operations rather than of diffuse arousal processes.

Finally, a third set of questions that becomes accessible by examining commissurotomized patients concerns the nature of the interactions between the separated hemispheres. Considerable debate has focused on the extent to which the two hemispheres are capable of processing information independently (in parallel), as opposed to having an interactive relationship whereby, for instance, one hemisphere takes charge and suppresses the other (Gazzaniga and Hillyard 1973; Trevarthen 1974; Lee-Teng and Sperry 1974; Franco 1977; Ellenberg and Sperry 1980; Gazzaniga 1987, Luck et al. 1989). Typically, failures of parallel processing in the separated hemispheres have been ascribed to a competition between them for a limited pool of "processing resources," presumably mediated by subcortical structures or pathways (e.g., Holtzman and Gazzaniga 1982, 1985; Holtzman et al. 1984). Related to this issue is the notion of an attentional capacity that may be allocated preferentially to one hemisphere or the other depending on task demands. Kinsbourne (1977), has suggested that brainstem activating systems can shift the balance of attention between the two hemispheres as a function of the nature of the required task. Some evidence for a unified attentional system that integrates information from the two hemispheres and directs attention to relevant spatial locations in either visual field can be found in the reports of Trevarthen (1974, 1987) and Holtzman et al. (1984).

In the present experiment, we investigated the mechanisms of interhemispheric interaction by presenting target stimuli unilaterally (to one visual field) on some trials and bilaterally (to the two hemispheres simultaneously) on others. The key question was whether the P300 can be fully developed in each hemisphere at the same time, or whether interhemispheric competition is invoked when target information is presented to both hemispheres simultaneously. To the extent that the overall amplitude of the P300 elicited by bilateral targets to the two hemispheres is reduced in relation to the sum of the individual P300s elicited by unilateral targets, interhemispheric interaction in the control of the P300 (presumably mediated subcortically) and of the associated cognitive processes would be implied. Although this question is also amenable to strictly behavioral investigation, an ERP analysis is particularly informative because interactions due to cognitive factors can be unconfounded from interactions due to motor interference.

RESULTS

Visual Experiments

Unilateral Names: Control Subjects

The ERPs elicited by all names were characterized by N1 (145 msec) and P2 (250 msec) components, both largest at the vertex. The N1 was slightly but significantly asymmetrical between the hemispheres, being larger contralaterally to the eliciting stimulus [for base-to-peak amplitude between 100 and 200 msec, visual field by hemisphere interaction, $F(1,6) = 13.9, p < .009$]. The P2 component was significantly larger in amplitude to target (6.6 μV) than to nontarget names (3.2 μV) [for base-to-peak amplitude between 150 and 220 msec, main effect of stimulus category, $F(1,6) = 43.11, p < .001$]. The P2 was also laterally asymmetrical, being larger over the right hemisphere for right visual field (RVF) stimuli and about the same amplitude over the two hemispheres for left visual field (LVF) stimuli [for base-to-peak amplitude between 200 and 300, visual field by hemisphere interaction, $F(1,6) = 9.95, p < .019$].

In addition to the N1 and P2 components, the target ERPs were characterized by a small N2 component (335 msec) and a large P300 wave peaking between 350 and 450 msec, followed by a broader positive slow wave (SW). The P300 component (mean latency 390 msec) was largest at the midline parietal site (17.0 μV) and was significantly larger than the component measured in the same latency zone in the nontarget (standard) ERPs [for base-to-peak amplitude between 300 and 700 msec, main effect of stimulus category, $F(1,6) = 27.12, p < .002$].

The ERPs (averaged across all seven control subjects) from the lateral parietal sites elicited by the target and nontarget (standard) names presented unilaterally either to the RVF or LVF are displayed in Figure 1. As is clear in this figure, the P300 was bilaterally symmetrical to both RVF (13.9 versus 13.8 μV) and LVF (12.8 versus 13.6 μV) targets at the parietal locations. By contrast, at the lateral central sites, the P300 showed a tendency to be larger ipsilateral to the visual field of target presentation; this was particularly evident in the target minus standard difference waves (Table 1) wherein the P300 amplitude was 1–3 μV larger over the central site ipsilateral to the field of target presentation [base-to-peak amplitude between 300 and 500 msec, visual field by hemisphere

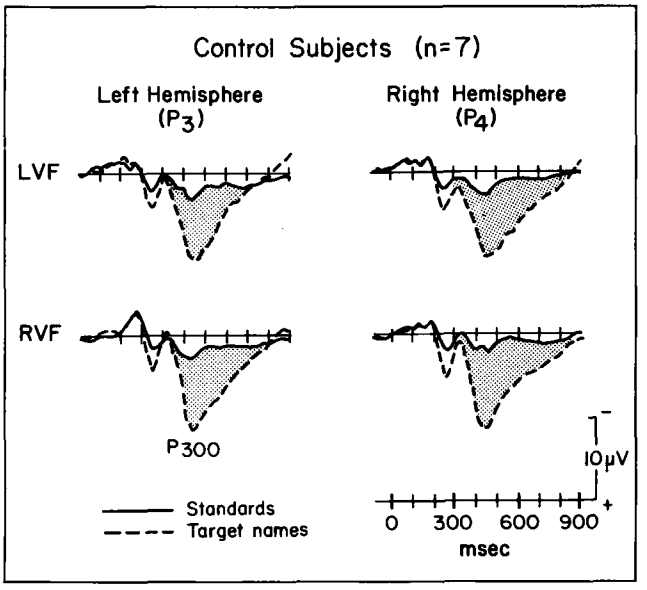

Figure 1. Grand average ERPs across all control subjects recorded over left and right parietal sites during unilateral presentations of names to either the right (RVF) or the left (LVF) visual field. In each case, ERPs elicited by standard and target names are compared.

Table 1. Base-to-Peak Amplitudes of P300 Components (in μV, with Standard Errors) in the Target Minus Standard Difference Waves

	Electrode Site		
	P3	*Pz*	*P4*
Control subjects (N=7)			
Unilateral names			
RVF	12.1 (1.9)	16.2 (2.3)	12.4 (1.3)
LVF	10.7 (2.1)	15.3 (2.7)	11.3 (1.8)
Control subjects (N=7)			
Bilateral names			
RVF	8.8 (1.3)	11.9 (1.8)	9.0 (1.8)
LVF	8.4 (1.7)	9.7 (2.4)	7.3 (1.7)
Bilateral	11.1 (1.6)	13.4 (2.2)	9.9 (2.2)
Split-brain subjects (N=4)			
RVF	8.4 (1.2)	10.5 (1.8)	9.1 (1.6)
LVF	6.1 (1.1)	10.3 (0.7)	10.9 (1.9)
Bilateral	9.0 (1.2)	14.1 (0.7)	13.0 (0.6)

interaction $F(1,6) = 14.88$, $p < .01$]. The lateral distribution of the later positivity measured in the difference waves as the mean amplitude between 500 and 700 msec and between 700 and 900 msec was uninfluenced by visual field of target presentation at either central or parietal locations.

Bilateral Names: Control Subjects

The ERPs elicited by the standard and target names in this condition were similar in most respects to those obtained during the unilateral visual runs with control subjects. The early part of the ERPs (< 200 msec) showed a somewhat more complex waveform, however, including a double-peaked N1 wave.

Again, only the ERPs to stimulus displays containing at least one target were characterized by large P300 and SW components (see Fig. 2). However, unlike the sharp P300 obtained with the unilateral name displays, the P300 to the bilateral name displays was broader and appeared to have two subpeaks at around 450 msec and 550 msec.

While both P300 subpeaks appeared by visual inspection to be roughly symmetrical between the right and left hemispheres irrespective of the field in which the target appeared, base-to-peak and mean amplitude measures revealed slight differences in their anterior–posterior and lateral distributions. The first peak (measured 400–500 msec poststimulus relative to 100 msec prestimulus activity) was significantly larger at the central scalp sites ipsilateral to the visual field of target presentation [for LVF, left and right hemisphere amplitudes were 8.4 versus 6.9 μV; for RVF, 6.8 versus 8.7 μV; target visual field by hemisphere interaction, $F(1,6) = 9.93$, $p < .02$]. The second positive peak (500–700 msec) tended to be larger parietally than centrally; it showed a similar but nonsignificant trend to be larger ipsilateral to the target presentation at the lateral central sites.

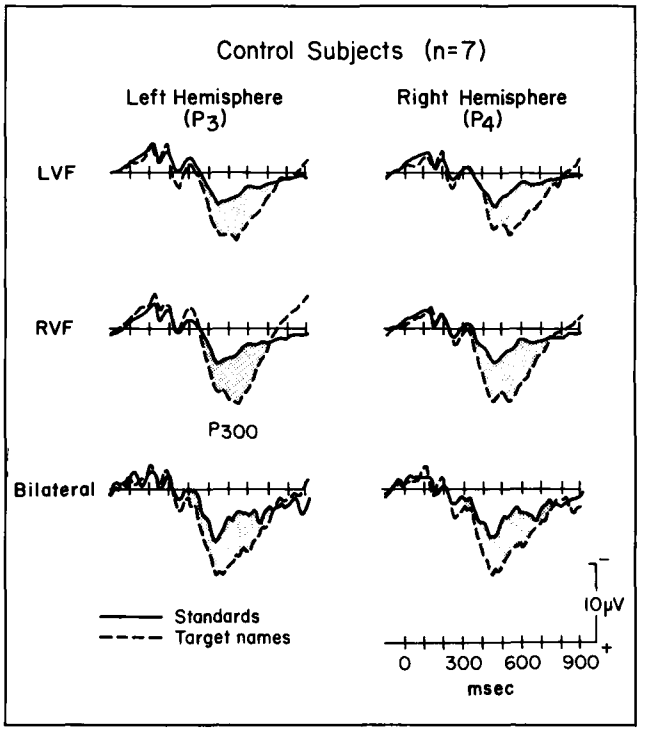

Figure 2. Grand average ERPs across all control subjects recorded over the left and right parietal sites during bilateral presentations of names to the right and left visual fields. The three rows show ERPs elicited by target names occurring in the left visual field (LVF), right visual field (RVF), or in both fields simultaneously (bilateral). In each case, ERPs elicited by standard and target names are compared.

P300s to Bilateral Targets

When both visual fields contained a target at the same time, the P3 was somewhat larger than when only one visual field contained a target. However, it is important to note that P300s to bilateral targets were smaller than would have been predicted from summing the responses to the unilateral targets (for peak amplitude in the target minus standard difference waves between 500 and 700 msec, $F(1,6) = 17.7$, $p < .006$).[1] This comparison is depicted in Figure 3. In the bilateral target case, both subpeaks were bilaterally symmetrical (peak amplitude between 400 and 500 msec collapsed across central and parietal sites for left versus right hemispheres: 13.1 versus 13.1 μV; between 500 and 700 msec, 11.7 versus 10.9 μV).

Bilateral Names: Split-Brain Subjects

The ERPs elicited by both the standard and target names were characterized by N1 (134 msec), P2 (228 msec), and N2 (322 msec) components, as in the control subjects. There were no significant differences between the target and standard ERPs in any of these components.

As in the controls, the ERPs to the displays containing at least one target included a large, parietally distributed P300 (averaging 9–16 μV, with a mean amplitude of 10.4 μV) peaking between 400 and 600 msec (mean of 539 msec), which was greatly reduced in the standard ERPs ($p < .01$ for standard-target comparisons on all P300 measures). Figure 4 shows the grand average ERPs at the lateral parietal sites from the four commissurotomized patients who showed a P300 in response to the target names. Subject #4, who showed a large, atypical negative wave in response to the targets, will be considered separately.

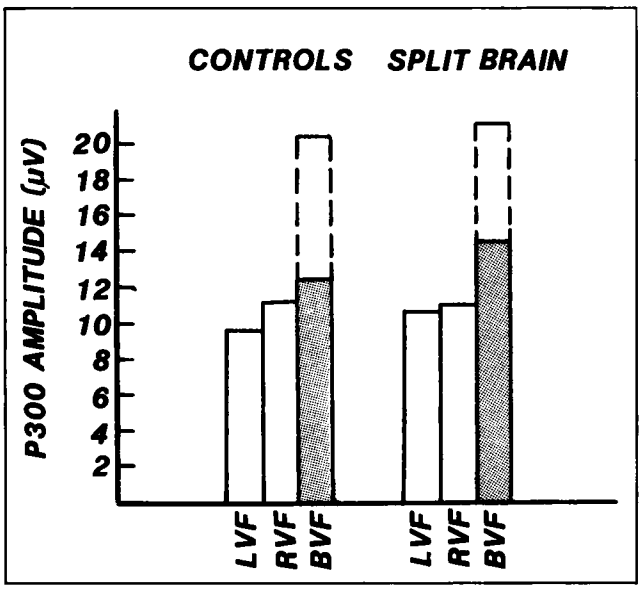

Figure 3. Mean peak amplitudes of the P300s measured in the target minus standard difference waves at the midline parietal site (Pz) across the seven control and four split-brain subjects following target name presentations in the LVF, RVF, and both visual fields simultaneously (BVF). The dashed lines depict the expected value of the bilateral P300 (BVF) if it were simply the sum of the LVF and RVF P300 amplitudes.

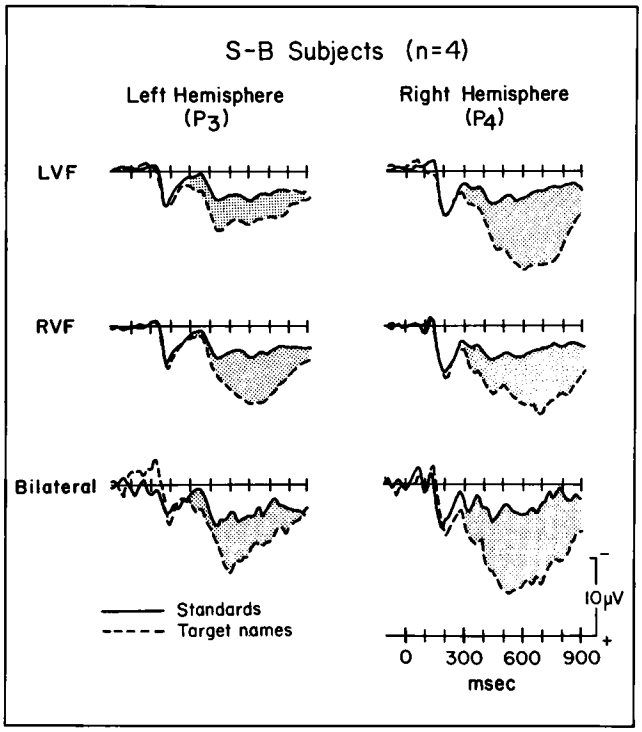

Figure 4. Grand average ERPs across four commissurotomized subjects recorded over the left and right parietal sites during bilateral presentations of names to the right and left visual fields. The three rows show ERPs elicited by target names occurring in the left visual field (LVF), right visual field (RVF), or in both fields simultaneously (bilateral). In each case, ERPs elicited by standard and target names are compared.

The lateral distribution of the P300 at the parietal sites was strongly dependent on the visual field of target presentation (see Figs. 4 and 5). Target names in the LVF elicited a P300 (measured as peak amplitude between 400 and 800 msec) that was highly asymmetrical, being larger over the contralateral (i.e., right) hemisphere (9.7 versus 14.6 μV). A similar, though slightly reduced, right hemispheric predominance (12.8 versus 16.7 μV) was observed in the P300 elicited by target names presented to both visual fields simultaneously (i.e., bilateral targets). In contrast, for RVF targets, the parietal P300s were of approximately equal amplitude over the left (11.5 μV) and right (2.2 μV) hemispheres. These distributional shifts were reflected in a significant visual field of the target by hemisphere interactions for the peak amplitude of the P300 at the parietal sites measured between 400 and 800 msec [$F(2,6) = 10.4$, $p < .05$], as well as for a measure of the mean amplitude between 500 and 700 msec epoch, wherein the P300 reached its maximum amplitude [$F(2,6) = 16.36$, $p < .006$].

Similar results were obtained for equivalent analyses

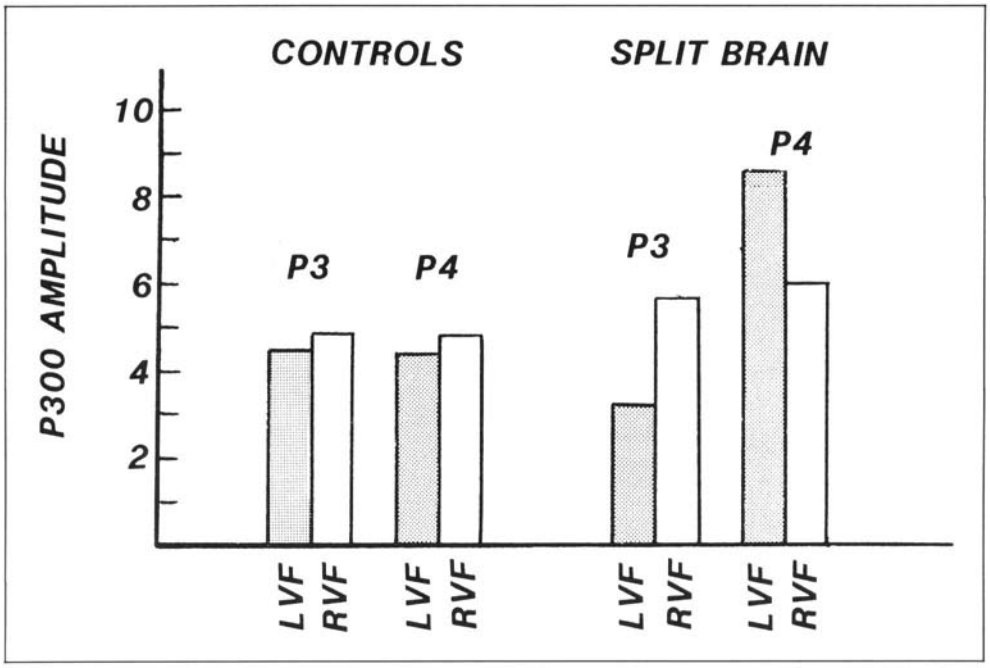

Figure 5. Comparison of the change in lateral parietal distribution of the P300 as a function of visual field of target presentation. Mean amplitudes of the P300 (measured between 500 and 700 msec) over the right (P4) and left (P3) parietal sites following LVF and RVF targets. Note that in control subjects P300s are unchanged in amplitude or laterality as a function of field of target presentation. For RVF targets the split-brain subjects show a similar pattern; however, for LVF targets, they show a strong contralaterally dominant asymmetry.

performed on the peak P300 amplitudes measured in the parietal difference waveforms (i.e., within the shaded areas in Fig. 4): specific comparisons showed that the right-greater-than-left P300 asymmetry was significant for LVF [$F(1,3) = 19.48$, $p < .02$] and bilateral targets [$F(1,3) = 16.57, p < .03$] but not for the RVF targets (see Table 1). The consistency of these asymmetries across the four subjects is illustrated in Figure 6.

As in the control subjects, the P300 elicited by bilateral targets was clearly substantially smaller in amplitude than that which would be expected by the sum of the amplitudes of the individual P300s elicited by unilaterally presented targets in the LVF and RVF [for peak amplitude, $F(1,3) = 22.01, p < .02$].

Because the P300 developed slowly and lasted for several hundred milliseconds, it is possible that it may be comprised of more than one late positive subcomponent; accordingly, separate mean amplitude measures of the difference waveforms were taken over successive 200 msec epochs between 300 and 900 msec poststimulus. Analyses of these measures (Table 2) revealed a complex relationship between the ERP and the visual field of target presentation.

The earliest epoch between 300 and 500 msec encompassed both the N2 deflection and the onset of the late positivity. Although there was a general trend toward right hemispheric predominance in late positive amplitudes, no statistically significant interactions with visual field of target were obtained.

The second analysis window between 500 and 700 msec included the peak of the parietally maximum P300 component. This mean amplitude measure showed greater P300 activity over the right than the left parietal scalp for LVF and bilateral target names, and bilaterally symmetrical potentials for RVF targets [main effect of hemisphere, $F(1,3) = 29.88$, $p < .01$, visual field by hemisphere interaction, $F(2,6) = 8.46, p < .04$].

Analyses of the lateral distribution of the positivity between 700 and 900 msec poststimulus indicated a right hemisphere preponderance for LVF, RVF, and bilateral target names at both central and parietal sites [main effect of hemisphere, $F(1,3) = 14.35, p < .03$].

Subject #4 displayed atypical ERPs, dominated by a large *negative* wave in response to target names (see Fig. 7). For this reason her data were not averaged or analyzed with the others. This broad negative ERP was somewhat larger over parietal than central electrode locations and was larger over the hemisphere contralateral to the visual field of target presentation.

Auditory Experiments

Control Subjects

The ERPs elicited by both target and standard tones were characterized by evoked N1 (122 msec) and P2 (201 msec) components. The N1 wave ranged between 5 and 8 μV in amplitude being largest at the vertex and reduced by approximately 20% at the parietal sites. The P2 component showed a significantly shorter latency for target (191 msec) than standard (211 msec) stimuli over all electrode locations [$F(1,6) = 13.03, p < .01$].

The largest differences between the ERPs to target and standard tones were in the later, endogenous components. The target ERPs were characterized by a small N200 component (227 msec), which marked the leading edge of the much larger P300 component (348 msec) that was largest (15.9 μV) at the midline parietal site.

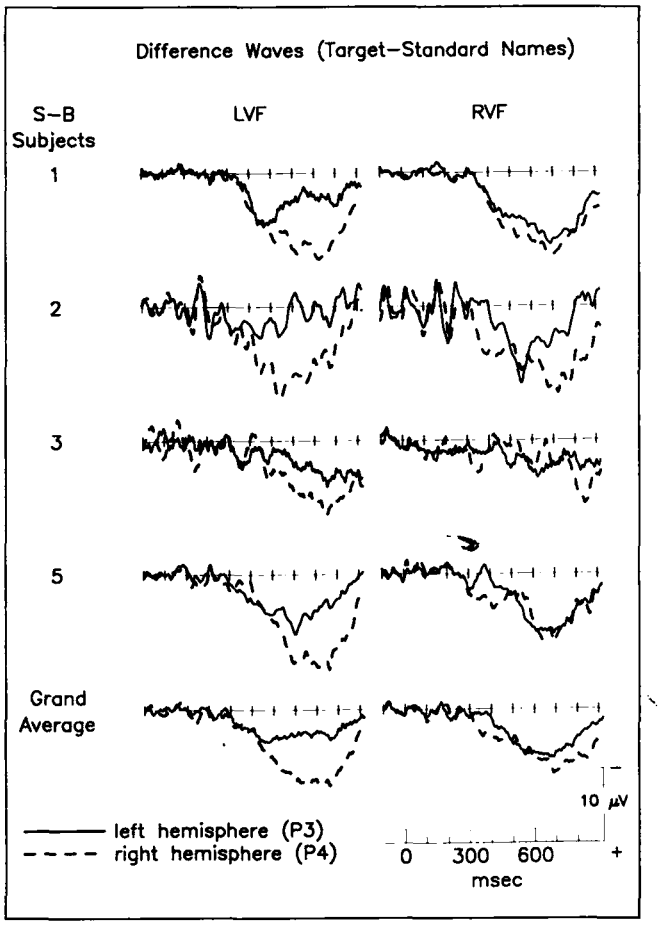

Figure 6. Comparison of the right and left parietal recordings of target minus standard "difference ERPs" elicited by targets presented to the left and right visual fields in four commissurotomized subjects. The corresponding grand average ERPs are shown in the bottom row.

The P300 was much larger in the target than the standard ERPs at all electrode sites [$F(1,6) = 17.45, p < .006$].

Neither the N200 nor the P300 component showed any lateral amplitude asymmetries over the parietal sites for either hand responding. This can be seen in Figure 8, which shows the standard and target ERPs recorded from the lateral electrode sites averaged across all seven control subjects and over right- and left-hand response conditions.

Split-Brain Subjects

The ERP components elicited by the standard and target tones in the patients were similar in morphology to those observed in the control subjects (Fig. 9). However, there were major differences between the two groups in the amplitudes and lateral distributions of the late endogenous components elicited by the target tones.

The N1 (113 msec) component showed a slight but nonsignificant tendency to be larger over the right than left hemisphere for both standard (−5.5 versus −4.2) and target (−4.4 versus −3.2μV) tones. The P2 (195msec)

Table 2. Mean Amplitudes of P300 Components (in μV, with Standard Errors) over Successive 200-msec Intervals Poststimulus in the Target Minus Standard Difference Waves

	Interval: 300–500 msec		
	P3	*Pz*	*P4*
Control subjects (N=7)			
Unilateral names			
RVF	4.7 (1.5)	8.7 (1.8)	6.0 (1.1)
LVF	4.5 (1.2)	8.3 (1.7)	4.9 (0.9)
Control subjects (N=7)			
Bilateral names			
RVF	1.8 (1.2)	5.1 (1.6)	3.5 (1.1)
LVF	2.6 (1.8)	3.7 (2.2)	1.7 (1.6)
Bilateral	3.3 (1.1)	5.3 (1.8)	2.6 (1.7)
Split-brain subjects (N=4)			
RVF	1.8 (0.4)	4.3 (1.0)	3.4 (0.7)
LVF	2.8 (0.4)	4.6 (0.1)	3.5 (0.8)
Bilateral	2.9 (1.6)	6.2 (1.0)	5.9 (0.6)

	Interval: 500–700 msec		
	P3	*Pz*	*P4*
Control subjects (N=7)			
Unilateral names			
RVF	5.1 (1.1)	7.6 (0.9)	5.4 (1.1)
LVF	4.2 (1.4)	7.5 (1.4)	5.6 (1.3)
Control subjects (N=7)			
Bilateral names			
RVF	4.9 (1.3)	6.9 (1.6)	4.9 (1.6)
LVF	4.6 (1.5)	5.8 (1.8)	4.5 (1.4)
Bilateral	4.3 (1.5)	5.4 (2.7)	2.9 (1.9)
Split-brain subjects (N=4)			
RVF	5.8 (0.8)	8.1 (1.5)	6.2 (1.6)
LVF	3.3 (0.9)	7.9 (0.8)	8.8 (0.9)
Bilateral	5.0 (2.2)	9.1 (2.2)	9.9 (1.6)

	Interval: 700–900 msec		
	P3	*Pz*	*P4*
Control subjects (N=7)			
Unilateral names			
RVF	0.1 (1.0)	2.6 (0.9)	1.7 (0.6)
LVF	−0.6 (1.0)	1.8 (1.5)	1.5 (0.8)
Control subjects (N=7)			
Bilateral names			
RVF	−1.9 (1.4)	−0.9 (1.4)	−0.4 (1.2)
LVF	0.4 (0.8)	−0.0 (1.2)	0.6 (0.8)
Bilateral	−0.7 (1.5)	0.1 (2.5)	−0.9 (1.3)
Split-brain subjects (N=4)			
RVF	3.9 (1.2)	6.8 (0.7)	6.6 (0.8)
LVF	2.6 (0.9)	6.3 (1.6)	7.6 (0.9)
Bilateral	2.6 (3.9)	5.8 (4.8)	8.2 (3.9)

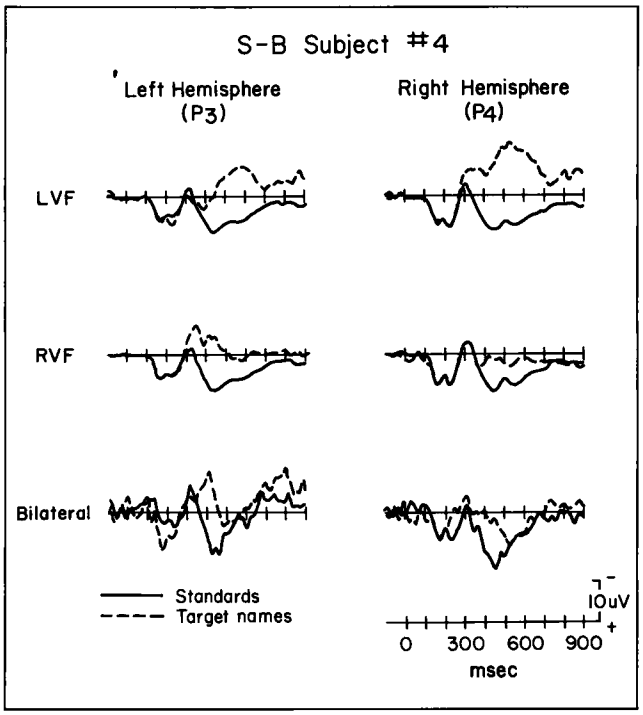

Figure 7. Comparison of the ERPs to standard and target names presented in one or both visual fields in split-brain subject #4. Note that targets elicit late negativity rather than an LPC in this subject.

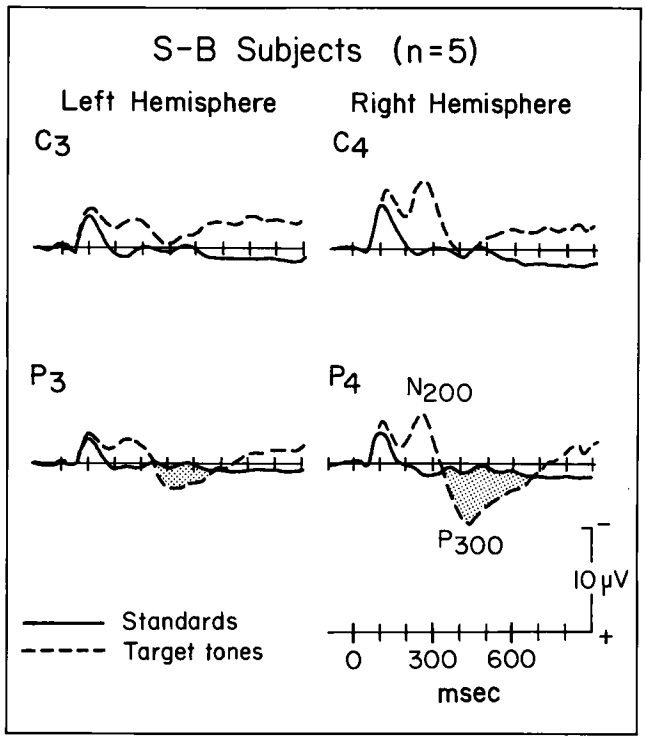

Figure 9. Grand average ERPs across five commissurotomized subjects recorded over central and parietal sites over the left and right hemispheres during binaural tone presentations. In each case, the ERPs elicited by target and standard tones are compared.

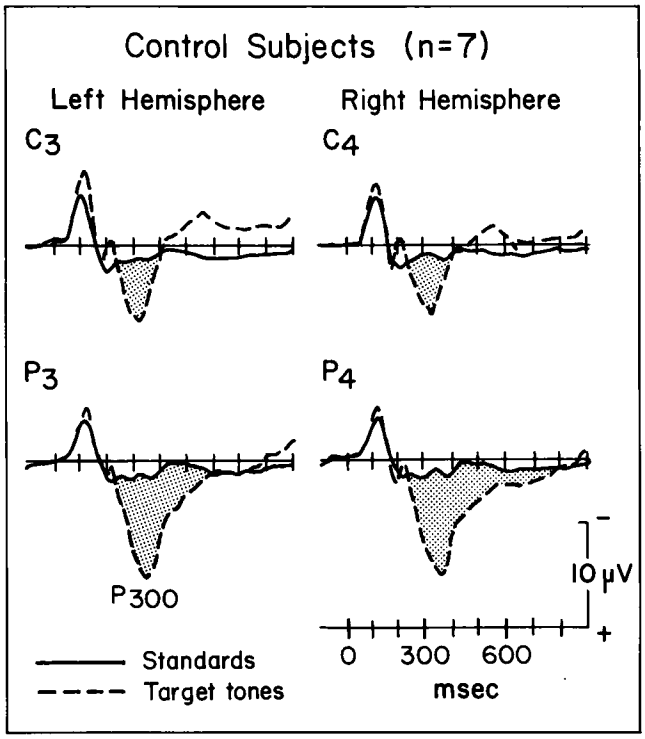

Figure 8. Grand average ERPs across all control subjects recorded over central and parietal sites over the left and right hemispheres during binaural tone presentations. In each case, the ERPs elicited by target and standard tones are compared.

was generally above baseline and at times difficult to discern in the raw waveforms, being interposed between the preceding N1 and following N2 components.

The standard and target ERPs differed markedly in their later components. The target tones elicited large N200 waves (243 msec) that were larger than those to the standard tones at lateral central sites [$F(1,4) = 11.6$, $p < .05$]. In addition, the N2 waves elicited by target tones were markedly asymmetric across the hemispheres [mean amplitude 200–300 msec, main effect of hemisphere, $F(1,4) = 7.77$, $p < .05$]; for example, centrally the N200 was nearly twice as large over the right (−7.5 μV) as the left hemisphere (−4 μV).

Following the N200 in the target ERPs was a parietally distributed P300 component (466 msec) that was either not present or greatly reduced in the standard ERPs. Unlike in the control subjects, the commissurotomized patients exhibited a strong right-greater-than-left asymmetry in both the N200 and P300 components of the target ERPs. In the target minus difference waveforms, these lateral asymmetries were significant for N200 [$F(1, 4) = 9.30$, $p < .04$] and P300 components [$F(1,4) = 12.10$, $p < .025$], each measured base-to-peak (see Table 3). The parietal N200–P300 measured peak-to-peak was highly asymmetrical [$F(1,4) = 39.37$, $p < .003$], with an amplitude over the right hemisphere (12.2 μV) that was almost twice as large as that over the left hemisphere (6.9 μV).

Table 3. Auditory Experiment: Means and Standard Errors (μV) of Base-to-Peak Amplitudes of N200 and P300 in the Target-Standard Difference Waves

	N200			*P300*		
	C3	*Cz*	*C4*	*P3*	*Pz*	*P4*
Controls (*N*=7)	−4.5 (1.5)	−4.0 (1.7)	−4.7 (1.3)	12.5 (2.3)	15.7 (2.0)	11.6 (1.5)
Split-brain (*N*=5)	−4.3 (1.2)	−8.0 (1.9)	−7.8 (2.1)	3.3 (1.6)	5.8 (2.3)	6.0 (2.1)

The consistency of these asymmetries among the five commissurotomized patients is shown in Figure 10. Although each of the subjects shows the N200–P300 peak-to-peak amplitude to be larger over the right than the left hemisphere, this lateral asymmetry was appreciably larger in the first three subjects than the other two. As in the visual experiments, subject #4's waveforms were quite unusual in that they were characterized by large negative rather than positive potentials in response to target tones.

DISCUSSION

Striking differences were observed between the commissurotomy patients and the neurologically intact controls in the lateral asymmetry of the visual P300 wave as a function of which hemisphere received the target information. In the control subjects the P300 was essentially symmetrical over the two hemispheres in response to lateralized visual target stimuli, whether they were presented in unilateral or bilateral sequences. The small asymmetries that were seen as a function of visual field of target presentation (more positive over the hemisphere ipsilateral to the target) can most likely be explained in terms of overlapping negative motor readiness potentials developing over the hemisphere opposite to the responding hand (Ragot and Remond 1979; Coles et al. 1988). A similar pattern of greater ipsilateral positivity was reported by Mangun and Hillyard (1990) for P300 waves elicited by target letters presented to the lateral visual fields.

In contrast, in each of the split-brain subjects the P300 elicited by lateralized visual targets was markedly asymmetrical. In four of five of these patients the asymmetry consisted of a substantially larger positivity over the right than the left hemisphere for left field target names, with a more symmetrical distribution for right field target names (Figs. 4 and 5). This dependence of P300 laterality on which hemisphere had received the target indicates that the P300 does not arise from a diffuse, bilateral system that is activated in the same manner regardless of which hemisphere is cued, as was found for the CNV (Gazzaniga and Hillyard 1973). Thus, these data do not support the idea that the P300 represents a diffuse relaxation of prior arousal (Karlin 1970; Näätänen 1967) or cessation of a baseline negativity (Desmedt 1981) that takes place simultaneously in the two hemispheres.

On the other hand, the pattern of P300 asymmetries observed in the name detection experiment was not indicative of totally independent generator systems in each hemisphere. Lateralized independent generators would be expected to show reversed ERP asymmetries for targets presented to the left versus right hemispheres and a simple additivity of these ERP amplitudes (in the target-standard difference waves) in response to the bilateral targets. Instead, the laterality of the P300 appears to reflect complex interactions between the two hemispheres; whereas the P300 was larger over the right side for left-field targets, it had about the same amplitude over both hemispheres for right-field targets. In response to bilateral targets the same right-greater-than-left asymmetry as for the left-field targets was seen, but the P300 amplitudes were only slightly augmented in relation to those elicited by unilateral targets, well below the summated amplitudes that would be expected if the hemispheres were activated independently. These results imply that subcortical systems that remain intact following commissurotomy are involved in the generation and/or control of the P300 components in the separated hemispheres. Experiments in squirrel monkeys support the idea that ascending subcortical projection systems play a permissive or triggering role in P300 production (Pineda et al. 1989).

It must be cautioned that the scalp distribution of the P300 in these patients may have been affected by factors other than the sectioning of the corpus callosum per se. P300 amplitudes are reportedly reduced unilaterally at scalp sites that overlie seizure foci in the temporal lobes of epileptic patients, in association with a reduction or absence of associated endogenous ERPs recorded within the affected temporal lobes themselves (Squires et al. 1983; McCarthy et al. 1987). The recorded scalp fields in the split-brain patients may also be subject to distortions due to inhomogeneities of current flow through the skull as a consequence of their history of craniotomy. Such factors as brain injury and disease, medication, and skull defects in themselves, however, would be expected to produce a *consistent* lateral asymmetry and/or distributional bias in the P300 rather than the observed trial-by-trial shifts of lateral distribution that depended on which

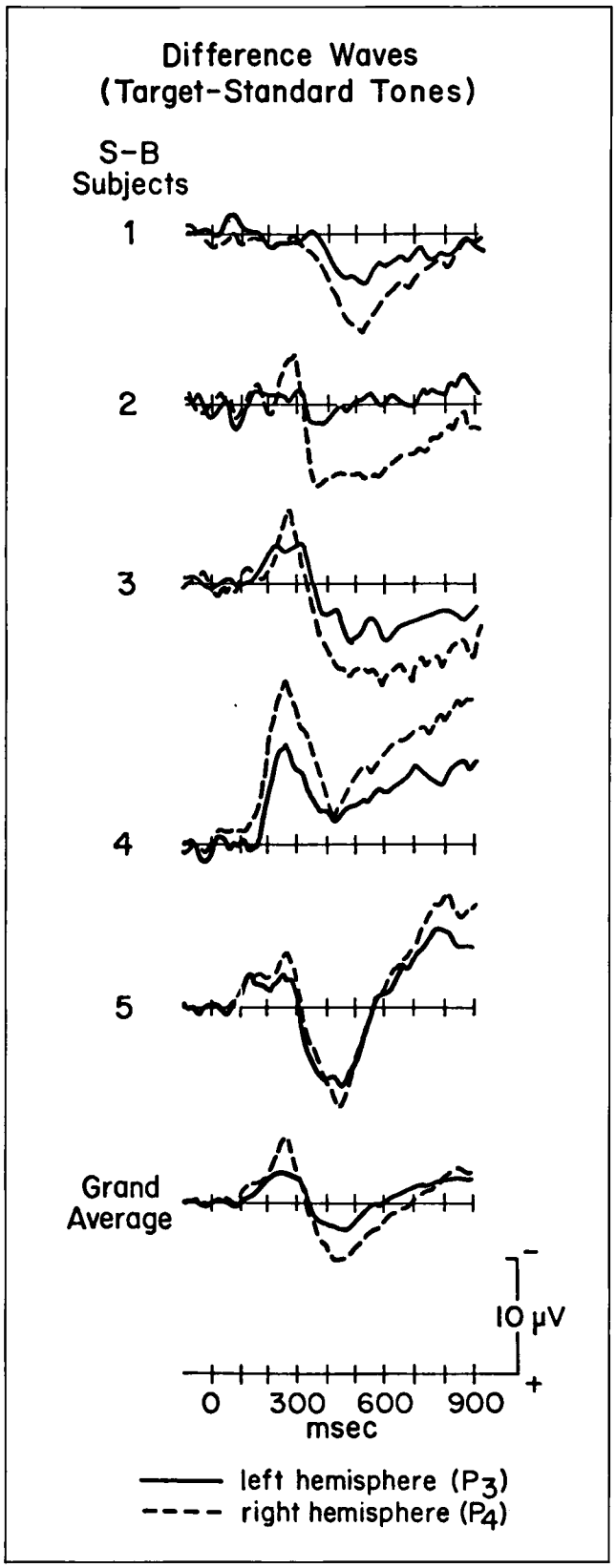

Figure 10. Comparison of right and left parietal recordings of the target minus standard "difference ERPs" for each of the commissurotomized subjects during the auditory detection task. The waveforms in the bottom row are the corresponding grand average responses averaged across all the subjects.

hemisphere received the target information. In fact, if we consider the P300 recorded over a given hemisphere, its amplitude was larger in response to unilateral targets presented to the contralateral than to the ipsilateral visual field (Fig. 5). This supports the hypothesis that P300 generators in the separated hemispheres were being activated in a lateralized manner due to the absence of interhemispheric transfer of target information.

The right-greater-than-left asymmetry of the auditory N200 and P300 components to binaural target tones in the split-brain patients was wholly unexpected. Since the tonal information undoubtedly reaches both hemispheres via bilateral auditory pathways, the asymmetric P300 might reflect hemispheric specialization for processing the tones in this task. This may be related to findings that some types of pitch discriminations are performed more accurately by the right hemisphere (Sidtis 1980), or to the hypothesis of lateralized attentional functions described above. However, in several follow-up investigations of patient J. W. (#3) we observed the same right hemisphere preponderance in response to oddball discriminations based on duration or phonemic cues. Another alternative possibility that the asymmetrical auditory P300 results from lateralized brain damage, seizure activity, or skull defects in these patients, however, cannot be ruled out on present evidence.

The finding of substantial P300 waves elicited by targets in both auditory and visual oddball paradigms is of interest in light of the report by Knight and associates (1989) that *unilateral* lesions at the junction of the posterior temporal/inferior parietal cortex produced a severe *bilateral* reduction of the P300 to auditory targets. To account for this remarkable finding, the authors suggested that P3 generation may be dependent on an "interhemispheric comparison of sensory data in the superior temporal planes." The present findings, however, indicate that at least a substantial portion of P300 activity does not depend on any such interhemispheric comparison that is mediated by the corpus callosum. Rather, each of the surgically separated hemispheres appears capable of producing substantial P300 activity without any transfer of stimulus information via the neocortical commissures.

A number of authors have suggested that attentional and alerting functions are represented asymmetrically in the two hemispheres (Trevarthen and Sperry 1973; Lee-Teng and Sperry 1974; Dimond 1976, 1979; Heilman and Van den Abell 1980; Ruff et al. 1981; Hom and Reitan 1982; Heilman et al. 1987). In particular, Heilman and Van den Abell reported a pattern of hemispheric activation in intact subjects that resembled the present findings in the split-brain patients; they found that the EEG of the left hemisphere was responsive only to lateralized stimuli in the right visual field, while the right hemisphere EEG could be activated by visual events in either field. These authors suggested accordingly that the right hemisphere was "dominant" for visual attention functions. In a similar

vein, Dimond (1976, 1979) has reported that lateralized visual targets are detected more accurately in the left visual field during prolonged periods of stimulation in split-brain subjects; he proposed that the right hemisphere is generally superior to the left at sustaining attention. In light of these hypotheses, it seems reasonable to suggest that the general right-sided preponderance of the P300 observed in the split-brain patients might also reflect the preferential activation of the right hemisphere in tasks that require the orienting of attention to significant events.

METHODS

Subjects

Control Subjects

Eight young adults, six women and two men (age range 19–28), were paid for participating in the experiments. Six of the subjects took part in both the visual and auditory experiments. Of the two remaining subjects, one took part only in the visual experiment and the other in the auditory experiment. Most had not participated in prior ERP experiments. All of the subjects were right-handed according to the Edinburgh Inventory (Oldfield 1971). Although the general nature of the experiment was explained to them, subjects were naive as to the specific hypotheses under investigation.

Commissurotomized Subjects

These patients had undergone complete or partial commissurotomy as treatment for severe epilepsy intractable to medication regime. Their respective case histories are summarized in Table 4.

Procedure: Visual Experiments

Bilateral Stimuli

Stimulus words (common first names) were presented on a video monitor under the control of a microprocessor (Apple IIe). Pairs of words were presented, one to each visual field for 180 msec. The medial aspect of each name was 1.2° from the fixation point at a viewing distance of 94 cm.

During all runs, subjects sat in a reclining chair and fixated a central spot on the video screen. The stimuli were either a man's or woman's first name according to the subject's gender. Random sequences were presented of the subject's name interposed among 17 other names; the names were chosen so as to be easily categorizable as a man's or a woman's and to be equivalent in length (i.e., number of letters) to the target name.

A pair of names was presented simultaneously, one in the right and one in the left visual field every 1500–1800 msec. The subject's task was to respond to the target stimulus (his/her own first name) with a button press. Target stimuli to the right visual field necessitated a right-hand response, whereas target stimuli to the left visual field required a left-hand response. A random 20% of the names in each field were targets. Hence, the probability of a target stimulus in both fields simultaneously was 0.04.

Each control subject participated in three experimental runs of 100 stimuli arranged according to these probabilities. Each commissurotomized subject participated in six such experimental runs.

Unilateral Stimuli

Each control subject also participated in six experimental runs equivalent to the previous conditions in all respects except that the stimuli were presented unilaterally, that is, to only one visual field per block. Subjects were requested to maintain fixation at the central point and to respond to targets with the hand ipsilateral to the visual field of presentation. Across the subjects, the order of visual field presentations was counterbalanced.

Procedure: Auditory Experiments

Tone bursts (100 msec duration, 60 dB SL) were delivered binaurally through headphones at the rate of one per second. Tone frequencies were either 1000 Hz ("low" tone) or 1500 Hz ("high" tone). Sequences of tones were prerecorded along with coded trigger pulses on an audio tape recorder.

Each experimental run consisted of 150 tones presented at a rate of one per second. The high and low tones were presented in a Bernoulli sequence, with the probability of one being 0.20 and the other 0.80. Subjects pushed a button on the occurrence of each target tone with either the right or the left hand. For each subject, high and low tones served as targets on different runs; hand usage was counterbalanced within and across subjects. Each subject participated in a minimum of three and a maximum of seven experimental runs.

Recording System

The electroencephalogram (EEG) was recorded using Ag/AgCl electrodes from six scalp sites, each referred to linked mastoids. Electrode impedances were less than 2 kΩ. Electrodes were placed according to the International 10–20 system at central (C3, Cz, C4) and parietal (P3, Pz, P4) midline and lateral locations. Vertical eye movements and blinks were monitored via an electrode placed on the lower orbital ridge, also referred to as linked mastoids. In addition, a bipolar, right-to-left external canthal montage was used to record lateral eye movements (EOG).

The system bandpass for recordings from the two midline and the lateral central sites was DC to 40 Hz (half-amplitude cutoff). The two lateral parietal and horizontal

Table 4. Commissurotomized Subjects

Subject	*Age at Surgery*	*Sex*	*Age at Experiment*	*Neurological Condition*	*Extent of Commissurotomy*[a]
#1. (P.S.)	13	M	17	Unknown etiology; left temporal focus with occasional propagation to the right	C.C.—one stage operation
#2. (V.P.)	24	F	26	Recurrent febrile seizures at 6 years; diffuse	C.C.—two stage operation
#3. (J.W.)	24	M	25	Concussive brain trauma at 13 years; right anterior temporal focus; diffusely abnormal EEG	C.C.—two stage operation
#4. (N.G.)	30	F	47	Calcification in central part of Rolandic fissure on right hemisphere; EEG abnormal in posterior left temporal lobe	C.C., A.C.
#5. (L.B.)	13	M	26	No distinct signs of damage in either hemisphere	C.C., A.C.

[a]C.C., corpus callosum; A.C., anterior commissure.

eye electrodes were recorded with an 8 sec time constant. The infraorbital activity was amplified with a bandpass down 3 dB at 0.15 and 150 Hz.

The EEG, EOG, subject's responses, and stimulus trigger codes were recorded on FM tapes and averaged offline by minicomputer. Each averaging epoch began 100 msec preceding stimulus onset and lasted for 924 msec thereafter.

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Note

1. The appropriate waveform comparisons to test the hypothesis of hemispheric independence in the generation of P300 are between the target minus standard difference wave amplitudes (shaded areas in Fig. 4). That is, if the separated hemispheres do not interact in producing P300 waves when bilateral targets are presented, the amplitude of the P300 difference wave elicited by bilateral targets (Fig. 4, bottom tracings) should equal the linear sum of the amplitudes of the difference P300s elicited by unilateral left and right visual field targets (Fig. 4, top and middle tracings). This can be derived as follows:

Let the P300 waves elicited by left, right, and bilateral targets be designated LT, RT, and BT, respectively. The smaller P300 elicited by left, right, and bilateral standard stimuli are termed LS, RS, and BS. The basic equations defining independence (linear summation) of the P300 waves in the two hemispheres are then given by

$$BT = LT + RT \quad (1)$$

$$BS = LS + RS \quad (2)$$

These equations may be subtracted from one another and rearranged as follows:

$$BT - BS = LT - LS + RT - RS \quad (3)$$

We can then substitute for the LS and RS terms of this equation from Eq. (2) and rearrange the terms taking into account the fact that a unilateral target was always accompanied by a standard stimulus in the opposite field in the present design, to attain the following:

$$[BT - BS] = [(LT + RS) - BS] + [(RT + LS) - BS] \quad (4)$$

The three terms within brackets in this equation are equivalent to the shaded areas (i.e., difference waves) at the bottom, top, and middle of Fig. 4, respectively. See Figure 3 for a more direct comparison.

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