Behavioral Neuroscience
1989, Vol. 103, No. 5, 1115-1138

Copyright 1989 by the American Psychological Association, Inc.
0735-7044/89/$00.75

Visual Evoked Potential Measures of Interhemispheric Transfer Time in Humans

Clifford D. Saron and Richard J. Davidson
University of Wisconsin—Madison

Four experiments testing right-handed adult males examined interhemispheric transfer time (IHTT) estimation with visual evoked potentials (EPs) elicited in response to hemiretinal presentations of checkerboard-flash stimuli. Experiment 1 was a study of the relation between reaction time (RT) and EP measures of IHTT. EP measures provided more valid estimates than RT measures because more subjects showed IHTT in the direction of anatomical prediction. Experiment 2 showed that EPs derived from lateral occipital sites provided more valid and longer estimates of IHTT compared with EPs from medial occipital sites. Experiment 3 showed no difference between random versus blocked hemiretinal stimuli. Experiment 4 showed that IHTT derived with a linked-ears reference provided more valid estimates than IHTT derived with a mid-frontal reference and that small changes in stimulus eccentricity did not influence IHTT. The findings of these experiments indicate that noninvasive estimates of visual IHTT can be obtained in humans.

How the two cerebral hemispheres interact and communicate has become a major question in research on hemispheric specialization (e.g., Lepore, Ptito, & Jasper, 1986). Interhemispheric communication has been hypothesized to play a major role in the development of functional hemispheric specialization (e.g., Denenberg, Hofmann, Rosen, & Yutzey, 1984; Witelson, 1986), and dysfunctions in this process have been implicated in various clinical disorders, including dyslexia (e.g., Davidson, Leslie, & Saron, 1989; Gladstone & Best, 1985; Leslie, Davidson, & Batey, 1985) and schizophrenia (e.g., Nasrallah et al., 1986; Schwartz, Winstead, & Walker, 1984). One important parameter of callosal function is the speed with which information is transferred between the hemispheres, referred to as *interhemispheric transfer time* (IHTT). Dysfunctions in IHTT have been implicated in some clinical disorders, and dyslexia is one of them (e.g., Davidson, Leslie, & Saron, 1989). The development of a valid and reliable method to estimate IHTT would enable studies of this process in subjects who present with various clinical disorders and in those who might be vulnerable to such conditions. Also, individual differences in IHTT could be examined in relation to the pronounced variability that has been observed in the size of the human corpus callosum (Demeter, Ringo, & Doty, 1988).

IHTT in humans was first estimated in reaction time (RT) studies (Poffenberger, 1912). IHTT was computed by subtracting the RT of a response made on the side ipsilateral to hemiretinal stimulation from the RT to contralateral stimulation. This RT difference was considered to be an estimate of IHTT. Many studies have been performed with this procedure (e.g., St. John, Shields, Krahn, & Timney, 1987; see Bashore, 1981, for a review). According to Bashore (1981), the average estimate of IHTT provided by this simple RT method across studies is approximately 3 ms. Although the RT method has been used in different contexts to provide estimates of IHTT, it has several limitations. The first emerges from consideration of physiological facts. The only type of callosal axon that could mediate an IHTT of 3 ms would have a large diameter (2.5–6 μm) and be myelinated. This type of commissural axon accounts for only approximately 10% of the callosal fibers in the human brain (Swadlow, Geschwind, & Waxman, 1979; Tomasch, 1954). According to Tomasch (1954), more than one half of the myelinated callosal axons have been found to be narrower than 1.5 μm, which would result in an IHTT that is considerably longer than the values obtained with RT methods.

Second, because RT methods of computing IHTT necessarily involve only one hand responding to a stimulus presented to only one hemisphere at a time, there is no way to measure a response from both sides of the brain at once. Thus, in principle, differences between conditions may involve variables other than just interhemispheric transfer. RT differences between conditions may be obtained as a function of a change in the overall state of the brain from one condition to the next rather than being associated specifically with interhemispheric transfer.

Electrophysiological methods of estimating IHTT have been used more recently to improve on RT studies. A goal of the

This research was supported by Grant 12-165 from the March of Dimes Birth Defects Foundation and by a grant from the Wisconsin Alumni Research Foundation to Richard J. Davidson.

We thank Peter Reiner for help in data collection and analysis; James Long for software support, and Andrew Tomarken, Fiona May, Andrea Straus, and two anonymous reviewers for comments on drafts of the manuscript. We gratefully acknowledge an equipment loan from the Teca Corporation and the Department of Rehabilitative Medicine, University Hospital, Madison, Wisconsin.

Correspondence concerning this article should be addressed to Clifford D. Saron, who is now at the Department of Neuroscience, Albert Einstein College of Medicine, 1300 Morris Park Avenue, Bronx, New York 10461, or Richard J. Davidson, Department of Psychology, University of Wisconsin, 1202 West Johnson Street, Madison, Wisconsin 53706.

electrophysiological approach has been to bypass the requirement for a manual response and to record simultaneously from both hemispheres the brain activity evoked by input to only one hemisphere. Such methods of estimating IHTT use latency differences between evoked potential (EP) components recorded from homologous sites over each hemisphere in response to unilateral input. These studies have used somatosensory stimuli (e.g., Gott, Hughes, & Binggeli, 1985; Gulmann, Wildschiødtz, & Ørbaek, 1982; Salamy, 1978), auditory stimuli (e.g., Mononen & Seitz, 1977), and visual stimuli (e.g., Andreassi, Okamura, & Stern, 1975; Ledlow, Swanson, & Kinsbourne, 1978; see Rugg, 1982, for a review of early studies).

The EP method of estimating IHTT is based directly on animal neurophysiological studies in which IHTT is inferred from conduction velocities measured directly in commissural axons (see Swadlow, 1985, for a review). In such studies, extracellular recordings are obtained from the cell bodies of neurons that send an axon across the corpus callosum. Stimulating electrodes are implanted in the contralateral hemisphere, and callosal efferent neurons are identified by their antidromic activation after electrical stimulation. Axonal conduction velocity is estimated from measurements of antidromic latency and from estimates of axonal conduction distance. Using such methods to study interhemispheric conduction velocities in the splenium of the rhesus monkey, Swadlow, Waxman, and Rosene (1978) found that the median antidromic interhemispheric latency was 7 ms. This value suggests that the axons studied were myelinated. Although in humans approximately 40% of the callosal axons are nonmyelinated (Tomasch, 1954), the values for IHTT that have been obtained in previous EP studies (8–15 ms) suggest similarly that the interhemispheric transfer process being measured is probably mediated by medium- or large-diameter myelinated axons (Swadlow et al., 1979). Thus, comparability with respect to substrates has been observed between estimates of IHTT derived from studies of the conduction velocities of callosal axons in animals and EP estimates of IHTT derived from measures of brain electrical activity recorded from the scalp in humans.

Despite the validation provided by the similarity of EP IHTT estimates to the values obtained in animal studies, many of the earlier studies suffered from methodological shortcomings, such as overly complex task requirements and insufficient stimulus repetitions for good wave form definition (Rugg, 1982). Rugg and his colleagues have conducted a series of studies that seek to advance previous approaches and more systematically assess the impact of stimulus parameters and recording montage on EP measures of IHTT (Lines, Rugg, & Milner, 1984; Rugg, Lines, & Milner, 1984, 1985; Rugg, Milner, & Lines, 1985).

The basic protocol of these experiments was as follows: Small (0.33°) LED stimuli were randomly presented to the left or right visual field (LVF or RVF, respectively, typically 4° from fixation) at a fixed interval of 2 s in a go–no-go RT paradigm. The go–no-go decision was made on the basis of the duration of the stimuli, with 5-ms go stimuli and 50- to 90-ms no-go stimuli, depending on the study. Each stimulus was preceded by a warning tone 600 ms prior to presentation. Subjects were required to respond with the hand ipsilateral to the stimulated visual field. Estimates of IHTT were derived by subtracting the latency of the negative EP component in the region of 160 ms poststimulus (N160) recorded from the directly stimulated hemisphere from the latency of the analogous peak recorded from the homologous site on the indirectly stimulated hemisphere. The overall estimate of IHTT obtained from lateral occipital recording sites in these studies was in the range of 8–15 ms. In a study of two acallosal individuals (Rugg, Milner, & Lines, 1985), clearly defined N160 peaks were recorded from only the directly stimulated hemisphere, further supporting the view that the latency shifts seen between the hemispheres correspond to transmission time across the corpus callosum.

Rugg and his colleagues (Lines, Rugg, & Milner, 1984; Rugg, Lines, & Milner, 1984, 1985; Rugg, Milner, & Lines, 1985) used a fixed interstimulus interval of 2.0 s. Curry (1984), using auditory stimuli with an interstimulus interval as short as 1.5 s, has shown that a contingent negative variation can be recorded in go–no-go tasks. Although not directly comparable to Rugg's studies, in which the warning tone did not contain response-relevant information, such data suggest that there may be prestimulus activity that does not return to baseline by the time of stimulus onset, which could obscure the components of interest.

Another potential problem with the Rugg studies (Lines, Rugg, & Milner, 1984; Rugg, Lines, & Milner, 1984, 1985; Rugg, Milner, & Lines, 1985) is the sampling rate of 3 ms per point. With that rate, a variation of only two samples in peak latency measurement could mean differences in IHTT estimates of 6 ms, which might account for a particular subject not showing the IHTT effects in the direction of anatomical prediction.

The use of the N160 component of the visual EP may not be the most appropriate one on which to base estimates of IHTT. In a recent study of the geometry of source generators of pattern-onset visual EPs, Maier, Dagnelie, Spekreijse, and van Dijk (1987) attempted to locate the cortex of origin for various components of the visual evoked response. Using an array of 24 electrodes spaced in 3-cm intervals over the occipital region and principal-components analysis to separate spatially distinct but time-overlapping components, the Maier group found two spatially distinct components for pattern-onset peripheral stimuli (one-half annulus with radii of 2° and 4°). They suggest that the CI or *P100 component* is extrastriate in origin, emanating from Areas 18 or 19. The CII or *N160 component* appears to have two overlapping generators, one striate and one extrastriate. The two components accounted for at least 93% of the power in the latency range of 71–171 ms poststimulus onset. These data suggest that the latency values measured from N160 visual EP components may reflect activity of Visual Areas 17–19. Because the richest callosally interconnected areas are extrastriate (Pandya & Rosene, 1985; Pandya & Seltzer, 1986), the contributions of Area 17 to the N160 component may confound estimates of IHTT. Whether these results generalize to responses elicited from the small stimuli of the Rugg studies (Lines, Rugg, & Milner, 1984; Rugg, Lines, & Milner, 1984, 1985; Rugg, Milner, & Lines, 1985) is unclear.

In another study of the topography of checkerboard-flash stimuli, Srebro (1987) made recordings from an array of 20 sites on the right side of the occipital scalp region and derived Laplacian responses that eliminated biases in the apparent spatial distribution of current sources caused by the particular reference electrode used (see Srebro, 1985). Stimuli (semicircular, from 1.2° to 7.6°) lasted 16.67 ms, with an interstimulus interval of 1.3 s. Subjects were instructed to report a faint brightness change in the central fixation point with a button press. Two spatially distinct components were identified in 6 subjects; the earlier of these (latency = 87 ms) was located more medially and was not sensitive to stimulus location (LVF vs. RVF). The later component was located more temporally (centered approximately 4 cm to the right of Oz, comparable with the lateral occipital sites previously described) and was sensitive to stimulated visual field (LVF latency = 136 ms; RVF latency = 162 ms). The latency difference between RVF and LVF stimuli was 26 ± 10 ms ($M \pm SD$). In each of two replications, all 6 subjects demonstrated effects in the anatomically predicted directions (range 14–42 ms). Because of the sampling rate, latency differences less than 7 ms could not be resolved. Srebro (1987) has interpreted the longer latency values (recorded from the right hemisphere) in response to RVF stimuli as indicative of transcallosal transfer time. Although estimates of IHTT were not the focus of the study, the data are important because they represent, to the best of our knowledge, the first reported measurement of IHTT using Laplacian-transformed evoked responses.

In this article, we report on a series of experiments that sought to simplify the procedure reported by the Rugg group (Lines, Rugg, & Milner, 1984; Rugg, Lines, & Milner, 1984, 1985; Rugg, Milner, & Lines, 1985) while retaining a task that would engage the subjects' attention and give a measure of task performance. The general purpose of the experiments was to examine different parametric features of this paradigm on estimates of IHTT. One major goal of this effort was to specify how EP estimates of IHTT should be obtained in future research requiring such measures. Experiment 1 examined the relation between RT and EP measures of IHTT collected at the same time. We felt that comparison of these two measures in the same subjects was important, for three reasons: (a) The estimates of IHTT from RT studies have been shorter than EP measures of IHTT (3 vs. 8–15 ms). (b) A close correspondence between the two measures would suggest that, in our paradigm, simple RT measures are adequate to estimate IHTT. (c) In light of the problems associated with RT measures, a lack of correspondence between the two measures would suggest that results based on EP measures should be favored. In Experiment 1, we also examined the effect of response hand on both EP and RT estimates of IHTT.

In Experiment 2, we compared EP measures of IHTT derived from medial and lateral occipital recording sites. We reasoned that the medial sites may reflect activity originating in primary sensory cortex and that the more lateral sites may reflect transcallosally interconnected secondary and tertiary processing areas. The increased physical separation of the lateral sites might also attenuate the recording of responses that did not originate in the hemisphere underlying that electrode.

Experiment 3 was a comparison of randomly presenting stimuli to the two visual fields and blocking the stimuli to one visual field at a time. Equipment limitations originally prevented our presenting stimuli randomly to the two visual fields.

Experiment 4 had two purposes: (a) to compare EP estimates of IHTT derived from linked-ears-referenced recordings with those obtained simultaneously with a mid–frontal reference site and (b) to assess the effect of decreasing the stimulus eccentricity from 2.8° to 1.8°. The importance of the contribution of the reference electrode to the pattern of scalp electroencephalogram (EEG) recordings has been stressed by Nunez (1981). Previous work characterizing the visual EP has often used a mid–frontal reference site (e.g., Halliday, Barrett, Blumhardt, & Kriss, 1979). Previous studies using visual EPs to estimate IHTT have used a linked-ears reference (e.g., Rugg et al., 1984).

The reduced eccentricity condition was included to test whether reducing the eccentricity of the stimulus would yield more clearly defined responses. More centrally located stimuli tend to activate regions of primary visual cortex nearer the occipital poles (Fox, Miezin, Allman, Van Essen, & Raichle, 1987; Miller, 1982). We reasoned that the callosally interconnected homologous secondary visual processing areas associated with the region of primary sensory cortex stimulated by a more centrally located stimulus would be more likely to be located on the lateral convexity and not in the calcarine fissure. Therefore, electrodes on the scalp surface over the occipital poles would be more optimally located to record EPs separately from each hemisphere.

EXPERIMENT 1

Method

Subjects

Nine subjects participated in the experiment. They were all right-handed men between the ages of 20 and 30 yr. Handedness was assessed with the Edinburgh Inventory (Oldfield, 1971). Subjects had to score 70% or higher in the right-handed direction to be included in the experiment. The visual acuity criterion was set at 20/40, both eyes corrected, as assessed with a Snellen chart.

Design

A simple RT task to unilaterally presented checkerboard-flash stimuli formed the basis of all data collection. There were four experimental conditions: RVF stimulus with a right-hand response (RVF–RH), RVF stimulus with a left-hand response (RVF–LH), LVF stimulus with an RH response (LVF–RH), and LVF stimulus with an LH response (LVF–LH).

The experiment consisted of four blocks of 100 stimuli, presented to one visual field at a time. For each block, the subject lifted his left or right index finger in response to each stimulus. Within a block, only one hand was used. Condition order was counterbalanced within subjects, and counterbalance order was randomized between subjects.

Procedure

The following description summarizes the approach taken for this and all subsequent experiments. Subjects were tested in a sound-attenuated room separate from the recording and projection rooms. They were seated at a table that held a response push-button, snap-action switch and a chin rest with forehead restraint. Subjects placed both arms straight out in front of them on the table. The switch was placed at a comfortable position for the subject on the same side of the table as the response hand for that block. The height of the table and chin rest were adjusted for maximum comfort.

The table faced a 61 × 91-cm rear-projection screen (3M Polacoat ¼-in. [6.3 mm] glass) and was placed so that the nasion-to-screen distance was 1.23 m. A black mask covered the screen, with cutouts for both visual field stimulus locations and a small fixation target.

A video camera that was mounted below the screen and focused only on the subject's eyes allowed for eye position monitoring. Two 150-W reflector spotlights directed at the wall above the projection screen provided symmetrical indirect lighting (49 cd/m^2 at the subject's eyes).

The stimuli were three- by four-check checkerboards 8.4 cm high and 6.3 cm wide (visual angle = 3.66° by 2.93°). The medial edge of the stimuli was 2.8° to the left or right of central fixation. The fixation point was a small (0.2°) circle with a cross in it. Three Kodak Ektagraphic projectors generated the stimulus and fixation images. The fixation point was visible throughout the experimental session. LVF or RVF checkerboard flashes were created with Gerbrands electromechanical shutters attached to the projector lenses and two identical stimulus slides. White noise (90 dB at 30.48 cm, A weighted) in the projection room masked the sound of the shutters in the subject room. Both shutters always opened with each stimulus to further minimize auditory differences between LVF and RVF stimuli. Only the lamp of the projector for the visual field to be stimulated was turned on. The fans of both projectors were always on.

The background illumination of the screen was 4.0 cd/m^2. The intensity of the white checks was 19.7 cd/m^2, yielding a contrast ratio of 79.7%. Stimulus intensity was equated between visual fields with Kodak wratten neutral-density filters and a Kodak variable neutral-density glass wedge. Coulbourn digital logic controlled stimulus presentation.

Each stimulus lasted 10 ms. A random (rectangularly distributed) interstimulus interval of 1.5–3.5 s was used. All stimuli were viewed binocularly. If subjects did not respond in the 1.5-s maximum RT epoch, the next stimulus was presented.

After a brief introduction to the nature of the experiment, each subject was instructed to centrally fixate during the presentation of stimuli and lift his index finger of the indicated hand off the button as quickly as possible in response to all stimuli. We chose a finger lift as the motor response for this task based on previous research (Milner & Lines, 1982).

RT Acquisition and Analysis

RT from stimulus onset to subject response was recorded (resolution = 0.1 ms) for each trial on an IBM Personal Computer. Mean, median, and upper-quartile RT for each of the four conditions for each subject were then computed.

Two methods were used to compute IHTT from the RT data. The first enabled us to compare separately for each hand the difference in RT between the two visual fields. For the right-hand condition, the RT in response to RVF presentations was subtracted from the RT in response to LVF presentations. For the left hand, the opposite subtraction was computed (RVF − LVF RTs). The second method enabled separate comparison of RT between hands for each visual field. Again, the ipsilateral condition was subtracted from the contralateral one. Positive values would indicate IHTTs in the anatomically predicted direction, with shorter RTs for conditions that did not require interhemispheric transfer in order to make a response.

Electrophysiological Data Acquisition and Analysis

EEG was recorded with an electrode cap (Electro-Cap Corp.) and Grass gold-cup ear clips. A Grass Model 7 polygraph with 7P5A AC preamps amplified and displayed the EEG. Electrode impedances were well below 5,000 Ω (typically 1,500 Ω). Recording sites were O1 and O2, which were referenced to linked ears. The EEG amplifier passband was 1–500 Hz (6 dB per octave). The output of the polygraph was low-pass filtered above 100 Hz before averaging with Rockland Model 424 dual filters (48 dB per octave).

Two channels of electrooculography (EOG) were recorded. Beckman miniature electrodes on the external canthi provided a horizontal eye movement signal, and electrodes on the supra- and suborbit measured vertical movements. The EOG was also amplified with Grass 7P5A preamps. Eye movements greater than 1° in any direction or eyeblinks were detected with four Schmidt triggers (one per polarity per EOG channel). The Schmidt trigger outputs were combined to generate an eye movement artifact detection signal that prevented averaging and flagged RT data for exclusion from analysis. Trigger thresholds were set prior to data collection for each subject.

A Teca Model TD-20 two-channel averager was used to derive the EPs from each lead for each of the four conditions. Each channel was sampled at 0.4 ms per point for 200 ms poststimulus onset. The 200-ms averaging epoch was chosen on the basis of pilot work. We found that time delays between wave forms recorded from homologous sites were clearly apparent in the 90- to 160-ms range. Before each subject's data collection, a 20-μV, 20-Hz calibration signal was used to standardize the gain for each channel. All EPs for this experiment were derived on-line. Each wave form was stored on an IBM Personal Computer for further analysis. The internal plotter on the TD-20 provided graphic output of the wave forms. These were overlaid and traced for between-site comparisons within a visual field.

Wave Form Quantification

Latency. Three wave form quantification procedures were used to estimate EP IHTT: (a) P100 peak latency differences between the hemispheres, (b) N160 peak latency differences, and (c) lag-to-maximum correlation. The *P100 latency* was defined as the latency of the greatest positivity between 88 and 140 ms. The *N160 latency* was defined as the latency of the greatest negativity between 130 and 195 ms. In the case in which adjacent points showed equal values, the earliest value was used. If two peaks of equal amplitude occurred within the allowable latency range, the earlier one was selected. Estimates of IHTT were computed by subtracting the latency of the peak expected to occur earlier from the latency of the corresponding peak recorded from the homologous scalp site.

The cross-lag correlation procedure was as follows: For each of the four conditions, a section of the wave form predicted to occur earlier was lagged 30 ms in both directions against the other wave form in 0.4-ms steps, generating a set of 150 cross correlations. The wave form section was a 40-ms-wide window, starting 100 ms after stimulus onset. The initial zero-lag correlation, maximum correlation, and its associated lag time were computed. Results that indicated a maximum correlation at the maximum lag time were eliminated from further analysis because no peak correlation value could be detected. In addition, wave form pairs with maximum correlations below .75 were rejected because we judged that a lack of similar

wave form features in the cross-lag time window recorded from homologous sites would be uninterpretable in terms of estimating IHTT. This judgment was based on our observation that the EP components recorded from the indirectly stimulated hemisphere often had the same general morphology as the corresponding earlier wave form components recorded from the directly stimulated hemisphere. Almost all wave form comparisons met these criteria. Of the 72 possible wave forms in this experiment, only 1 was excluded on this basis. Typical maximum correlation values were .95.

The window width and starting times were chosen to capture the typical P100 component of the EPs elicited during this task. Based on EP estimates of IHTT cited previously, a 30-ms lag test represented a reasonable outside limit for maximum wave form overlap, allowing for individual differences. We examined the lag correlations in both directions so as not to artificially bias the analysis in the direction of anatomical prediction.

Amplitude. Amplitude data were obtained to further characterize the EPs generated in this paradigm. Amplitude values for each peak type were obtained by subtracting the amplitude value of the first wave form point from the amplitude of the detected peak (P100 or N160). The first point was chosen as a baseline amplitude reference point because the averager lacked an absolute-amplitude readout. This strategy was not followed under two conditions: (a) if the first point was visibly not representative of the mean early activity (before 20 ms) of the EP and (b) if this early activity was not close (within 1 μV) to the zero-amplitude graticule mark of the averager display and the wave form did not appear to be DC offset (roughly symmetrical about the zero line, with typically larger negative than positive components). In these cases, measurements were taken from the wave form point closest to the zero-amplitude graticule line. All of the amplitude values for this experiment were obtained relative to the first point of the wave form.

Results

RT Data

RT measures for each hand–visual field combination were computed separately for each subject in the following manner: Single-trial RTs associated with eye movements and those below 100 ms or above 500 ms were excluded from further analysis. These time criteria were selected to limit the inclusion of spurious responses and eliminated 1.3% of the raw data. The time criteria did not eliminate the EEG data associated with them. The average number of trials per condition was 92. Mean, median, and fastest quartile RT values were computed from trials meeting criteria. Each of these three dependent measures was separately examined with a two-way analysis of variance (ANOVA) with visual field and hand as variables. None of the three dependent measures yielded significant main effects for visual field or hand. There was a significant Visual Field × Hand interaction for mean RT-derived data, $F(1, 8) = 6.18$, $p = .037$, and a marginal Visual Field × Hand interaction for the upper-quartile-derived results, $F(1, 8) = 5.23$, $p = .052$. To examine the separate contributions of the four conditions to the mean-RT-derived interaction, two-tailed t tests were performed for data from each hand between visual fields and for each visual field between hands. The LVF comparison revealed a significant difference between hands, $t(8) = 2.33$, $p = .048$. Table 1 displays mean RT by condition. Note that the condition means are in the anatomically predicted directions.

Table 1
Reaction Times by Visual Field and Hand Conditions

Response hand	Stimulus to left visual field	Stimulus to right visual field
Left	247.8 ± 9.3	261.3 ± 26.5
Right	260.4 ± 17.1	253.3 ± 21.5

Note. Values are expressed in milliseconds ($M \pm SD$; $n = 9$) and are of individual subject reaction time means for all conditions.

Table 2
Reaction Time Estimates of Interhemispheric Transfer Time (IHTT) by Visual Field and Hand Conditions

Stimulus or response	IHTT (ms)	p	Effect[a]
Stimulus			
Left visual field	12.6 ± 16.2	.05	67
Right visual field	8.0 ± 17.7	.21	67
Response			
Left hand	13.5 ± 21.1	.09	78
Right hand	7.09 ± 14.5	.18	67

Note. IHTT ($M \pm SD$; $n = 9$) and p values are from t tests for a difference from zero for reaction time estimates of IHTT derived from mean RT data for all conditions. Positive values indicate IHTT estimates in the predicted direction. None of the IHTT values were significantly different from a mean of 0 ms at the Bonferroni-corrected alpha level of .0125 ($df = n - 1$).
[a]Percentage of subjects in each condition who showed effects in the direction of anatomical prediction.

IHTT estimates were computed from the mean-derived RTs separately for each subject in two ways: (a) as differences between hands within a visual field and (b) between visual fields within a hand. These values are presented in Table 2. To examine whether any of the IHTT values were significantly different from 0 ms, a two-tailed t test was performed on the values for each condition. None of the conditions reached the Bonferroni-corrected alpha level (.0125). Positive IHTTs indicate results in the anatomically predicted direction. The percentage of subjects showing this effect is also presented.

Differences between the two methods of IHTT computation were examined with an ANOVA with type (by visual field or by hand) as a variable. There was no effect for type, $F(1, 8) = 0.18$, $p = .68$.

EP Data

Figure 1 shows grand average wave forms for each of the four experimental conditions (LVF–LH, $n = 8$; LVF–RH, $n = 8$; RVF–LH, $n = 9$; and RVF–RH, $n = 9$). If, within a condition for a given subject, either O1 or O2 wave forms were confounded with 60-Hz noise or lacked clearly visible P100 and N160 peaks, both were eliminated from the grand average. Of 72 wave forms, 4 were eliminated.

Stimulus onset was coincident with the beginning of the wave forms. The mean number of trials averaged to compute each subject's evoked response was 92. The P100 and N160 peaks of the wave form on the side contralateral to stimu-

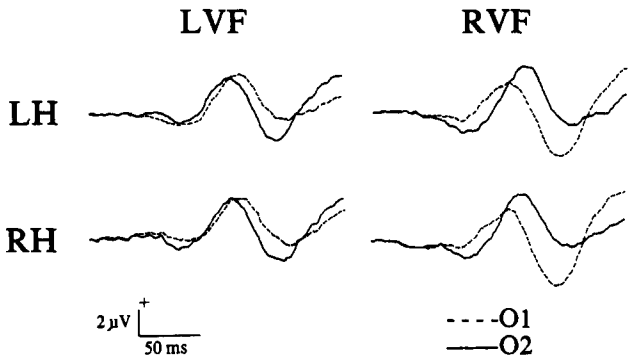

Figure 1. Grand average wave forms from each of the four stimulus–response conditions of Experiment 1 (left visual field stimulus [LVF] and left-hand response [LH], $n = 8$; LVF and right hand [RH], $n = 8$; right visual field [RVF] and LH, $n = 9$; and RVF–RH, $n = 9$) for Scalp Sites O1 and O2 referenced to linked ears. (The average number of trials from each subject for each condition was 92.)

lation (the direct pathway) occurred earlier than the same peaks on the wave form recorded from the opposite hemisphere (indirect pathway) for both visual field conditions. The response hand did not visibly influence the latency differences between the EPs recorded from each side of the scalp.

Peak Latency Data

P100 and N160 latency results. The means for each visual field–hemisphere combination across hands for P100 and N160 latency values are listed in Table 3. Note that for both peak types, these data are in the anatomically predicted directions, with earlier peaks recorded from sites over the directly stimulated hemisphere. P100 and N160 values were examined separately with three-way ANOVAS, with visual field, hand, and hemisphere as variables. For the P100 data, no main effect for any factor was found. There was a highly significant Visual Field × Hemisphere interaction, $F(1, 8) = 56.65$, $p = .0001$ (Table 3). P100 means across hands were compared within a visual field between hemispheres and within a hemisphere between visual fields with two-tailed t tests. Two comparisons were significant: RVF between hemispheres, $t(7) = 5.4$, $p = .001$, and left hemisphere between visual fields, $t(5) = 4.81$, $p < .005$. The other two comparisons revealed marginal effects ($p < .08$) in the expected directions. No other P100 two- or three-way interactions were found.

The analyses of the N160 latency data paralleled the P100 results. No main effect for any factor was found. As predicted, there was a highly significant Visual Field × Hemisphere interaction, $F(1, 5) = 64.65$, $p = .0002$. No other two- or three-way interaction was found. Means were also compared within a visual field between hemispheres and within a hemisphere between visual fields with two-tailed t tests. All four comparisons were significant: RVF between hemispheres, $t(6) = 4.2$, $p = .006$; LVF between hemispheres, $t(4) = 2.83$, $p < .05$; right hemisphere between visual fields, $t(4) = 3.4$, $p < .03$; and left hemisphere between visual fields, $t(4) = 2.71$, $p = .05$. These data indicate that when N160 peaks were detectable, their latency values consistently demonstrated results in the anatomically predicted directions.

P100 and N160 IHTT estimates. Estimates of IHTT were computed separately from the P100 and N160 latency data by subtracting the latency of the peak expected to occur earlier from the latency of the corresponding peak recorded from the homologous scalp site. We performed t tests on the IHTT estimates for each of the visual field–hand conditions to test the significance of the difference from 0 ms. The results for IHTT estimates derived from both peak types are presented in Table 4. Only RVF P100 IHTT estimates were significantly different from 0 ms at the Bonferroni-corrected alpha. P100 and N160 IHTT values were most similar for the right-hand conditions. The overall percentage of subjects showing IHTT values in the anatomically predicted direction did not differ between peak types. However, the sample sizes were smaller for the N160 data due to the greater number of ill-defined N160 peaks.

Cross-Lag Correlation Analysis

EP estimates of IHTT for each condition computed on the basis of the cross-lag correlation procedure are presented in Table 5. The procedure computed the zero-lag correlation, maximum correlation, and lag in milliseconds of the maximum correlation between wave forms recorded from homologous sites with a 40-ms-wide window beginning at 100 ms poststimulus. Lag values at the 30-ms limit of the initial analysis (one instance) and maximum correlation values below .75 (one instance) were eliminated. Note the exceptionally high maximum correlations. These values demonstrate

Table 3
P100 and N160 Peak Latencies Across Hands by Visual Field and Hemisphere

	P100 latencies (ms)		N160 latencies (ms)	
Visual field	O1	O2	O1	O2
Left				
$M \pm SD$	116.2 ± 4.5	110.8 ± 5.9	152.0 ± 8.5	146.6 ± 5.5
n	7	7	5	5
Right				
$M \pm SD$	107.2 ± 6.0	118.0 ± 2.8	145.9 ± 4.4	156.3 ± 7.6
n	8	8	7	7

Note. Values are for Scalp Sites O1 (left hemisphere) and O2 (right hemisphere) for each visual field.

Table 4
P100 and N160 Evoked Potential Estimates of Interhemispheric Transfer Time by Visual Field and Response Hand Conditions

	P100 data				N160 data			
Condition	*n*	*M* ± *SD*	*p*	Effect[a]	*n*	*M* ± *SD*	*p*	Effect[a]
LVF–LH	8	10.00 ± 9.1	.02	88	6	5.87 ± 6.3	.07	66
LVF–RH	8	2.70 ± 4.9	.16	62	5	3.84 ± 4.4	.12	80
RVF–LH	8	11.60 ± 8.7	.007[b]	75	9	5.91 ± 5.8	.02	89
RVF–RH	9	10.13 ± 4.6	.0002[b]	100	7	13.37 ± 11.6	.02	86

Note. Means (±*SD*) and *p* values are from *t* tests (for a difference from zero) of interhemispheric transfer time estimates derived from P100 and N160 latency values for each visual field–hand condition. LVF = left visual field; RVF = right visual field; LH = left hand; RH = right hand.
[a]Percentage of subjects showing effects in the anatomically predicted direction. [b]Significant *p* values at the Bonferroni-corrected alpha level.

the substantial similarity of the wave form sections from homologous sites that were displaced in time. To examine whether the lag values were significantly different from zero, two-tailed *t* tests were performed (Table 5). Both RVF conditions were significant at the Bonferroni-corrected alpha level, as in the P100 IHTT results presented earlier.

Differences among the four conditions for zero-lag and maximum correlations and lag were examined with an ANOVA with visual field and hand as variables. There were no main effects or interactions for zero-lag or maximum correlation. There was a main effect of visual field on lag, $F(1, 8) = 8.41$, $p = .02$. LVF lag values were consistently faster than RVF values: LVF, $M \pm SD = 4.8 \pm 5.8$ ms; RVF, $M \pm SD = 9.3 \pm 3.3$ ms. There was also a significant Visual Field × Hand interaction, $F(1, 4) = 16.1$, $p < .02$. Paired comparisons indicated significant differences between visual fields for the right-hand conditions, $t(6) = 6.36$, $p = .0007$, and between hands for the LVF conditions, $t(5) = 3.15$, $p < .03$. Visual inspection of the individual subject wave forms for the LVF-RH condition revealed latency shifts in the leading edges of the P100 peaks for 3 subjects (Table 5). These latency shifts were not reflected in the falling edge of the P100 peaks and thus fell outside the cross-lag correlation window, which began at 100 ms poststimulus. The lag values obtained for these subjects were therefore not representative of the actual latency shifts in these subjects' data and contributed to the low mean for this condition.

Comparison of the Peak-Derived and Lag Correlation IHTT Measures

We chose not to include the N160 data in this comparison because of the small sample sizes of the LVF condition (left hemisphere, $n = 6$; right hemisphere, $n = 5$). The IHTT estimates obtained from the lag correlation procedure and the IHTT estimates obtained from the P100 peak latency difference method were compared by computing separate correlations between them for each visual field–hand condition. The two methods of IHTT estimation were moderately correlated (Table 6).

Comparison Between RT and EP Estimates of IHTT

The IHTT estimates obtained from the P100 latency and lag correlation EP measures and the IHTT estimates obtained from the mean-derived RT data were compared by computing separate correlations between each EP method and each RT IHTT computation type (by visual field or by hand) separately for each visual field–hand condition. As with the previous comparisons, the N160-based IHTT estimates were not included in this analysis because of the small sample size. The correlations between RT IHTT and EP estimates based on the lag correlation procedure ranged between .86 and −.41. The mean correlation was .19, and none of the correlations reached the Bonferroni-corrected alpha level. The

Table 5
Lag Correlation Evoked Potential Estimates of Interhemispheric Transfer Time (IHTT) by Visual Field and Response Hand Conditions

Condition	*n*	Z*r*	M*r*	Lag (ms)	*p*	Effect[a] (%)
LVF–LH	8	.70 ± .35	.97 ± .02	6.4 ± 6.1	.02	88
LVF–RH	7	.79 ± .23	.97 ± .13	2.7 ± 5.1	.21	86
RVF–LH	8	.51 ± .27	.93 ± .07	8.9 ± 3.7	.0002[b]	100
RVF–RH	9	.51 ± .27	.97 ± .06	9.7 ± 3.1	.0001[b]	100

Note. Mean (±*SD*) values of zero-lag correlation (Z*r*), maximum correlation (M*r*), lag, and *p* values are from *t* tests for a difference from zero for evoked potential estimates of IHTT (i.e., lag values) for each stimulus–hand condition based on a 40-ms window starting at 100 ms poststimulus. LVF = left visual field; RVF = right visual field; LH = left hand; RH = right hand.
[a]Percentage of included subjects showing IHTT values in the anatomically predicted direction. [b]Significant *p* values at the Bonferroni-corrected alpha level.

Table 6
Correlations Between Lag Correlation and P100 Interhemispheric Transfer Times by Visual Field and Response Hand Conditions

Condition	*n*	*r*	*p*[a]
LVF–LH	8	.91	.002[b]
LVF–RH	7	.67	.10
RVF–LH	8	.53	.17
RVF–RH	9	.70	.03

Note. Comparison of correlation coefficients for the lag correlation and peak latency difference interhemispheric transfer time estimates, separately by condition. LVF = left visual field; RVF = right visual field; LH = left hand; RH = right hand.
[a]Probability $r = 0$. [b]Significance at the Bonferroni-corrected alpha level.

correlations between RT IHTT and EP estimates based on the peak latency data ranged from .74 to −.29, with a mean correlation of .11. Again, none were significant at the Bonferroni-corrected alpha level. Of the 32 possible correlations between EP and RT IHTT indices (16 for each method of EP IHTT computation), 22 were positive.

P100 and N160 Amplitude Data

P100 and N160 amplitude data were examined in the same manner as their corresponding latency values. Three-way ANOVAs with visual field, hemisphere, and hand as variables were used. For the P100 data, no main effects were found. In addition, the expected Visual Field × Hemisphere interaction did not reach significance, $F(1, 8) = 4.36$, $p = .07$. The Visual Field × Hemisphere interaction for N160 amplitude was significant, $F(1, 5) = 17.78$, $p = .008$. Paired comparisons of these data revealed significant left-hemisphere differences between visual fields, $t(4) = 3.14$, $p < .04$, and differences between the hemispheres for RVF stimuli, $t(6) = 3.89$, $p = .008$. There were no other significant effects for the N160 amplitude data. The mean amplitude values for each visual field–hemisphere condition across hands for both peak types are presented in Table 7.

Discussion

The most distinguishing feature of these data is that EP measures of IHTT provided results in the anatomically predicted direction more reliably than RT estimates obtained from the same subjects at the same time. The RT estimates were in the predicted direction in 70% of the computations of IHTT. The EP IHTT estimates were in the anatomically predicted direction in 94% of the IHTT computations based on the lag correlation procedure and in 81% of the peak-based data. The EP data closely resemble the pattern of response predicted by a sensory-relay model of the corpus callosum in which, by virtue of the constancy of the anatomy, a delay will always be imposed as information crosses from one hemisphere to the other.

The mean RT differences within a hand and between visual fields is 10.3 ms, combining results from both hands. Examination of our individual subject data revealed 1 subject with consistently large IHTT values (IHTT $M = 38.3$ ms). This subject increased the overall means 3.5 ms. However, an IHTT estimate of 6.8 ms is still considerably longer than the 3.6-ms value that was obtained in a recent study by St. John et al. (1987), the 3-ms value cited in the review by Bashore (1981), and the 1.8-ms value reported for Experiment 2 of Lines et al. (1984). The broad range of experimental designs within the general paradigm of RT measurement in response to hemifield stimulation makes interpreting the results of a single study problematic. The most important difference between the St. John et al. study and our study is that they presented stimuli randomly at different eccentricities within and between the two visual fields and that the response key was positioned at the midline. These design features would serve to inhibit attentional biases and effects of stimulus–response spatial compatibility. The presence of such effects in our study might serve to enhance differences between crossed and uncrossed RTs, thereby increasing the estimated IHTT values we obtained. In addition, differences in stimulus characteristics between the two studies may also have contributed to the differing IHTT results. Other studies have reported values closer to those we found. For example, Maddess (1975) found a 25-ms difference between ipsilateral and contralateral stimulation, and Berardi, Fiorentini, and

Table 7
P100 and N160 Peak Amplitudes Across Hands by Visual Field and Hemisphere Conditions

	P100 amplitude (μV)		N160 amplitude (μV)	
Visual field	O1	O2	O1	O2
Left				
M ± *SD*	3.5 ± 1.0	3.6 ± 1.4	−1.9 ± 1.9	−3.2 ± 1.3
n	7	7	5	5
Right				
M ± *SD*	2.7 ± 1.4	3.8 ± 1.3	−4.5 ± 1.4	−2.0 ± 1.0
n	8	8	7	7

Note. Values are for Scalp Sites O1 (left hemisphere) and O2 (right hemisphere) for each visual field.

Gravina (1988) recently reported crossed versus uncrossed differences in the range of 10 ms for some subjects.

Although the values of our RT estimates of IHTT are close to those obtained from EPs, they are uncorrelated. This finding suggests that the two measures reflect different processes. One would expect that spatial compatibility effects and motor priming would influence the EP data less than the RT measures. The latencies of the P100 and N160 components on which all the EP estimates of IHTT were based was considerably earlier than the 256-ms average RT response time. Presumably, the effects of spatial compatibility and motor priming would probably take place in the interval between the arrival of visual information in secondary visual areas (as reflected by the P100–N160 complex) and the initiation of response execution. In this case, IHTT estimates based on earlier responses (EPs vs. RT) would be freer of confounding factors and be more likely to truly reflect IHTT.

Estimates of IHTT derived from each peak type were, across conditions, within 2 ms of each other (P100 IHTT = 8.6 ms; N160 IHTT = 7.2 ms). The overall percentage of subjects showing effects in the anatomically predicted directions for the two peak types were nearly identical (81% vs. 80% for P100 and N160 peaks, respectively). There were, however, fewer subjects with clearly defined N160 peaks (33 P100 vs. 27 N160 instances of detectable pairs of homologous peaks from a maximum of 36).

The longer IHTT estimates found in response to RVF stimuli for both peak and lag correlation methods is similar to the pattern of values obtained by Rugg, Lines, and Milner (1985). The experiments to be reported below also obtained a similar trend. A basis for such a visual field asymmetry may lie in differences in the pattern of callosal inputs from the two visual fields. Van Essen, Newsome, and Bixby (1982) and Maunsell and Van Essen (1987) have demonstrated in macaques marked asymmetries in the density of callosal projections in dorsal compared with ventral occipital cortex and within a single visual field along the horizontal meridian. Van Essen, Newsome, and Maunsell (1984) found marked individual differences in both the size and visual field topography of extrastriate cortex in the 6 macaques studied. Their investigations have focused on asymmetries within a single hemisphere. However, the irregular and patchy pattern of callosal connections and topographical variability they have described raises the possibility of similar differences between the hemispheres. Visual field IHTT asymmetries could result if measured speed of transfer is related to degree of cortical interconnection. In addition, differences in the latencies of EP peaks could result from asymmetries in the size and location of stimulated cortex.

IHTT estimates obtained in response to RVF stimuli were more often in the anatomically predicted direction than LVF estimates for each of the three wave form quantification methods (100% for lag correlation procedure). Recent studies on anatomical asymmetries in human occipital cortex may help explain this finding and contribute to the interpretation of visual field asymmetries in IHTT. Kertesz, Black, Polk, and Howell (1986) analyzed magnetic resonance images from 20 subjects grouped by sex and handedness. They found increased left-hemisphere occipital width measurements in 90% of the right-handers. These results agree with an earlier computerized tomography study by LeMay (1977) showing larger left-hemisphere occipital length in 78% and greater width in 71% of right-handed subjects. The anatomical asymmetry in our sample would probably result in larger regions of left compared with right occipital cortex being stimulated when receiving input from identical stimuli. The more reliable RVF IHTT estimates may be a function of larger initially stimulated left-hemisphere regions resulting in larger callosally connected right-hemisphere regions being stimulated. This increased bihemispheric activation would increase the probability of recording callosally mediated responses from a given recording montage.

The peak amplitude data, in contrast to the latency results, differentiated the two peak types. Most notable, there was no Visual Field × Hemisphere interaction for P100 amplitude compared with the strong interaction for the N160 amplitude. The pattern of findings is consistent with the suggestions of Maier et al. (1987) that the P100 component is of extrastriate origin and the N160 component consists of overlapping striate and extrastriate generators. In this case the lack of asymmetry in P100 amplitude would be predicted by a sensory-relay model of callosal function connecting homologous regions of Visual Areas 18 and 19. The asymmetry in N160 amplitude would result if, in addition to the extrastriate response, regions of Area 17 that are not callosally connected were differentially stimulated by a unilateral input. The increased response amplitude recorded from the directly stimulated hemisphere would then reflect both of these components.

Comparisons of our amplitude results with previous studies are difficult because of the myriad differences in stimulus size, intensity, and duration among the experiments. Various amplitude effects have been reported in experiments recording occipitally derived EPs in response to hemifield stimuli. Studies have reported no amplitude asymmetries for P100 or N160 (Andreassi et al., 1975; Novak, Wiznitzer, Kurtzberg, Giesser, & Vaughan, 1988 [N75–P100 only]), greater peak amplitudes from the directly stimulated (contralateral) hemisphere for P100 and N160 (Shagass, Amadeo, & Roemer, 1976), greater ipsilateral P100 peak amplitude (e.g., Blumhardt, Barrett, Halliday, & Kriss, 1978), and greater ipsilateral P100 amplitudes associated with greater contralateral N160 amplitudes (e.g., Lines et al., 1984; Rugg, Lines, & Milner, 1985).

EXPERIMENT 2

In Experiment 2, we compared EP measures of IHTT derived from medial and from lateral occipital recording sites. Previous studies (Rugg et al., 1984; Rugg, Lines, & Milner, 1985; Rugg, Milner, & Lines, 1985) have relied principally on the lateral montage. Our initial findings (Experiment 1) were based on medial occipital sites. The purpose of this experiment was to directly compare recordings from these two regions. We hypothesized that the medial sites may reflect more activity originating from the primary sensory cortex than the more lateral sites that may reflect a greater proportion of transcallosally interconnected secondary and ter-

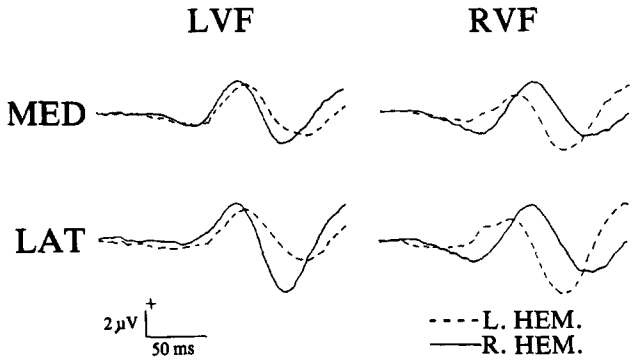

Figure 2. Grand average wave forms from each of the four stimulus–response conditions of Experiment 2 (left visual field stimulus (LVF) and medial recording sites [MED], $n = 11$; LVF and lateral recording sites [LAT], $n = 10$; right visual field [RVF] and MED, $n = 11$; and RVF–LAT, $n = 12$. Medial sites were O1 and O2 and lateral sites were O3 and O4, referenced to linked ears. All responses were made with the left hand. L. HEM. = left hemisphere; R. HEM. = right hemisphere.)

tiary processing areas. In addition, the greater distance between the lateral sites might attenuate the confounding effects of responses that did not originate in the hemisphere underlying that electrode.

Method

Subjects

Twelve right-handed men with the same characteristics as described in Experiment 1 were tested in this experiment. The data recorded from Sites O1 and O2 from 6 of these subjects were included in Experiment 1, and the remaining 6 subjects were new to the study.

Design

The task and stimuli were the same as in Experiment 1. However, subjects responded only with the left hand in this study, forming two task conditions (LVF–LH and RVF–LH) with recordings from two regions, medial (Sites O1 and O2) and lateral (Sites O3 and O4). The inclusion of an extra hand condition would have made the length of the experiment impractical. In Experiment 1, we reported that all interactions with hand were accounted for by responses made during the right-hand condition. On the basis of these data, we chose to include only the left-hand condition. The order of stimulus conditions was counterbalanced with other experimental conditions that are reported in additional experiments.

Electrophysiological Data Acquisition and Analysis

The details of electrophysiological recording were the same as those described for Experiment 1, except for the addition of two occipital recording sites (O3 and O4). These were located midway between the standard EEG Recording Sites O1 and T5 for the left hemisphere and O2 and T6 for the right hemisphere (approximately 3 cm lateral to O1 and O2). All EEG data were stored on FM tape (Hewlett-Packard 3968). Wave forms from Sites O1 and O2 were derived on-line. Wave forms O3 and O4 were derived off-line. The EOG artifact detection signal that was input on-line to the Teca averager was also recorded on FM tape so that both on- and off-line analyses contained the identical epochs. To check the effects of recording data on FM tape and of averaging on-line, we compared the two types of data. Wave forms obtained on-line were indistinguishable from the same data analyzed off-line. Wave form quantification procedures were the same as described in Experiment 1. No RT data were analyzed for this or any subsequent experiment.

Results

The grand average wave forms for LVF and RVF conditions for both occipital regions are shown in Figure 2. Wave forms not showing clear P100 and N160 peaks or showing excessive noise were excluded from the grand averages and further analysis as before. Of the 96 recorded wave forms, 8 were eliminated. The number of subjects included in each grand average was as follows: LVF–medial = 11, LVF–lateral = 10, RVF–medial = 11 and RVF–lateral = 12. Note that the wave forms at Sites O3 and O4 reveal larger latency differences than the Site O1 and O2 recordings for both visual fields, visible particularly in the P100 component.

Figure 3 displays the individual subject wave forms recorded from medial and lateral sites that were analyzed in this experiment. The vertical bars indicate the position of

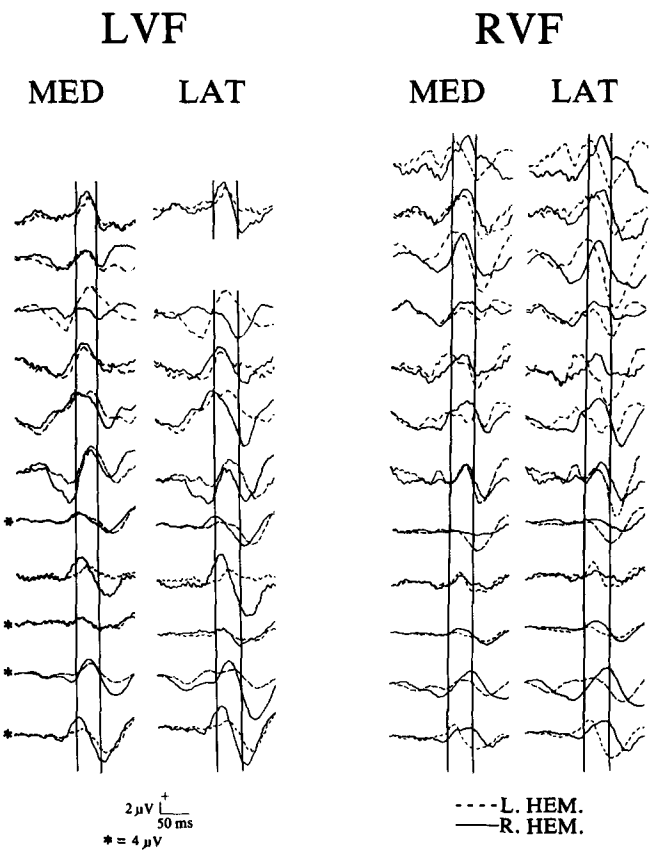

Figure 3. Individual subject wave forms recorded from medial (MED) and lateral (LAT) sites that were analyzed in Experiment 2. (These are the wave forms that comprise the grand averages displayed in Figure 2. The vertical bars indicate the position of the cross-lag correlation window. LVF = left visual field; RVF = right visual field; L. HEM. = left hemisphere; R. HEM. = right hemisphere.)

Table 8
P100 and N160 Peak Latencies by Visual Field, Region, and Hemisphere

	Left hemisphere		Right hemisphere	
Latency	O3	O1	O2	O4
P100				
Left visual field				
$M \pm SD$	116.9 ± 6.8	116.8 ± 6.8	110.6 ± 8.4	106.9 ± 9.0
n	10	11	11	10
Right visual field				
$M \pm SD$	105.5 ± 7.0	111.8 ± 10.0	121.5 ± 8.0	120.9 ± 8.2
n	11	10	10	11
N160				
Left visual field				
$M \pm SD$	164.1 ± 8.4	157.8 ± 9.4	150.1 ± 8.6	149.8 ± 8.9
n	9	8	8	9
Right visual field				
$M \pm SD$	146.9 ± 6.6	151.2 ± 8.0	159.1 ± 13.5	161.1 ± 14.5
n	12	11	11	12

Note. Means ($\pm SD$) are expressed in milliseconds for medial (O1 and O2) and lateral (O3 and O4) occipital sites for each visual field.

the cross-lag correlation window. The wave forms from both regions were quantified as described for Experiment 1, and estimates of IHTT were obtained with the P100, N160, and cross-lag correlation methods.

Peak Latency Data

P100 and N160 latency results. The mean P100 and N160 latencies for lateral and medial sites for both visual fields are presented in Table 8. The expected pattern of shorter latencies for the directly stimulated pathway was obtained with each peak type for both regions and visual fields. These peak latency data were examined separately for each peak type with a three-way ANOVA with visual field, hemisphere, and region as variables. The analysis of the P100 data revealed a main effect for region, $F(1, 11) = 16.72$, $p < .002$, with lateral sites yielding slightly shorter overall latencies: medial P100 latency, $M \pm SD = 116.2 \pm 6.1$ ms; lateral P100 latency, $M \pm SD = 113.2 \pm 6.4$ ms.

As was found in Experiment 1, there was a highly significant P100 Visual Field × Hemisphere interaction, $F(1, 9) = 46.35$, $p = .0001$, with shorter latencies associated with the directly stimulated pathway. A Visual Field × Region × Hemisphere interaction, $F(1, 7) = 8.85$, $p = .02$, was also found. For both hemispheres, directly stimulated lateral sites yielded shorter latencies than directly stimulated medial sites. This pattern was not obtained in recordings taken from the indirectly stimulated lateral compared with medial sites. Separate two-way ANOVAs with visual field and hemisphere as variables were computed for each region to decompose this three-way interaction. The strength of the Visual Field × Hemisphere interaction was much greater for the lateral compared with the medial recording sites: medial Visual Field × Hemisphere interaction, $F(1, 8) = 12.72$, $p = .007$; lateral Visual Field × Hemisphere interaction, $F(1, 8) = 94.77$, $p < .0001$.

The analysis of the N160 data also demonstrated a strong Visual Field × Hemisphere interaction, $F(1, 9) = 71.05$, $p < .0001$, with shorter latencies associated with the directly stimulated pathway. Again, as seen in the P100 data, a Visual

Table 9
P100 and N160 Evoked Potential Estimates of Interhemispheric Transfer Time by Visual Field and Region Conditions

	P100 data				N160 data			
Condition	n	$M \pm SD$	p	Effect[a]	n	$M \pm SD$	p	Effect[a]
LVF–medial	12	6.0 ± 8.7	.04	73	8	7.7 ± 8.3	.03	88
LVF–lateral	10	10.0 ± 8.8	.006[b]	90	9	14.3 ± 12.0	.006[b]	89
RVF–medial	10	9.7 ± 9.8	.012[b]	80	11	7.9 ± 10.2	.03	91
RVF–lateral	12	15.4 ± 8.8	.0002[b]	100	12	14.2 ± 10.8	.0008[b]	100

Note. Means ($\pm SD$) and p values are from t tests (for a difference from zero) of interhemispheric transfer time estimates derived from P100 and N160 latency values for each visual field–region condition. LVF = left visual field; RVF = right visual field.
[a]Percentage of subjects showing effects in the anatomically predicted direction. [b]Significant p values at the Bonferroni-corrected alpha level.

Table 10
Lag Correlation Evoked Potential Estimates of Interhemispheric Transfer Time by Visual Field and Region Conditions

Condition	*n*	Zr	Mr	Lag (ms)	*p*	Effect[a] (%)
LVF–medial	11	.76 ± .37	.98 ± .02	4.4 ± 5.6	.03	81
LVF–lateral	10	.62 ± .40	.96 ± .03	9.1 ± 7.3	.004[b]	90
RVF–medial	9	.65 ± .28	.94 ± .06	8.0 ± 4.8	.001[b]	100
RVF–lateral	11	.22 ± .57	.96 ± .05	14.2 ± 6.5	.0001[b]	100

Note. Mean (±*SD*) values of zero-lag correlation (Zr), maximum correlation (Mr), lag, and *p* values of *t* tests for a difference from zero for evoked potential estimates of IHTT (i.e., lag values) for each stimulus–region condition based on a 40-ms window starting at 100 ms poststimulus. LVF = left visual field; RVF = right visual field; *medial* and *lateral* refer to Sites O1 and O2 and O3 and O4, respectively.
[a]Percentage of subjects showing IHTT values in the anatomically predicted direction. [b]Significant *p* values at the Bonferroni-corrected alpha level.

Field × Region × Hemisphere interaction, $F(1, 5) = 11.70$, $p < .02$, was found. For both visual fields, the latency differences between the hemispheres were larger in lateral compared with medial sites. Separate two-way ANOVAs with visual field and hemisphere as variables were again computed for each region to decompose this three-way interaction. The effect size for the Visual Field × Hemisphere interaction was larger for the lateral compared with medial sites: medial Visual Field × Hemisphere, $F(1, 6) = 24.88$, $p < .003$; lateral Visual Field × Hemisphere, $F(1, 6) = 109.40$, $p < .0001$.

P100 and N160 IHTT estimates. Estimates of IHTT were computed separately from the P100 and N160 latency data as in Experiment 1. We performed *t* tests on the IHTT estimates for each of the visual field–region combinations to test the significance of the difference from a mean of zero. These estimates and their corresponding *t* values are presented in Table 9. Note that for both peak types, laterally derived IHTT estimates are longer than corresponding medial sites. These IHTT estimates were further examined with a two-way ANOVA with visual field and region as variables. As expected from the results presented earlier, a main effect for region was found for the P100-derived IHTT values, $F(1, 11) = 12.70$, $p = .004$, with medially derived IHTT $M \pm SD = 6.5 \pm 5.5$ ms ($n = 9$) and lateral P100 IHTT $M \pm SD = 11.1 \pm 3.5$ ms ($n = 9$). This effect was in the same direction, although marginal for the N160-derived IHTT values, $F(1, 11) = 4.27$, $p = .06$, with medial N160 IHTT = 9.3 ± 4.9 ms, $n = 7$, and lateral N160 IHTT = 14.4 ± 4.1 ms, $n = 9$.

Cross-Lag Correlation Data

The values from the cross-lag correlation procedure are presented in Table 10. Both lateral and one medial lag estimate were significant at the Bonferroni-corrected alpha level. An ANOVA with visual field (LVF vs. RVF) and region (medial vs. lateral) as variables was performed on zero-lag correlation, maximum correlation, and lag values. There was a main effect for region on the zero-lag correlation (Zr), $F(1, 11) = 7.93$, $p = .02$. The zero-lag correlation values for the wave forms recorded from medial sites were consistently higher than those of the laterally recorded wave forms: medial Zr, $M \pm SD = .71 \pm .33$; lateral Zr, $M \pm SD = .41 \pm .53$. The relatively large zero-lag correlation in the medial compared with the lateral recording sites is consistent with the suggestion that the medial sites are more sensitive to activity in both hemispheres compared with the lateral sites.

The ANOVA on the lag values revealed a significant region main effect, $F(1, 11) = 9.16$, $p = .01$, with medial-site-derived estimates of IHTT consistently shorter than those from the lateral sites: medial (Sites O1 and O2) lag, $M \pm SD = 6.0 \pm 5.4$ ms; lateral (Sites O3 and O4) lag, $M \pm SD = 11.8 \pm 7.2$ ms. There was no main effect for visual field, $F(1, 11) = 2.49$, $p = .15$. The Visual Field × Region interaction was significant, $F(1, 6) = 8.45$, $p < .03$. This interaction is a function of larger differences in IHTT between the two visual fields for the lateral compared with the medial recordings, with left-to-right hemisphere transfer (RVF IHTT) longer compared with right-to-left hemisphere transfer (LVF IHTT).

Comparisons Among the Three EP Measures

Lag correlation and peak latency IHTT estimates. The IHTT estimates obtained from the lag correlation procedure and from the peak latency-difference method for both peak types were compared by computing correlations between lag correlation IHTT estimates and each type of peak-derived IHTT estimate within each visual field–region condition. Overall, P100 IHTTs were correlated with lag correlation results, and the N160 IHTTs were not. Correlations between IHTT derived from P100 latencies and lag correlations ranged from .42 to .90, with a mean of .63, whereas the correlations between N160 and lag correlation IHTT ranged from −.22 to .37, with a mean of .01. These results reflect the fact that window position of the lag correlation procedure was selected to capture the P100 component of the wave forms and therefore should be more correlated with P100-derived IHTT values.

P100 and N160 IHTT. IHTT values derived from P100 and N160 peaks were directly compared with a two-way ANOVA with visual field and peak type as variables. This analysis was performed separately for each region. No main effects or interactions were found for either region. These results demonstrate that the overall estimates of IHTT obtained from the two peak measures did not differ. Correla-

Table 11
P100 and N160 Peak Amplitudes by Visual Field, Region, and Hemisphere

	Left hemisphere		Right hemisphere	
Amplitude	O3	O1	O2	O4
P100				
Left visual field				
$M \pm SD$	2.8 ± 1.3	3.1 ± 1.3	3.5 ± 1.8	4.0 ± 2.3
n	10	11	11	10
Right visual field				
$M \pm SD$	2.4 ± 1.7	2.3 ± 1.4	3.4 ± 1.4	3.5 ± 1.6
n	11	10	10	11
N160				
Left visual field				
$M \pm SD$	−3.1 ± 2.5	−2.2 ± 2.2	−3.3 ± 3.3	−6.2 ± 4.2
n	9	8	8	9
Right visual field				
$M \pm SD$	−4.9 ± 2.6	−3.4 ± 1.8	−2.1 ± 1.8	−2.9 ± 2.6
n	12	11	11	12

Note. Means ($\pm SD$) are expressed in microvolts for medial (O1 and O2) and lateral (O3 and O4) occipital sites for each visual field.

tions between P100 and N160 estimates of IHTT were performed within each region–visual field condition to further investigate the relation between these methods. Interestingly, the two measures were not correlated. The correlations ranged from −.35 to .35, with a mean of .11. These results suggest that although mean IHTTs from both peak types did not differ, they reflect different interhemispheric transfer processes.

IHTT across conditions. To examine the relation between medially and laterally derived IHTT, correlations were computed between regions for each visual field, separately for each IHTT computation method. LVF P100 and N160 IHTT were highly correlated between regions (P100 LVF, $r = .93$, $p = .0001$, $n = 10$; N160 LVF, $r = .95$, $p = .0008$, $n = 7$). LVF lag correlation IHTT estimates were not as highly correlated between regions ($r = .46$, $n = 10$). RVF IHTT between regions were also positively correlated, with each IHTT method yielding similar results (RVF IHTT: P100, $r = .64$, $p = .04$, $n = 10$; N160, $r = .66$, $p = .03$, $n = 11$; lag correlation IHTT: $r = .66$, $p = .05$, $n = 9$). These results provide evidence that individual differences in IHTT are preserved between regions and are a demonstration of the reliability of wave form quantification procedures, particularly the IHTT estimates based on peak detection.

The estimates of IHTT obtained in response to LVF stimulation reflect the transfer of information from the right to the left hemisphere. Conversely, IHTT values from RVF stimulation reflect the transfer of information from the left to the right hemisphere. The relation between speed of transfer in each direction was investigated by computing correlations between visual fields within a region, again separately for each method of IHTT derivation. Significant negative correlations for both peak types were obtained from lateral sites. This finding suggests that faster transfer time in one direction is associated with slower transfer in the opposite direction (P100, $r = -.69$, $p = .04$, $n = 9$; N160, $r = -.74$, $p = .02$, $n = 9$). Comparisons of medially derived peak IHTTs were less negatively correlated between visual fields than were the lateral data (P100, $r = -.13$, $n = 9$; N160, $r = -.56$, $n = 7$). Laterally derived lag correlation IHTT values showed a slight negative relation ($r = -.21$, $n = 9$). Medial lag correlation IHTT values were also negatively correlated between visual fields (lag correlation, $r = -.47$, $n = 8$).

P100 and N160 Amplitude Data

Mean P100 and N160 amplitude values are listed in Table 11. ANOVAs with visual field, region, and hemisphere as variables were used to examine these results. The analyses on the P100 amplitude data revealed a main effect for hemisphere, $F(1, 11) = 7.8$, $p < .02$. P100 amplitude recorded over the right hemisphere is larger than the same peak recorded over the left hemisphere (left $M \pm SD = 2.6 \pm 0.8$ μV, $n = 8$; right $M \pm SD = 3.5 \pm 1.7$ μV, $n = 8$). These results must be qualified by a Region × Hemisphere interaction, $F(1, 11) = 7.48$, $p < .02$. We computed t tests between regions across visual fields separately for each hemisphere and between hemispheres across visual fields separately for each region. Both hemisphere comparisons were significant: medial left versus right hemisphere, $t(8) = 2.25$, $p = .05$; lateral left versus right hemisphere, $t(8) = 2.37$, $p = .05$. The difference in P100 amplitude between hemispheres for the lateral region was larger than for the medial region (1.1 vs. 0.7 μV). The Visual Field × Hemisphere interaction was not significant, a result consistent with the findings in Experiment 1.

The N160 amplitude data demonstrated a strong main effect for region, $F(1, 11) = 18.24$. Lateral sites (averaged across visual field and hemisphere) produced larger N160 amplitudes than the medial sites produced (medial amplitude, $M = -3.1$ μV; lateral amplitude, $M = -4.3$ μV). In contrast to the P100 results, there was a strong Visual Field × Hemisphere interaction for N160 amplitude, $F(1, 9) = 23.60$, $p = .0009$, with the directly stimulated hemisphere

producing larger N160 components compared with the indirectly stimulated hemisphere.

Discussion

Three important latency findings emerged from this experiment: (a) Longer estimates of IHTT were obtained from lateral compared with medial occipital recording sites; (b) P100 and N160 IHTT values were not correlated, although they did not differ; and (c) LVF and RVF IHTT values were inversely correlated.

The pattern of longer laterally derived IHTT values was consistent across all three methods of IHTT computation. The only Rugg et al. study that reported P100 latency data (Rugg, Lines, & Milner, 1985) obtained IHTT values from lateral electrode placements nearly identical with ours (Rugg study, LVF = 10 ms, RVF = 17 ms; our study, LVF = 10.0 ms, RVF = 15.4 ms). However, because no medial site data were presented, a direct comparison between regions for this study was not possible. Lines et al. (1984) reported N160-based IHTT values for both medial and lateral sites. The values they obtained in response to their "bright" stimuli mirror our findings (Lines study, medial N160 IHTT = 7.2 ms, lateral = 12.05 ms; our study, medial N160 IHTT = 7.8 ms, lateral = 14.3 ms). This similarity is noteworthy because the simple RT response requirement of Experiment 2 of the Lines et al. study closely resembles ours. The no-go visual EPs reported by Rugg et al. (1984) do not show occipital region differences in N160 IHTT, which may be accounted for by the effects of the choice RT procedure. No data are presented for the go visual EPs, so inferences about the effects of a motor response on IHTT in the same subjects cannot be made from this study. Using a task identical to their 1984 study, Rugg, Milner, and Lines (1985) found longer N160 IHTT values recorded from lateral compared with medial occipital sites.

We obtained a significant region effect for the zero-lag correlation values, with lateral sites having lower initial correlations compared with the medial sites. This increased similarity between medially recorded wave form sections from the two hemispheres is consistent with the possibility that the response recorded at an individual medial site was subject to influences arising in both hemispheres. Given the proximity of our stimuli to the fovea, we expected that the major sources of the EPs we recorded would be the occipital poles. This source orientation could generate overlapping fields at medial sites. The shorter estimates of IHTT from the medial sites may be due to the general mixing of responses from both hemispheres at each site. We expect that recording from more lateral sites results in an attenuation of this mixing effect and reflects responses generated primarily in one hemisphere.

We know of no other study that has examined correlations between P100 and N160 IHTT values. The uncorrelated P100 and N160 IHTT values suggest a transfer of different information. A precise interpretation of this finding is difficult due to our limited understanding of the time course and synchronization of serial callosal transfers.

Arguably, the most interesting finding that emerged from this experiment was the inverse relation between LVF and RVF IHTTs. This finding suggests that faster transfer time in one direction is associated with slower transfer in the opposite direction. The correlation between LVF and RVF IHTT obtained from the lateral sites was −.69 for P100-based estimates and −.74 for N160-based estimates. The similarity of effect for both peak types is striking, considering the absence of a relation between the two peak types within a visual field, and may reflect the stability of this inverse visual field IHTT relation. No other investigation has reported correlations in IHTT between the visual fields with either behavioral or electrophysiological methods.

In light of the lack of similar data, interpretations of these findings are inherently speculative. However, both anatomical and functional perspectives on the corpus callosum may be useful in considering this phenomenon. Because research has shown that the right occipital region is smaller than the left (e.g., Kertesz et al., 1986) in right-handed subjects, we would expect fewer projections from the left to the right hemisphere because the number of axons is determined primarily by target availability. This decreased number of projections might result in slower transfer time (see Marzi, 1986). Note that the standing asymmetry between visual fields in IHTT is seen in the lag correlation and P100 IHTT values, but not in the N160 IHTT values. The lack of asymmetry between visual fields in N160-derived IHTT may be a function of greater striate contribution to the N160 compared with the P100 components, because the anatomical asymmetry between occipital regions clearly extends beyond the striate area (Kertesz et al., 1986).

In contrast with an anatomical view of this phenomenon, changes in hemispheric activation may also need to be considered when interpreting these findings. Levy (1985), citing evidence of increased arousal asymmetries in commissurotomized subjects compared with normal subjects points out the crucial role of the corpus callosum in regulating the activation levels of the two hemispheres. The relation between activation level and speed of transfer is not clear, nor is the relative impact of the activation of the initially stimulated compared with the receiving hemisphere. Sergent (1983) summarized evidence that the right hemisphere may perform simple visual detection tasks better than the left hemisphere (cf. Hellige & Webster, 1979). If the processing requirements of our task (a simple visual detection) selectively activate the right hemisphere, left-hemisphere activation may actually decrease because of callosally mediated inhibitory influences on the left hemisphere (Zaidel, 1986) from the activated right hemisphere. This pattern of increased right- and decreased left-hemisphere activation may account for the observed inverse relation in IHTT between visual fields.

Another feature of this experiment may also have affected asymmetries in activation between the hemispheres. All responses were made with the left hand. This response requirement presumably would result in greater activation of the right instead of the left motor cortex independent of which visual field was stimulated. If this asymmetry of tonic motor cortex activation affected secondary visual processing areas, then left-hemisphere inhibition could result from callosally mediated inhibitory input from the activated right hemi-

Table 12
P100 and N160 Peak Latencies by Visual Field, Hemisphere, and Stimulus-Presentation Conditions

	Blocked		Mixed	
Latency	O3	O4	O3	O4
P100				
Left visual field				
$M \pm SD$	117.8 ± 5.6	104.8 ± 10.9	121.1 ± 9.3	106.7 ± 6.7
n	4	4	5	5
Right visual field				
$M \pm SD$	101.8 ± 7.2	119.0 ± 5.4	100.8 ± 11.1	122.1 ± 9.3
n	5	5	6	6
N160				
Left visual field				
$M \pm SD$	165.6 ± 15.3	146.1 ± 8.6	167.9 ± 21.5	144.5 ± 3.6
n	3	3	3	3
Right visual field				
$M \pm SD$	145.1 ± 6.0	154.8 ± 15.7	148.1 ± 7.6	157.6 ± 14.7
n	6	6	5	5

Note. Means ($\pm SD$) are expressed in milliseconds for blocked and mixed stimuli recorded from left- and right-hemisphere lateral occipital sites (O3 and O4).

sphere. Of course, these possibilities are not mutually exclusive; right-hemisphere specialization for the task and a left-hand response requirement could act together to increase right-hemisphere activation.

EXPERIMENT 3

In Experiment 3, we investigated the effects of randomly presenting stimuli to the two visual fields and of blocking them to one visual field at a time. Studies by Posner (e.g., Posner, Snyder, & Davidson, 1980) have demonstrated performance advantages in simple hemifield luminance detection when subjects received cues indicating stimulus position shortly before stimulus onset. This performance advantage was hypothesized to be due to a shift in visual attention independent of shifts in eye position. Although Posner et al. (1980) found these effects weakened when stimulus location was blocked, the pattern of effects was maintained. The assumption in presenting stimuli randomly to the two visual fields without location cuing is that attention is divided equally between them (Hardyck, Chiarello, Dronkers, & Simpson, 1985). This experiment sought to examine whether attentional biases to one hemispace arising from foreknowledge of stimulus location would affect EP estimates of IHTT. The experiment was designed only to investigate possible differences between blocked and random stimulus presentation and was not intended as a general investigation of the effects of attention on IHTT. Equipment limitations in earlier experiments prevented our presenting stimuli randomly to the two visual fields.

Method

Subjects

Six of the subjects from Experiment 2 participated in this experiment. The data from the mixed conditions represented additional trials that were run when the data reported for these subjects were collected in Experiment 2.

Design

The stimuli were identical to those presented in the first two experiments. All responses were made with the left hand. There were three experimental conditions: RVF–blocked, RVF– and LVF–mixed, and LVF–blocked. The order of these conditions was counterbalanced within subjects, and counterbalance order was randomized among subjects. There were 100 stimuli in each blocked condition and 200 stimuli in the mixed condition. Stimuli were presented in sets of 100.

Procedure

The blocked trials were identical to those described for Experiments 1 and 2. For the mixed trials, only one shutter opened for each stimulus. In these conditions, both projector lamps were always on, and Coulbourn digital logic randomly selected which visual field was to receive a stimulus. The probability for a stimulus occurring in one visual field was set at 50%.

Electrophysiological Data Acquisition and Analysis

Considering the results of Experiment 2, which demonstrated stronger results in the anatomically predicted directions for lateral occipital sites, we chose to analyze only wave forms recorded from Sites O3 and O4, referenced to linked ears, for this experiment.

Results

Peak Latency Data

P100 and N160 latency results. Table 12 presents the mean P100 and N160 latencies for blocked and mixed stimulus-presentation conditions obtained from lateral occipital sites (O3 and O4) referenced to linked ears.

Table 13
P100 and N160 Evoked Potential Estimates of Interhemispheric Transfer Time by Visual Field and Stimulus-Presentation Conditions

	P100				N160			
Condition	*n*	*M* ± *SD*	*p*	Effect[a] (%)	*n*	*M* ± *SD*	*p*	Effect[a] (%)
LVF–blocked	4	13.0 ± 13.3	.15	100	3	19.5 ± 19.2	.22	67
LVF–mixed	5	14.4 ± 6.7	.009[b]	100	3	22.3 ± 18.1	.16	100
RVF–blocked	5	17.3 ± 9.4	.015	100	6	9.7 ± 11.1	.08	100
RVF–mixed	6	21.3 ± 9.1	.002[b]	100	5	9.5 ± 9.2	.08	100

Note. Means (±*SD*) and *p* values are from *t* tests (for a difference from zero) of interhemispheric transfer time estimates derived from P100 and N160 latency values for each visual field–condition combination. LVF = left visual field; RVF = right visual field; *blocked* = all stimuli presented to the same visual field in a run of 100 stimuli; *mixed* = stimuli randomly presented to the two visual fields across two blocks of 100 trials.
[a]Percentage of subjects showing effects in the anatomically predicted direction. [b]Significant *p* values at the Bonferroni-corrected alpha level.

These peak latency data were examined with a three-way ANOVA with visual field, hemisphere, and condition as variables. The only significant effect was the expected Visual Field × Hemisphere interaction found for both P100 and N160 latency values: P100 Visual Field × Hemisphere, $F(1, 4) = 43.57, p < .003$; N160 Visual Field × Hemisphere, $F(1, 4) = 13.48, p = .02$.

P100 and N160 IHTT estimates. Estimates of IHTT and *t* tests comparing the IHTT values to zero were computed as in Experiments 1 and 2. These estimates and their corresponding *t* values for P100- and N160-derived IHTT values are presented in Table 13. Note that only the P100 mixed condition showed a significant difference from 0 ms at the Bonferroni-corrected alpha level, although 100% of the subjects showed P100 IHTT estimates in the anatomically predicted direction for every condition. The sample sizes for N160 IHTT values were small due to the lack of clearly defined N160 peaks.

Cross-Lag Correlation Data

IHTT values were obtained from the cross-lag correlation procedure as previously described. Four data points were rejected because the lag values for subject–condition combinations were beyond the 30-ms maximum lag used in the lag correlation procedure. These data revealed IHTTs in the direction of anatomical prediction for 100% of the remaining subjects for each condition.

An ANOVA with visual field (LVF vs. RVF) and condition (blocked vs. mixed) as variables was performed on zero-lag correlation, maximum correlation, and lag values. There were no main effects or interactions for any of the dependent variables.

P100 and N160 Amplitude Data

As was the case in Experiments 1 and 2, no P100 Visual Field × Hemisphere interaction was obtained. However, this interaction was obtained for N160 amplitude, $F(1, 4) = 8.03$, $p < .05$, with larger responses recorded from the directly stimulated hemisphere. No main effect for condition or interactions with condition were obtained for the amplitude data.

Discussion

These data indicate that there were no important differences between estimates of IHTT when stimulus location was blocked and those resulting from random presentations. This finding was obtained for all three methods of wave form quantification. These results are consistent with a recent study by Rugg, Milner, Lines, and Phalp (1987). In that study the authors added an attention condition to the same basic paradigm they have used to investigate IHTT. Subjects were asked to attend to one visual field and to detect only short-duration "target" stimuli occurring in the attended visual field. EPs were recorded to the nontarget stimuli, which were more numerous and did not require a response. Although the basic latency advantage for the directly stimulated hemisphere was obtained, there was no difference between attended and unattended conditions. The average ipsi- and contralateral P100 latency difference (from lateral occipital sites, collapsed across visual field) was 14.6 ms for the attended condition and 14.2 ms for the unattended condition. However, there was a main effect for attention on the amplitude of the P100. In another recent study, Neville and Lawson (1987) demonstrated large differences in occipital EPs as a function of directed attention. Their experiment varied attention to one visual field while flash stimuli were randomly presented to both visual fields during a movement-detection task. P100 amplitudes and latencies were increased in the attended condition compared with center-attended or opposite visual field–attended conditions. An examination of the P100 components by an enlargement of the published grand average wave forms reveals latency advantages for the direct projection for both visual fields in the attended condition. The wave forms from the unattended condition do not contain clearly visible P100 peaks.

Although neither of these studies sought to specifically examine the effect of attention on EP estimates of IHTT, they do suggest that attentional bias may affect EPs recorded occipitally in response to hemiretinal stimuli, at least during

a choice RT task. This hypothesis would argue for controlling such bias by randomly varying stimulus location. In addition, in the random-location condition, responses to stimuli from both visual fields are closely spaced in time, and order effects owing to marked changes in subjects' state are minimized. However, our data indicate that in the context of these measures with these stimuli, no differences were found between blocked and mixed stimuli. It is important to note that the purpose of this experiment was to examine specifically the manipulation of stimulus-presentation method, not to test the general effects of attentional biases on IHTT. Such effects may be obtained in paradigms that require the detection of particular stimulus features as has been shown in numerous studies (e.g., Mangun & Hillyard, 1987).

EXPERIMENT 4

Experiment 4 had two purposes: (a) to compare EP estimates of IHTT derived from linked-ears-referenced recordings with those obtained simultaneously with a mid–frontal reference site and (b) to assess the effect of decreasing the stimulus eccentricity from 2.8° to 1.8°.

Studies characterizing the visual EP have often used a mid–frontal reference site (e.g., Blumhardt et al., 1978; Blumhardt & Halliday, 1979; Halliday et al., 1979), whereas experiments that use visual EPs to estimate IHTT have recorded with a linked-ears reference (e.g. Rugg et al., 1984). In light of these differences in recording montage, we wished to directly compare IHTT estimates derived from recordings with each of these two references.

The reduced eccentricity condition was included to test whether more medial stimuli would yield more clearly defined responses. As we noted earlier, the retinotopography of the visual system results in more centrally located stimuli activating regions of primary visual cortex nearer the occipital poles. We included a less eccentric stimulus location to maximize the likelihood that the areas of visual cortex responsible for transferring a representation of such a stimulus between the hemispheres would be located on the lateral convexity, that is, under the electrodes and not in the calcarine fissure. Because the EEG is most sensitive in recording proximal radially oriented dipoles (Rose, Smith, & Sato, 1987), such a source orientation would be optimal to record EPs separately from each hemisphere.

Method

Subjects

Six subjects who participated in Experiment 2 but not in Experiment 3 were tested in this experiment. The linked-ears and larger eccentricity stimuli (the outer condition) responses reported here constitute a subset of the data that were reported in Experiment 2.

Design

Both reference electrode comparisons and the outer condition used stimuli identical to those presented in Experiments 1 and 2. For the inner condition, the angle to the medial edge of the stimuli decreased from 2.8° to 1.8°. As in the previous two experiments, all responses were made with the left hand. There were four experimental conditions: RVF–outer, RVF–inner, LVF–outer, and LVF–inner. The order of these conditions was counterbalanced within subjects, and counterbalance order was randomized among subjects. There were 100 stimuli in each condition, with stimulus location within a condition blocked. All reference electrode comparisons were made on EPs recorded from the outer stimulus (normal) location.

Electrophysiological Data Acquisition and Analysis

The overall methods for this experiment are the same as reported in Experiment 2. Again, considering the results of Experiment 2, we chose to analyze wave forms recorded from Sites O3 and O4 for this experiment. The mid–frontal reference was placed midway between Fz and Fpz sites. The mid–frontally referenced channels were recorded on additional Grass Model 7P5 EEG preamps and displayed on a Grass Model 7 polygraph. These data were recorded on FM tape for off-line analysis. EPs recorded with the linked-ears reference site were averaged on-line.

Results

Reference Site Comparisons

Peak Latency Data

P100 and N160 latency results. The mean P100 and N160 latencies for the two reference sites obtained from Occipital Sites O3 and O4 are presented in Table 14. The most notable feature of these data was the small latency difference between the hemispheres found for LVF frontally referenced P100s. All other conditions and peaks revealed the expected latency shifts.

These peak latency data were examined with a three-way ANOVA with visual field, hemisphere, and reference (linked ears vs. mid–frontal) as variables. A visual field main effect for P100 latency was found, $F(1, 5) = 25.5$, $p < .004$. P100 latency values recorded in response to LVF were earlier compared with RVF stimuli: LVF P100 latency, $M \pm SD = 111.8 \pm 7.4$ ms; RVF P100 latency, $M \pm SD = 114.5 \pm 6.3$ ms. There was no main effect for the hemisphere or reference variable. The expected Visual Field × Hemisphere interaction was obtained, $F(1, 5) = 6.27$, $p = .05$. In addition, there was a significant Visual Field × Hemisphere × Reference interaction, $F(1, 3) = 11.24$, $p < .04$. To examine the three-way interaction in more detail, the P100 data from each reference site were analyzed separately with two-way ANOVAS with visual field and hemisphere as variables. The analysis of the frontal reference data revealed a significant main effect for visual field, $F(1, 5) = 24.01$, $p < .02$, but no Visual Field × Hemisphere interaction, $F(1, 5) = 0.13$, $p = .74$. The linked-ears reference site analysis also revealed a significant main effect for visual field, $F(1, 5) = 9.01$, $p = .03$. However, there was a strong Visual Field × Hemisphere interaction, $F(1, 5) = 40.51$, $p < .002$. Two-tailed t tests within each visual field between hemispheres and within each hemisphere between visual fields were performed to further examine this interaction. All four comparisons were significant: LVF, $t(5) = 4.28$, $p < .008$; RVF, $t(5) = 3.82$, $p < .02$; left hemisphere, $t(5) = 5.02$, $p = .004$; and right hemisphere, $t(5) = 5.79$, $p = .002$.

Table 14
P100 and N160 Peak Latencies by Visual Field, Hemisphere, and Reference Electrode

	Linked ears		Mid-frontal	
Latency	O3	O4	O3	O4
P100				
Left visual field				
$M \pm SD$	116.2 ± 7.9	108.3 ± 8.3	107.2 ± 11.1	110.7 ± 9.2
n	6	6	5	5
Right visual field				
$M \pm SD$	108.7 ± 5.6	122.5 ± 10.2	107.8 ± 4.7	115.6 ± 12.9
n	6	6	4	4
N160				
Left visual field				
$M \pm SD$	163.3 ± 4.1	151.6 ± 9.2	171.5 ± 10.1	151.3 ± 11.4
n	6	6	6	6
Right visual field				
$M \pm SD$	148.8 ± 7.3	167.5 ± 11.0	146.2 ± 11.1	173.1 ± 11.6
n	6	6	6	6

Note. Means ($\pm SD$) are expressed in milliseconds for linked-ears and mid-frontal reference electrode sites recorded from left- and right-hemisphere lateral occipital sites (O3 and O4) for each visual field.

No Visual Field main effect was found for the N160 peak latency data. The Visual Field × Hemisphere interaction was unusually strong, $F(1, 5) = 226.63$, $p < .0001$. The Visual Field × Hemisphere × Reference Site interaction was also significant, $F(1, 5) = 10.79$, $p = .02$. This three-way interaction was further analyzed as was done for the P100 data. Separate two-way ANOVAs with visual field and hemisphere as variables were performed on the N160 data for each reference site. In contrast to the P100 data, both analyses revealed significant Visual Field × Hemisphere interactions. However, the magnitude of the effect was greater for the linked-ears reference site: linked ears N160 Visual Field × Hemisphere, $F(1, 5) = 248.01$, $p < .0001$; frontal N160 Visual Field × Hemisphere, $F(1, 5) = 99.73$, $p = .0002$. Two-tailed t tests on these interactions revealed significant differences for all comparisons for both reference sites.

P100 and N160 IHTT estimates. Estimates of IHTT were computed as in previous experiments. These estimates and their corresponding p values from t tests for a difference from zero for both P100 and N160 IHTT are presented in Table 15. Note that for the P100 values, only the linked-ears reference site provided P100 peak latency estimates of IHTT that were significantly different from 0 ms, with results for both visual fields significant at the Bonferroni-corrected alpha level. This effect of reference electrode was not present for the N160 IHTT values. Overall, N160 data displayed higher percentages of subjects with IHTTs in the anatomically predicted direction compared with the P100 data.

Cross-Lag Correlation Data

The results from the cross-lag correlation procedure for both reference sites revealed that the RVF linked-ears condition was the only condition that yielded lag values that were significantly different from 0 ms at the Bonferroni-corrected alpha level.

An ANOVA with visual field (LVF vs. RVF) and condition (linked ears vs. mid-frontal) as variables was performed on zero-lag correlation, maximum correlation, and lag values. There were no main effects or interactions for any of the

Table 15
P100 and N160 Evoked Potential Estimates of Interhemispheric Transfer Time by Visual Field and Reference Electrode Conditions

	P100 data				N160 data			
Condition	n	$M \pm SD$	p	Effect[a] (%)	n	$M \pm SD$	p	Effect[a] (%)
LVF–ears	6	8.0 ± 4.6	.008[b]	83	6	11.8 ± 7.7	.014	100
LVF–frontal	5	−3.5 ± 7.0	.32	40	6	20.1 ± 9.4	.003[b]	100
RVF–ears	6	13.9 ± 8.9	.012[b]	100	6	18.7 ± 9.1	.004[b]	100
RVF–frontal	4	7.8 ± 12.8	.31	75	6	26.8 ± 6.7	.0002[b]	100

Note. Means ($\pm SD$) and p values are from t tests (for a difference from zero) of interhemispheric transfer time estimates derived from P100 and N160 latency values for each visual field–reference condition. LVF = left visual field; RVF = right visual field; *ears* = linked ears reference; *frontal* = mid-frontal reference site. Wave forms were recorded from lateral occipital leads.
[a]Percentage of subjects showing effects in the anatomically predicted direction. [b]Significant p values at the Bonferroni-corrected alpha level.

Table 16
P100 and N160 Peak Latencies by Visual Field, Hemisphere, and Stimulus Position

Latency	Outer		Inner	
	O3	O4	O3	O4
P100				
Left visual field				
$M \pm SD$	116.3 ± 7.9	108.2 ± 8.3	119.0 ± 9.3	109.8 ± 8.1
n	6	6	5	5
Right visual field				
$M \pm SD$	108.7 ± 5.6	122.5 ± 10.2	106.9 ± 11.0	120.0 ± 2.6
n	6	6	5	5
N160				
Left visual field				
$M \pm SD$	163.3 ± 4.1	151.6 ± 9.3	160.6 ± 7.3	146.6 ± 5.8
n	6	6	5	5
Right visual field				
$M \pm SD$	148.8 ± 7.3	167.4 ± 11.0	146.7 ± 6.1	162.8 ± 5.7
n	6	6	5	5

Note. Means ($\pm SD$) are expressed in milliseconds for inner (1.8°) and outer (2.8°) stimulus locations recorded from left- and right-hemisphere outer occipital sites for each visual field.

dependent variables, indicating that there was no difference in IHTT estimates between the two reference sites with this method of wave form quantification.

P100 and N160 Amplitude Data

ANOVAs with visual field, hemisphere, and reference site as variables were used to examine these data. The pattern of findings was similar to that for previously reported results. The Visual Field × Hemisphere interaction was only significant for N160 data, $F(1, 5) = 17.3$, $p < .009$. In addition, a main effect for reference was found for the N160 amplitude data, $F(1, 5) = 7.92$, $p < .04$, with the frontal reference showing overall greater amplitude compared with the linked-ears site (frontal N160, $M \pm SD = -6.1 \pm 2.8$ μV; linked-ears N160, $M \pm SD = -5.1 \pm 2.5$ μV).

Effects of Stimulus Position

Based on the data reported earlier, stimulus position comparisons were made with the linked-ears reference data because only for this reference did high percentages of subjects show IHTTs in the anatomically predicted directions for both P100- and N160-derived estimates.

Peak Latency Data

P100 and N160 latency results. Table 16 presents the mean P100 and N160 latency values for the two stimulus locations obtained from Occipital Sites O3 and O4. The mean latency values for both stimulus positions for both peak types were in the anatomically predicted directions.

Each type of peak latency data was examined with a three-way ANOVA with visual field, hemisphere, and location (inner vs. outer) as variables. No main effect for location was found for either peak type. A main effect for visual field was found for the P100 latency data, $F(1, 5) = 33.09$, $p = .002$, with LVF latency values shorter than RVF values (LVF, $M = 110.8$ ms; RVF, $M = 114.9$ ms), consistent with results reported previously for the reference site comparisons. There was no interaction of location with any other variable, indicating that decreasing the eccentricity of the visual field stimuli did not affect the morphology of EPs. As expected, a strong Visual Field × Hemisphere interaction was obtained for both peak types: P100, $F(1, 5) = 26.27$, $p < .004$; N160, $F(1, 5) = 233.52$, $p < .0001$. Two-tailed t tests within each visual field between hemispheres and within each hemisphere between visual fields, collapsed across stimulus position, were performed to further examine these interactions. For the P100 values, only the left-hemisphere comparison failed to reach significance. All of the N160 latency comparisons were significant.

P100 and N160 IHTT estimates. P100 and N160 estimates of IHTT and their corresponding p values from t tests for a difference from zero are presented in Table 17. For the P100 IHTT estimates, only the outer stimulus locations yielded estimates of IHTT that were significantly different from 0 ms at the Bonferroni-corrected alpha level, suggesting a more consistent pattern of results in the anatomically predicted direction for the outer stimulus location. This pattern differed from the N160 IHTT estimates, all of which were in the anatomically predicted direction. The LVF–inner and RVF–outer conditions were significantly different from 0 ms at the Bonferroni-corrected alpha level.

These IHTT estimates were further examined with two-way ANOVAs with visual field and location as variables. No main effects or interactions were found for either dependent measure.

Cross-Lag Correlation Data

The data from 1 subject for the RVF–inner condition failed to meet criterion for this procedure because the greatest com-

Table 17
P100 and N160 Evoked Potential Estimates of Interhemispheric Transfer Time by Visual Field and Stimulus Position Conditions

	P100				N160			
Condition	*n*	*M* ± *SD*	*p*	Effect[a] (%)	*n*	*M* ± *SD*	*p*	Effect[a] (%)
LVF–inner	5	9.3 ± 10.5	.12	80	5	13.9 ± 8.9	.001[b]	100
LVF–outer	6	8.0 ± 4.6	.008[b]	83	6	11.8 ± 7.7	.014	100
RVF–inner	5	13.1 ± 11.0	.06	100	5	16.2 ± 9.8	.02	100
RVF–outer	6	13.9 ± 8.9	.012[b]	100	6	18.7 ± 9.2	.004[b]	100

Note. Means (±*SD*) and *p* values are from *t* tests of interhemispheric transfer time estimates derived from P100 and N160 latency values for inner (1.8°) and outer (2.8°) stimulus locations recorded from left- and right-hemisphere lateral occipital sites for each visual field.
[a]Percentage of subjects showing effects in the anatomically predicted direction. [b]Significant *p* values at the Bonferroni-corrected alpha level.

puted correlation was less than .75, and that was at the maximum lag value of 30 ms. All subjects had IHTTs in the anatomically predicted direction in response to RVF stimulation for both stimulus positions. LVF stimulation resulted in 83% of IHTTs in the anatomically predicted direction, again for both stimulus positions. An ANOVA with visual field (LVF vs. RVF) and location (inner vs. outer) as variables was performed on zero-lag correlation, maximum correlation, and lag values. There were no main effects or interactions for any of the dependent variables.

P100 and N160 Amplitude Data

Mean P100 and N160 amplitude values for each visual field, hemisphere, and stimulus position condition were examined with ANOVAS with visual field, hemisphere, and stimulus position as variables. Consistent with results reported above, the only significant N160 amplitude finding was the expected Visual Field × Hemisphere interaction, $F(1, 5) = 15.20$, $p = .01$, in the predicted directions, with contralateral conditions resulting in larger amplitude peaks. The P100 amplitude data revealed a main effect for hemisphere, $F(1, 5) = 10.72$, with greater amplitudes found over the right hemisphere (left, $M \pm SD = 2.3 \pm 1.8$ μV; right, $M \pm SD = 3.6 \pm 1.8$ μV).

Discussion

Reference Electrode Comparison

The main finding from the simultaneous comparison of reference electrode sites was that P100 measures were more affected by the switch from a linked-ears to a mid–frontal reference than either the N160 data or the results from the lag correlation procedure. Frontally referenced P100 IHTT estimates were less reliable and shorter. Only 40% of subjects showed IHTTs in the anatomically predicted direction for the LVF–frontal condition compared with 83% for the linked-ears reference. The lag correlation results demonstrate slightly greater reliability for the linked-ears recordings. Surprisingly, 100% of the subjects had N160-based IHTTs in the anatomically predicted directions for both reference sites, and frontally referenced responses were larger in amplitude. The differential effect of reference site on P100 and N160 data supports the suggestion that these two components are not generated in the same location (Maier et al., 1987), as has been discussed. The greater N160 amplitude from frontally referenced recordings may reflect the axial alignment of the recording montage relative to components of this response originating in striate cortex.

We chose to include the frontal reference site based on previous work investigating the characteristics of visual EPs to hemiretinal stimulation (e.g., Blumhardt, Barrett, & Halliday, 1977; Halliday et al., 1979). Note that in a comparison of IHTT estimates obtained from recordings referenced to linked ears and a noncephalic site, Rugg, Lines, and Milner (1985) found no evidence of any differences.

Effects of Stimulus Position

In the second part of this experiment, the smaller visual angle conditions were included to maximize the likelihood that the source generators of the EPs would be located near the occipital poles and not more medially in the calcarine fissure. Wider angle stimulation of the visual hemifields has yielded the well-known paradoxical effect in which visual EPs do not show the anatomically predicted amplitude asymmetry (Barrett, Blumhardt, Halliday, Halliday, & Kriss, 1976). Our data show that overall, there was little effect of eccentricity on IHTT. The stimuli used in the original Barrett et al. (1976) study were full semicircular hemifield stimuli that extended from the midline to 16°. In subsequent work, Blumhardt et al. (1978) found that when these full hemifield stimuli are reduced to semicircular "scotomata," the paradoxical amplitude asymmetry disappears. Our stimuli more closely resemble the scotomata stimuli because they did not extend from the midline and were small in visual angle subtended. Our data suggest that at least with the small-sized stimuli used in this study, the degree of eccentricity within the range tested does not affect EP estimates of IHTT.

GENERAL DISCUSSION

In this article we describe a method of estimating IHTT from visual EPs that yields values that are in the anatomically predicted direction and consistent with physiological esti-

mates of transcallosal conduction time. The percentage of the 15 unique subjects across all experiments (based on Sites O3 and O4 linked-ears wave forms, except Sites O1 and O2 for 3 subjects from Experiment 1, standard stimulus position and left-hand response) showing IHTT estimates in the predicted direction and greater than 3 ms (chosen as a physiologically reasonable minimum value) for the three methods of wave form quantification was as follows: lag correlation data = 93% (LVF, 11 of 13 subjects; RVF, 14 of 14 subjects), P100 data = 81% (LVF, 10 of 13 subjects; RVF, 12 of 14 subjects), and N160 data = 76% (LVF, 9 of 12 subjects; RVF, 12 of 15 subjects).

We consider these percentages to be acceptable. In fact, they are higher than has been achieved with any other single-session method for estimating IHTT. We recognize that a measure of a basic process such as IHTT should result in estimates that are in the direction of anatomical prediction in 100% of the cases. However, the realization of this ideal is mitigated by several important factors. Homan, Herman, and Purdy (1987) have recently studied the relation between underlying cerebral structures and the 10/20 system electrode locations. Although in general the 10/20 system performed well with respect to underlying cortical landmarks, there were considerable individual variability and interhemispheric differences in the location of homologous left- and right-sided electrodes (see also Myslobodsky & Bar-Ziv, 1989). A second source of noise is individual differences in retinotopic projections (e.g., Stensaas, Eddington, & Dobelle, 1974). Finally, evoked-response latency jitter (Woody, 1967) may also contribute to the appearance of IHTT estimates that are in the direction opposite anatomical prediction. Each of these limitations can be addressed, however. Recording from additional sites in conjunction with the use of source localization methods (e.g., Thickbroom, Carroll, & Mastaglia, 1985; Thickbroom, Mastaglia, Carroll, & Davies, 1984) will facilitate the precise localization of the sources for the P100 component of the checkerboard-flash evoked response. Magnetoencephalographic techniques also hold great promise for the precise specification of the sources of evoked magnetic fields (e.g., Beatty, Barth, Richer, & Johnson, 1986; Rose et al., 1987). In addition to these methods, electrode placement based on the individual neuroanatomy of a subject, obtained by magnetic resonance imaging, would eliminate the variability associated with the disparity between bone landmarks and the underlying cortical regions to which they nominally refer. Latency correction procedures can be used to limit the effects of latency jitter in broadening EP peaks and potentially distorting the observed peak latency. When source localization methods are combined with latency correction procedures, we believe that the percentage of subjects showing IHTT effects in the anatomically predicted direction in this paradigm will approach 100%.

In the context of establishing a valid method to estimate IHTT, we have several noteworthy findings bearing on the specific details of the recording paradigm. In Experiment 1, we found that the percentage of subjects showing IHTT in the direction of anatomical prediction was greater for the EP measures compared with the RT measures. The RT estimates were in the predicted direction in 70% of the computations of IHTT, whereas the EP IHTT estimates (based on the lag correlation procedure) were in the anatomically predicted direction in 94% of the computations. Correlations computed between the EP and RT measures of IHTT showed no consistent pattern of relation. This result suggests that they were reflecting different processes. Manual RT measures of IHTT in response to visual stimuli have been hypothesized to reflect the transfer of information about the motor response (Milner & Lines, 1982), whereas EP measures in response to similar stimuli have been suggested to reflect the transfer of sensory information (Lines et al., 1984). These previous reports in conjunction with our findings underscore the complexity and heterogeneity of interhemispheric transfer and indicate that measures reflecting the transfer of different types of information are not necessarily correlated.

In Experiment 2, we found that lateral occipital recording sites (O3 and O4) yielded longer IHTT estimates compared with medial recording sites (O1 and O2). In addition, lateral sites were more often in the anatomically predicted direction, and the zero-lag correlation for lateral leads was lower than for the medial sites. Taken together, these findings suggest that the medial leads may reflect activity from both hemispheres (indexed by the high zero-lag correlation), which consequently diminishes the latency difference between the wave forms recorded from each hemisphere. In this paradigm, therefore, the lateral occipital sites provide a better metric of IHTT than the medial sites. In addition, we found an inverse relation between transfer time in different directions. Faster transfer time in one direction was associated with slower transfer time in the opposite direction. In light of the consistent difference in transfer time between the visual fields, with RVF stimulation associated with slower transfer time compared with LVF stimulation, the pattern of findings suggests that slower transfer from the left to the right hemisphere is associated with faster transfer from the right to the left hemisphere. This effect held for P100 and N160 IHTT estimates, even though they were uncorrelated within a visual field.

In the third experiment, we found that EP estimates of IHTT obtained from presenting stimuli randomly to the two visual fields did not differ from those obtained from stimuli blocked to one visual field at a time. This finding suggests that slight biases in visual attention introduced by blocking stimuli to one visual field at a time do not systematically influence IHTT estimates. Whether more explicit attentional manipulations will affect IHTT estimates is not answered by our data.

In the final experiment, we found that a linked-ears reference yielded IHTT estimates more consistent with anatomical prediction compared with a mid-frontal reference that was obtained simultaneously for P100 and lag correlation IHTT estimates. Although we obtained more valid results for these measures with the linked-ears reference, some concern about the use of this reference has been expressed in studies of electrophysiological asymmetries (e.g., Davidson, 1988; Nunez, 1981). Nunez (1981) argues that such a reference will attenuate the magnitude of observed asymmetry because linking the ears provides a low-resistive shunt between the two sides of the head that artifactually forces

the two sides to be at the same potential. Whether estimates of IHTT can be improved by the use of references that do not have this problem requires study in future research.

In the final experiment, we also found little difference between IHTT estimates derived in response to stimuli 2.8° and 1.8° from central fixation. The difference between eccentricities may have been too small to reveal any difference in IHTT estimates based on the visual EP. With larger differences in eccentricity, IHTT differences may emerge.

EP estimates of IHTT were derived in three ways in each of these studies: (a) latency differences between the P100 component in the response ipsilateral compared with contralateral to the side of stimulation, (b) latency differences between the N160 component in the response ipsilateral compared with contralateral to the side of stimulation, and (c) the cross-lag correlation between a section of the wave form recorded from each hemisphere. The P100 and lag correlation estimates were only moderately correlated, and neither correlated with N160 IHTT estimates. In Experiment 1, the average correlation between P100 and lag correlation estimates (across conditions) was .70, and in Experiment 2, it was .62. These correlations are insufficiently high to consider these methods interchangeable. Because the highest percentage of subjects show effects in the direction of anatomical prediction when IHTT is computed with the cross-lag correlation procedure, we recommend that this procedure be used when a single index of visual transfer time is required. However, the specific parameters of the cross-lag procedure, such as window start position, window width, and inclusion of multiple window start positions from which results are then aggregated, must be systematically explored in future research.

Overall, our findings indicate that valid measures of IHTT can be obtained in response to brief hemiretinal exposures of checkerboard-flash stimuli by estimating latency differences in the P100 and N160 regions of the visual evoked response derived from lateral occipital recording locations (O3 and O4), referenced to linked ears. These measures are already proving useful in elucidating problems in interhemispheric interaction in certain clinical disorders (e.g., Davidson, Saron, Leslie, & Reiner, 1985). Differences in IHTT between certain clinical groups and normals rest on the assumption that such measures show temporal stability. To examine this question, we (Saron & Davidson, 1989) recently assessed the test–retest stability of EP measures of IHTT in a paradigm similar to the studies presented in this article. Eighteen right-handed subjects were tested on two occasions 3 weeks apart. The mean P100 IHTT test–retest correlation was .81, and the mean N160 IHTT test–retest correlation was .87. These findings indicate that EP measures of IHTT are stable. However, the simple stimuli and visual modality of this paradigm probably restrict these assessments to the functioning of the callosal splenium, through which almost all visual transfer fibers course (Pandya & Seltzer, 1986).

The fact that fewer than 100% of subjects show effects in the anatomically predicted direction is viewed as a product of the limitations of existing recording and analysis procedures, which are in principle possible to overcome.

References

Andreassi, J. L., Okamura, H., & Stearn, M. (1975). Hemispheric asymmetries in the visual cortical evoked potential as a function of stimulus locations. *Psychophysiology, 12,* 541–546.

Bashore, T. R. (1981). Vocal and manual reaction time estimates of interhemispheric transmission time. *Psychological Bulletin, 89,* 352–368.

Barrett, G., Blumhardt, L., Halliday, A. M., Halliday, E., & Kriss, A. (1976). A paradox in the lateralisation of the visual evoked response. *Nature, 261,* 353–355.

Berardi, N., Fiorentini, A., & Gravina, A. (1988). Functional dissociation of the hemispheres in the discrimination of complex gratings near the vertical meridian. *Vision Research, 28,* 491–496.

Beatty, J., Barth, D. S., Richer, F., & Johnson, R. A. (1986). Neuromagnetometry. In M. G. H. Coles, E. Donchin, & S. W. Porges (Eds.), *Psychophysiology: Systems, processes and applications* (pp. 26–40). New York: Guilford.

Blumhardt, L. D., Barrett, G., & Halliday, A. M. (1977). The asymmetrical visual evoked potential to pattern reversal in one half field and its significance for the analysis of visual field defects. *British Journal of Ophthalmology, 61,* 454–461.

Blumhardt, L. D., Barrett, G., Halliday, A. M., & Kriss, A. (1978). The effect of experimental "scotomata" on the ipsilateral and contralateral responses to pattern-reversal in one half-field. *Electroencephalography and Clinical Neurophysiology, 45,* 376–392.

Blumhardt, L. D., & Halliday, A. M. (1979). Hemisphere contributions to the composition of the pattern-evoked potential waveform. *Experimental Brain Research, 36,* 53–69.

Curry, S. H. (1984). Contingent negative variation and slow waves in a short interstimulus interval Go–NoGo task situation. *Annals of the New York Academy of Sciences, 425,* 171–176.

Davidson, R. J. (1988). EEG measures of cerebral asymmetry: Conceptual and methodological issues. *International Journal of Neuroscience, 39,* 71–89.

Davidson, R. J., Leslie, S. C., & Saron, C. D. (1989). *Reaction time measures of interhemispheric transfer time in reading disabled and normal children.* Manuscript submitted for publication.

Davidson, R. J., Saron, C., Leslie, S. C., & Reiner, P. D. (1985). Visual evoked potential estimates of interhemispheric transfer time: Comparison of dyslexics and normals [Abstract]. *Journal of Clinical and Experimental Neuropsychology, 7,* 634.

Demeter, S., Ringo, J. L., & Doty, R. W. (1988). Morphometric analysis of the human corpus callosum and anterior commissure. *Human Neurobiology, 6,* 219–226.

Denenberg, V. H., Hofmann, M. J., Rosen, G. D., & Yutzey, D. A. (1984). Cerebral asymmetry and behavioral laterality: Some psychobiological considerations. In N. A. Fox & R. J. Davidson (Eds.), *The psychobiology of affective development* (pp. 77–117). Hillsdale, NJ: Erlbaum.

Fox, P. T., Miezin, F. M., Allman, J. M., Van Essen, D. C., & Raichle, M. E. (1987). Retinotopic organization of human visual cortex mapped with positron-emission tomography. *Journal of Neuroscience, 7,* 913–922.

Gladstone, M., & Best, C. T. (1985). Developmental dyslexia: The potential role of interhemispheric collaboration in reading acquisition. In C. T. Best (Ed.), *Hemispheric function and collaboration in the child* (pp. 87–118). New York: Academic Press.

Gott, P. S., Hughes, E. C., & Binggeli, R. L. (1985). Interhemispheric transmission: Assessment with vibratory somatosensory evoked potentials. *International Journal of Neuroscience, 27,* 121–130.

Gulmann, N. C., Wildschiødtz, G., & Ørbaek, K. (1982). Alteration of interhemisphere conduction through corpus callosum in chronic schizophrenia. *Biological Psychiatry, 17,* 585–594.

Halliday, A. M., Barrett, G., Blumhardt, L. D., & Kriss, A. (1979). The macular and paramacular subcomponents of the pattern evoked response. In D. Lehmann & E. Callaway (Eds.), *Human evoked potentials: Applications and problems* (pp. 135–151). New York: Plenum Press.

Hardyck, C., Chiarello, C., Dronkers, N. F., & Simpson, G. V. (1985). Orienting attention within visual fields: How efficient is interhemispheric transfer? *Journal of Experimental Psychology: Human Perception and Performance, 11,* 650–666.

Hellige, J. B., & Webster, R. (1979). Right hemisphere superiority for initial stages of letter processing. *Neuropsychologia, 17,* 653–660.

Homan, R. W., Herman, J., & Purdy, P. (1987). Cerebral location of international 10–20 system electrode placement. *Electroencephalography and Clinical Neurophysiology, 66,* 376–382.

Kertesz, A., Black, S. E., Polk, M., & Howell, J. (1986). Cerebral asymmetries on magnetic resonance imaging. *Cortex, 22,* 117–127.

Ledlow, A., Swanson, J. M., & Kinsbourne, M. (1978). Differences in reaction times and average evoked potentials as a function of direct and indirect neural pathways. *Annals of Neurology, 6,* 525–530.

LeMay, M. (1977). Asymmetries of the skull and handedness: Phrenology revisited. *Journal of Neurological Science, 32,* 243–253.

Lepore, F., Ptito, M., & Jasper, H. H. (Eds.). (1986). *Two hemispheres—one brain: Functions of the corpus callosum.* New York: Liss.

Leslie, S. C., Davidson, R. J., & Batey, O. B. (1985). Purdue pegboard performance of disabled and normal readers: Unimanual versus bimanual differences. *Brain and Language, 24,* 359–369.

Levy, J. (1985). Interhemispheric collaboration: Single-mindedness in the asymmetric brain. In C. T. Best (Ed.), *Hemispheric function and collaboration in the child.* New York: Academic Press.

Lines, C. R., Rugg, M. D., & Milner, A. D. (1984). The effect of stimulus intensity on visual evoked potential estimates of interhemispheric transmission time. *Experimental Brain Research, 57,* 89–98.

Maddess, R. J. (1975). Reaction time to hemiretinal stimulation. *Neuropsychologia, 13,* 213–218.

Maier, J., Dagnelie, G., Spekreijse, H., & van Dijk, B. W. (1987). Principal components analysis for source localization of VEPs in man. *Vision Research, 27,* 165–177.

Mangun, G. R., & Hillyard, S. A. (1987). The spatial allocation of visual attention as indexed by event-related brain potentials. *Human Factors, 29,* 195–211.

Marzi, C. A. (1986). Transfer of visual information after unilateral input to the brain. *Brain and Cognition, 5,* 163–173.

Maunsell, J. H. R., & Van Essen, D. C. (1987). Topographic organization of the middle temporal visual area in the macaque monkey: Representational biases and the relationship to callosal connections and myeloarchitectonic boundaries. *Journal of Comparative Neurology, 266,* 535–555.

Miller, N. R. (Ed.). (1982). *Walsh and Hoyt's clinical neuro-ophthalmology (Vol. 1, 4th ed.).* Baltimore, MD: Williams & Wilkins.

Milner, A. D., & Lines, C. R. (1982). Interhemispheric pathways in simple reaction times to lateralized light flashes. *Neuropsychologia, 20,* 171–179.

Mononen, L. J., & Seitz, R. R. (1977). An AER analysis of contralateral advantage in the transmission of auditory information. *Neuropsychologia, 15,* 165–173.

Myslobodsky, M. S., & Bar-Ziv, J. (1989). Locations of occipital EEG electrodes verified by computed tomography. *Electroencephalography and Clinical Neurophysiology, 72,* 362–366.

Nasrallah, H. A., Andreasen, N. C., Coffman, J. A., Olson, S. C., Dunn, V. D., Erhardt, J. C., & Chapman, S. M. (1986). A controlled magnetic resonance imaging study of corpus callosum thickness in schizophrenia. *Biological Psychiatry, 21,* 274–282.

Neville, H. J., & Lawson, D. (1987). Attention to central and peripheral visual space in a movement detection task: An event-related potential and behavioral study. I. Normal hearing adults. *Brain Research, 405,* 253–267.

Novak, G. P., Wiznitzer, M., Kurtzberg, D., Giesser, B. S., & Vaughan, H. G. (1988). The utility of visual evoked potentials using hemifield stimulation and several check sizes in the evaluation of suspected multiple sclerosis. *Electroencephalography and Clinical Neurophysiology, 71,* 1–9.

Nunez, P. L. (1981). *Electric fields of the brain: The neurophysics of EEG.* New York: Oxford University Press.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychologia, 9,* 97–113.

Pandya, D. N., & Rosene, D. L. (1985). Some observations on trajectories and topography of commissural fibers. In A. G. Reeves (Ed.), *Epilepsy and the corpus callosum* (pp. 21–39). New York: Plenum Press.

Pandya, D. N., & Seltzer, B. (1986). The topography of commissural fibers. In F. Lepore, M. Ptito, & H. H. Jasper (Eds.), *Two hemispheres—one brain: Functions of the corpus callosum* (pp. 47–73). New York: Liss.

Poffenberger, A. T. (1912). Reaction time to retinal stimulation with special reference to the time lost in conduction through nerve centers. *Archives of Psychology 23,* 1–73.

Posner, M. I., Snyder, C. R., & Davidson, B. J. (1980). Attention and the detection of signals. *Journal of Experimental Psychology, 109,* 160–174.

Rose, D. F., Smith, P. D., & Sato, S. (1987). Magnetoencephalography and epilepsy research. *Science, 238,* 329–335.

Rugg, M. D. (1982). Electrophysiological studies. In J. G. Beaumont (Ed.), *Divided visual field studies of cerebral organisation* (pp. 129–146). London: Academic Press.

Rugg, M. D., Lines, C. R., & Milner, A. D. (1984). Visual evoked potentials to lateralized visual stimuli and the measurements of interhemispheric transmission time. *Neuropsychologia, 22,* 215–225.

Rugg, M. D., Lines, C. R., & Milner, A. D. (1985). Further investigation of visual potentials elicited by lateralized stimuli: Effects of stimulus eccentricity and reference site. *Electroencephalography and Clinical Neurophysiology, 62,* 81–87.

Rugg, M. D., Milner, A. D., & Lines, C. R. (1985). Visual evoked potentials to lateralised stimuli in two cases of callosal agenesis. *Journal of Neurology, Neurosurgery and Psychiatry, 48,* 367–373.

Rugg, M. D., Milner, A. D., Lines, C. R., & Phalp, R. (1987). Modulation of visual event-related potentials by spatial and nonspatial visual selective attention. *Neuropsychologia, 25,* 85–96.

St. John, R., Shields, C., Krahn, P., & Timney, B. (1987). The reliability of estimates of interhemispheric transmission times derived from unimanual and verbal response latencies. *Human Neurobiology, 6,* 195–202.

Salamy, A. (1978). Commissural transmission: Maturational changes in humans. *Science, 200,* 1409–1411.

Saron, C. D., & Davidson, R. J. (1989). Reliability of evoked potential estimates of interhemispheric transfer time: Further studies [Abstract]. *Psychophysiology, 26,* S53.

Schwartz, B. D., Winstead, D. K., & Walker, W. G. (1984). A corpus callosal deficit in sequential analysis by schizophrenics. *Biological Psychiatry, 19,* 1667–1676.

Sergent, J. (1983). Role of the input in visual hemispheric asymmetries. *Psychological Bulletin, 93,* 481–512.

Shagass, C., Amadeo, M., & Roemer, R. (1976). Spatial distribution

of potentials evoked by half-field pattern-reversal and pattern-onset stimuli. *Electroencephalography and Clinical Neurophysiology, 41,* 609–622.

Srebro, R. (1985). Localization of visually evoked cortical activity in humans. *Journal of Physiology, 360,* 233–246.

Srebro, R. (1987). The topography of scalp potentials evoked by pattern pulse stimuli. *Vision Research, 27,* 901–914.

Stensaas, S. S., Eddington, D. K., & Dobelle, W. H. (1974). The topography and variability of the primary visual cortex in man. *Journal of Neurosurgery, 40,* 747–755.

Swadlow, H. A. (1985). The corpus callosum as a model system in the study of mammalian cerebral axons: A comparison of results from primate and rabbit. In A. G. Reeves (Ed.), *Epilepsy and the corpus callosum* (pp. 55–74). New York: Plenum Press.

Swadlow, H. A., Geschwind, N., & Waxman, S. G. (1979). Commissural transmission in humans. *Science, 204,* 530–531.

Swadlow, H. A., Waxman, S. G., & Rosene, D. L. (1978). Latency variability and the identification of antidromically activated units in mammalian brain. *Experimental Brain Research, 32,* 439–443.

Thickbroom, G. W., Carroll, W. M., & Mastaglia, F. L. (1985). Dipole source derivation: Application to the half-field pattern evoked potential. *International Journal of Bio-Medical Computing, 16,* 17–28.

Thickbroom, G. W., Mastaglia, F. L., Carroll, W. M., & Davies, H. D. (1984). Source derivation: Application to topographic mapping of visual evoked potentials. *Electroencephalography and Clinical Neurophysiology, 59,* 279–285.

Tomasch, J. (1954). Size, distribution and number of fibers in the human corpus callosum. *Anatomical Record, 119,* 119–135.

Van Essen, D. C., Newsome, W. T., & Bixby, J. L. (1982). The pattern of interhemispheric connections and its relationship to extrastriate visual areas in the macaque monkey. *Journal of Neuroscience, 2,* 265–283.

Van Essen, D. C., Newsome, W. T., & Maunsell, J. H. R. (1984). The visual field representation in striate cortex of the macaque monkey: Asymmetries, anisotropies, and individual variability. *Vision Research, 24,* 429–448.

Witelson, S. F. (1986). Wires of the mind: Anatomical variation in the corpus callosum in relation to hemispheric specialization and integration. In F. Lepore, M. Ptito, & H. H. Jasper (Eds.), *Two hemispheres—One brain: Functions of the corpus callosum* (pp. 117–137). New York: Liss.

Woody, C. D. (1967). Characterization of an adaptive filter for the analysis of variable latency neuroelectric signals. *Medical & Biological Engineering & Computing, 5,* 539–553.

Zaidel, E. (1986). Callosal dynamics and right hemisphere language. In F. Lepore, M. Ptito, & H. H. Jasper (Eds.), *Two hemispheres—One brain: Functions of the corpus callosum* (pp. 435–459). New York: Liss.

Received January 14, 1988
Revision received December 16, 1988
Accepted December 28, 1988 ■