Sound localization in callosal agenesis and early callosotomy subjects: brain reorganization and/or compensatory strategies

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Summary
In order to evaluate the callosal involvement in sound localization, the present study examined the response accuracy of acallosal and early callosotomized subjects to monaural and binaural auditory targets presented in three-dimensional space. In these subjects, bilateral localization cues, such as interaural time and level differences, are integrated at the cortical and subcortical levels without the additional support of the callosal commissure. Because acallosal and early-callosotomized subjects have developed with this reduced source of binaural activation of cortical cells, they might have perfected their ability to use monaural sound localization cues. This hypothesis was tested by assessing localization performance under both binaural and monaural listening conditions. Five subjects with callosal agenesis, one callosotomized subject operated early in life and 19 control subjects were asked to localize broad-band noise bursts (BBNBs) of fixed intensity in the horizontal plane in an anechoic chamber. BBNBs were delivered through randomly selected loudspeakers. Two conditions were tested: (i) localization of a stationary sound source; and (ii) localization of a moving sound source. Listeners had to report the apparent stimulus location by pointing to its perceived position on a graduated perimeter. The results indicated that the acallosal subjects were less accurate than controls, but only in the binaural moving sound condition. More interestingly, in the monaural testing conditions, some of the acallosal subjects and the early-callosotomized subject performed significantly better than control subjects. This suggests that, because of the absence of the corpus callosum, these subjects compensate for their reduced access to cortically determined binaural cues by making more efficient use of monaural cues.

Keywords: corpus callosum; monaural auditory localization; binaural auditory localization; moving sounds; cerebral plasticity

Abbreviations: BBNB = broad-band noise burst; LEO = left ear obstructed; REO = right ear obstructed; SPL = sound pressure level

Introduction
The corpus callosum is the principal neocortical commissure and allows the transfer of sensory and motor information between the hemispheres. In the auditory system, the corpus callosum interconnects different cortical areas, in particular the primary auditory area, which receives input from both ears, thereby providing for the integration of binaural cues (Imig and Brugge, 1978; Kelly and Wong, 1981; Imig et al., 1982, 1986; Code and Winer, 1985; Jouandet et al., 1986; Rouiller et al., 1991; Poirier et al., 1995). In fact, sound localization depends upon the combined operation of binaural and monaural cues. Binaural cues refer to the discrepancies of inputs between the ears in terms of timing and intensity, whereas monaural cues arise from the spectral filtering of sounds, in particular by the pinna and the head (Irvine, 1987; Moore, 1991). Because the corpus callosum interconnects the auditory areas, it may contribute to sound localization by allowing the interhemispheric integration of binaural inputs. Anatomical and electrophysiological studies in the cat suggest that auditory callosal projecting and recipient neurones are involved in sound localization. Imig et al. (1986) described anatomical subunit bands of cells connected through the corpus callosum that have receptive fields, suggesting that they may be sensitive to specific spatial positions of the sound. Cells possibly involved in sound-
source localization were also described by Middlebrooks and Pettigrew (1981). Poirier et al. (1989, 1995) examined this problem more directly by recording in the auditory portion of the callosum of normal cats. The results showed that callosal fibres are involved in the processing of both the null interaural time delay, which simulates auditory midline localization, and specific, non-zero interaural time delays, suggesting that these fibres prefer sounds situated at spatial locations other than the midline. Hence, the preferred delay(s) simulating specific locations in space suggested that different fibres code different positions throughout the auditory field. The response profiles of these fibres were thus characterized by heterogeneity in their responsiveness to binaural stimulation, a finding which supports the notion that the corpus callosum is involved in sound localization.

By contrast, neurobehavioural experiments carried out in animals suggest that callosal section has little or no effect on auditory localization behaviour (Moore et al., 1974; Casseday and Neff, 1975; Brunk et al., 1979). The absence of an effect may result from the use of experimental paradigms that do not provide an accurate assessment of sound localization. Indeed, one of the difficulties in some of these studies resides in the use of a two-choice test of sound localization, in which the sound source is lateralized to the left or the right of the animal’s midline. According to Jenkins and collaborators, this is considered to be a poor test of higher auditory processing (Jenkins and Masterton, 1982; Jenkins and Merzenich, 1984). Other factors which could have masked the presence of deficits include small sample size (Moore et al., 1974), the type of stimulus (i.e., pure tones, which are mainly treated subcortically) and long stimulus duration, which would allow scanning by movement of the head (Moore et al., 1974; Casseday and Neff, 1975; Brunk et al., 1979). In fact, using a multiple-source paradigm and a binaural presentation, Poirier et al. (1993) found that acallosal individuals displayed a deficit throughout the auditory field. This finding suggests that the additional binaural input provided by the corpus callosum is a necessary prerequisite for the accurate localization of sounds in space, at least in the binaural condition.

Because acallosal and early-callosotomized subjects have developed with this reduced source of binaural cortical activation, they may have learned to use monaural cues more efficiently to compensate for the lack of the additional interaural comparison normally provided by the corpus callosum. Normal subjects, tested under the monaural listening condition created by plugging one ear, a condition in which interaural differences are eliminated, could still, in theory, estimate sound position on the azimuth through the use of spectral cues (Searle et al., 1976; Butler and Flannery, 1980; Flannery and Butler, 1981; Martin and Webster, 1987; Humanski and Butler, 1988; Musicanet et al., 1990). However, it has been shown that, with one ear blocked, subjects tend to displace the perceived location of the sound source towards the side of the unobstructed ear. Sensory-deprived subjects, on the other hand, can localize a sound source in the azimuth on the appropriate side using monaural cues only. For instance, Slattery and Middlebrooks (1994) studied sound localization in five unilaterally deaf subjects and showed that three of them displayed little or no localization bias towards the functional ear. In the same vein, we recently found that some totally blind subjects can localize correctly sound presented on the side of the obstructed ear (Lessard et al., 1998). The fact that early blind and unilaterally deaf subjects perform better than normally hearing subjects may be attributed to learning and/or reorganization in the neuronal populations involved in the processing of monaural cues. Similar compensatory strategies may be used by acallosal and early-callosotomized subjects, who may have perfected their ability to use monaural cues to compensate for the reduced source of binaural activation.

In the present study, two experiments examined the localization ability for stationary and moving sounds of acallosal and early-callosotomized subjects compared with matched control subjects. The first experiment, a baseline binaural listening condition, was carried out to further assess the extent of the localization abilities under these optimal conditions. The second experiment explored the sound localization abilities of these subjects under monaural listening conditions. In the light of the results obtained by Poirier et al. (1993, 1995) and the fact that acallosal subjects have developed with a reduced source of binaural activation, it was expected that they would show localization deficits in the binaural condition. By contrast, because these individuals have developed without the additional binaural activation provided by the corpus callosum, we expected the acallosal and early-callosotomized subjects to display better use of monaural cues, and hence that their performance would be better than that of neurologically intact subjects in the monaural listening condition.

**Methods**

**Subjects**

This investigation was carried out on two groups of subjects: an experimental group and a control group. The experimental group was composed of five acallosal individuals and one early-callosotomized subject who was not included in the statistical analysis because of the different nature of his pathology. The control group consisted of 18 neurologically intact subjects matched with the experimental subjects for gender, age and manual dominance. Informed written consent was obtained from all subjects.

**Acallosal subjects**

Case M.G., a 27-year-old, left-handed man, is the youngest child of four. His complete history has been described elsewhere (Sauerwein et al., 1981; Lassonde et al., 1988). He was seen by a neurologist for the first time at the age of 4
years and 11 months because of prolonged enuresis, poor motor coordination and retarded language acquisition. Both CT and MRI scans confirmed complete agenesis of the corpus callosum with preservation of the anterior commissure. His global IQ on the Ottawa–Wechsler scale is 77. M.G. was taking anti-depressant medication (Prozac) at the time of the evaluation.

Case L.G., a 34-year-old, right-handed woman, is the third child of the same family as M.G. Her detailed case history has been reported before (Sauerwein et al., 1981; Lassonde et al., 1988). She was born prematurely in the seventh month of pregnancy after a particularly difficult breach birth. She was first hospitalized at the age of 3 1/2 years because of a light cranial trauma due to a fall. The EEG showed slow dysrhythmia without epileptic activity. At the age of 6 years, she was rehospitalized for elective mutism and ataxia. Neurological examination revealed agenesis of the corpus callosum. The diagnosis was confirmed by a CT scan at the age of 17 years. MRI performed when she was 22 years old revealed the presence of the anterior commissure. At the time of testing, L.G. was taking anticonvulsive medication (carbamazepine) because she manifested symptoms of epileptic activity, which were later diagnosed as being pseudoseizures. L.G. obtained a full scale IQ of 78 on the Ottawa–Wechsler scale.

Case S.G., a 35-year-old, right-handed woman, is the oldest sister of M.G. and L.G. A CT scan, performed because of the familial incidence of callosal agenesis, revealed an intact anterior commissure but complete callosal agenesis. S.G. was asymptomatic except for slow acquisition of walking, which reflects the motor incoordination that is often observed in callosal agenesis during development. She has an IQ of 84 on the WAIS-R (Wechsler Adult Intelligence Scale—Revised). MRI performed in 1997 showed the presence of the anterior commissure.

Case S.Pe., a 31-year-old, right-handed man, is the youngest child of his family. He was born with hypertelorism and cleft lip and palate. The latter was corrected surgically at the age of 4 months. A basal transpalatal encephalocele was also diagnosed and was surgically removed by bifrontal craniotomy at the age of 18 months. At this time, he was diagnosed as having congenital absence of the corpus callosum. A left hydrocele was detected at the age of 4 years. Two prepalatal fistulas were also corrected surgically. S.Pe. showed some growth retardation, hypothyroidism and hypopituitarism, which were treated with growth hormone therapy and thyroxine. He was not on medication at the time of testing. A recent MRI, performed in February 1996, confirmed the absence of both the corpus callosum and the anterior commissure. The posterior commissure was visualized. The MRI also showed bilateral prefrontal atrophy related to previous surgical interventions. Intellectual assessment with the WAIS-R revealed a global IQ of 107.

Case S.Po. is a 28-year-old, left-handed man. He is the youngest child of his family. He left school in sixth grade and started to work at the age of 13 years. At the age of 23 years, he underwent a derivation for hydrocephaly. A recent MRI showed complete agenesis of the corpus callosum. S.Po. obtains a global IQ of 75 on the WAIS-R.

**Early-callosotomized subject**

Case S.D. (referred to as early-callosotomized or subject E.-C.), a 20-year-old, right-handed man, was operated at the age of 6 years and 10 months. At the age of 3 years, he began to experience epileptic seizures, which soon became intractable. His preoperative EEG showed a right centroparietal focus with frequent secondary generalizations. After the callosotomy in March 1982, he stopped having seizures for 10 years but a recent EEG showed a new independent epileptic focus in the left frontotemporal region. Completeness of the callosal section was confirmed by MRI. E.-C. has an IQ of 75 on the Wechsler Intelligence Scale for Children—Revised (WISC-R). It is noteworthy that, like acallosal subjects, he does not show typical disconnection symptoms in most interhemispheric communication tasks (Lassonde et al., 1986, 1991).

Prior to experimentation, all subjects underwent audiometric testing with standard pure tones to measure detection thresholds for frequencies between 125 and 8000 Hz. All showed normal thresholds for both ears and exhibited essentially symmetrical audiograms displaying a difference of no more than 10 dB sound pressure level (SPL) between the two ears at any given frequency.

**Apparatus and stimuli**

The apparatus consisted of 16 loudspeakers mounted on a graduated semicircular perimeter (radius 50 cm) placed inside an anechoic chamber (measuring 1.5 × 3 × 1.6 m; Poirier et al., 1993). To assign a numerical value to a subject’s response, a circular indicator graduated in degrees was placed below the perimeter. This system was ±1° accurate in the determination of the actual and perceived azimuthal position. All surfaces (floor, walls and ceiling) were covered with thick acoustic foam wedges to absorb sound reflections. The loudspeakers were hidden from the subject’s view by a strip of black fabric to eliminate cues about the number and location of sound sources. The loudspeakers were separated by ~10° and were positioned 5°, 16°, 26°, 37°, 47°, 58°, 68° and 78° to the left and to the right of the middle of the semicircular perimeter.

The subject was seated in the centre of the perimeter facing the sound sources. The speakers were positioned at ear level, 50 cm from the middle of the interaural line. A headrest at the back of the chair ensured reliable immobilization of the head, which is necessary to maintain a constant ear position. In the fixed sound source condition, the pericentral field was defined arbitrarily as the space containing the loudspeakers located at ±5° and ±16° and the lateral fields were defined as the spaces containing the loudspeakers situated at ±26°, ±37°, ±47°, ±58°, ±68° and ±78°. Similarly, in the moving sound source
condition, the pericentral field was arbitrarily defined as the space contained between loudspeakers located at ±5°, ±16° and ±26° (maximal size of the field 52°) and the lateral fields (maximal size of the left and right fields 52°) were defined as the space between the loudspeakers situated –26° and –78° (left hemifield) and between +26° and +78° (right hemifield). Moving sound sources that travelled over a distance of 10° (±5°), 32° (±16°) and 52° (±26°) over the midline were considered as three independent measures of pericentral field location, and stimuli travelling over the same length on each side were considered to constitute the lateral fields.

The stimuli used were broad-band noise bursts (BBNBs). The SPL was determined at the estimated centre of the subject’s head by means of a wave analyser (model 2230; Bruel and Kjaer, Norcross, Georgia, USA) and a 12.7 mm condenser microphone. The SPL was maintained at 40 dB (20 µPa). A computer (386 processor; ProSys, Proactive Systems, Glen Allen, VA, USA) controlled the presentation of the stimuli, which were produced by a white-noise generator (model 81–02; Coulbourn Instruments, Allentown, VA, USA) gated by an electronic switch (model 84-04; Coulbourn) and calibrated with an amplifier and two attenuators (models 84–02 and 84–05; Coulbourn).

**Procedure**

The experiment required the presence of two experimenters: one who remained outside the experimental chamber and controlled the stimulus presentation and another who was seated behind the subject to reassure him or her in the closed chamber, to ascertain that he or she maintained correct head position and to record the subject’s responses. Prior to testing, the different tasks were explained in detail to the subjects. The subjects were first asked to localize a sound source under binaural listening to establish baseline performance. The subjects then had to localize the sound source under monaural listening, i.e. with either the left or the right ear blocked in random order across subjects. The order of presentation of the fixed or moving sound was also randomized across subjects. To remind the subject to keep their head aligned centrally, each trial was initiated with a 0.5 s warning buzzer located in front of the subject above the perimeter at midline. Responses, ranging from ±180° azimuth, were recorded in degrees. The trials in which subjects were unsure of their perception were repeated at the end of each block. In all experiments, subjects were required to localize the fixed sound source by touching the calibrated degree indicator with the index finger of either their dominant or their non-dominant hand. The procedure was then repeated with the other hand. To localize moving sound sources, subjects touched the calibrated degree indicator at the position where they thought the beginning and the end of the stimulus had occurred by using first the index finger of their dominant hand and then the index finger of their non-dominant hand. The order of the pointing hand was randomized across subjects.

**Baseline condition**

**Binaural listening**

**Fixed sound source condition.** On each trial, two BBNBs of 30 ms per stimulus, separated by an interburst interval of 30 ms (90 ms total stimulus duration), were delivered through a randomly selected loudspeaker on the sound perimeter. BBNBs were repeated five times for each position, giving a total of 80 presentations for each responding hand. Plotted presentations for both hands corresponded to a total of 160 trials. The stimuli were administered in five blocks of 16 trials with a short rest period between blocks. The order of stimulus presentation within blocks was pseudorandomized for each subject. Four practice trials were administrated in order to familiarize the subject with the apparatus, the tasks and the response requirements. During this training session, verbal feedback about the accuracy of the response was given to the subject.

**Moving sound source condition.** In this condition, the stimulus was presented randomly in the left or right hemispace or across the midline. The apparent movement travelled in either direction (left to right or right to left) over a distance of 10°, 32° or 52°, depending on the number of loudspeakers involved (two, four or six). These three distances were used in order to verify whether performance varied with the length of the trajectory. Apparent movement was produced by activating successive loudspeakers with broad-band noise stimuli. Because of the electrostatic nature of the speakers, the sound, which would have been produced if one speaker had simply been turned off and the other one on, would not have been a smooth moving sound but one which had a trough between successive plateaus. Therefore, the decay time (set at 10 ms) of the stimulus from one loudspeaker was straddled with the rise time (also set at 10 ms) of the stimulus of the contiguous loudspeaker. The summed output of two speakers, which corresponds to the amplitude of the stimulus, would then give the impression of a continuous sound. Various signal durations from 50 to 370 ms were used across trials. This control was necessary to prevent the subjects from estimating the length of the trajectory by the use of a sound duration cue. Central presentations involved trajectories which began and ended on either side of the vertical meridian, whereas lateral trajectories had a midpoint situated at ~52°. The stimulus was presented six times in each position (left, right and pericentral), giving a total of 54 presentations for each hand. Plotted presentations for both hands corresponded to a total of 108 trials. Stimuli were administered in blocks of 18 trials with frequent breaks. The order of presentation within blocks was varied randomly between the subjects. Four practice trials were given in order to familiarize the subject with the apparatus and the procedure. During this training session, the subject received verbal feedback about his or her performance.
Monaural listening

The procedure was the same as in the binaural experiment except that all testing was carried out with a single ear by randomly obstructing either the right ear [right ear obstructed (REO)] or the left ear [left ear obstructed (LEO)] with an earplug. The ear was obstructed with a soft foam earplug (mean standard attenuation 37.5 dB SPL) and covered by a hearing protector muff (mean standard attenuation 29 dB SPL). To ensure that no sound could be perceived with the earplug and a hearing protector muff in place, a preliminary psychophysical study was carried out with both ears occluded. This test served to confirm the efficacy of the preparation. Thus, the BBNBs were delivered randomly at different intensities ranging from 25 to 60 dB SPL in steps of 5 dB SPL, from one of four positions (±16° and ±68°). BBNBs were repeated five times for each position, giving a total of 20 presentations. The same procedure was repeated for moving stimuli. The BBNBs were delivered randomly from four different trajectories on the sound perimeter. None of the subjects reported hearing a stimulus presented within 25–60 dB SPL.

Baseline performance

Binaural listening

Fixed sound source condition. Pointing accuracy was determined by calculating the absolute errors (in degrees of arc) between the perceived and actual target positions. The means and standard deviations of the errors obtained for each spatial position ([±5°, ±16°, ±26°, ±37°, ±47°, ±58°, ±68° and ±78°]) were computed for all subjects. The error scores were averaged for the four pericentral positions ([±5° and ±16°] and the six left and six right positions ([±26°, ±37°, ±47°, ±58°, ±68° and ±78°]). The error scores, grouped according to their right, left or pericentral positions, were then submitted to ANOVA with group (acallosal subjects and control subjects) as the between-subjects variable and position (left, pericentral, right) as the within-subject variable. The analysis revealed a main effect of only position [F(2,63) = 13.42, P < 0.001]; all subjects performed more accurately in the centre of the auditory field than in the lateral fields (Fig. 1).

No group effect was observed. Figure 2 illustrates the correspondence between each target position and the pointing responses for the control subjects, the acallosal subjects and the callosotomized subject. The performance of all subjects was quite accurate at each location tested, particularly for the pericentral positions. The variability of performance for all groups is also illustrated in Fig. 2 (bar at each data point). The three groups of subjects were essentially comparable in terms of their variability.

Moving sound source condition. Here, the error scores were evaluated by computing the absolute difference (in degrees of arc) between the perceived and actual beginning and end of the sound trajectory. A mean error score was then calculated by a simple formula: |sum error beginning| + |sum error end|/number of trials. This error score was computed for each of the three trajectories (10°, 32° or 52°) in each field (left and right hemispheres and pericentral field).

Results

Preliminary analyses

Because of the high number of factors, four preliminary ANOVAs (analyses of variance) were conducted to determine whether subjects displayed different levels of performance when using their right versus left hand. These analyses were performed separately for each of the two conditions (fixed and moving sound sources) in each experiment. Moreover, in order to maintain the homogeneity of the experimental group, the callosotomized subject was not included in these analyses.

The mean error scores obtained in the binaural condition using a fixed sound source were submitted to ANOVA with group (acallosal subjects and control subjects) as the between-subjects variable and hand (left and right) as the within-subject variable. The analysis revealed no effect of hand [F(1,134) = 0.4097, P > 0.05]; all subjects performed equally well with either hand. The mean error scores of the monaural experiment were also submitted to ANOVA with group (acallosal subjects and control subjects) as the between-subjects variable and condition (LEO and REO) and hand (left and right) as within-subject variables. No significant main effect of hand was revealed for either group [F(1,268) = 0.0462, P > 0.05]. Similarly, no hand effect was observed in the moving sound source experiments [binaural, F(1,428) = 0.0801, P > 0.05; monaural, F(1,856) = 0.3658, P > 0.05]. Therefore, the data for both hands in both the binaural and the monaural condition were pooled for the analysis.

Fig. 1 Mean error scores of the experimental and control groups in each field (left, pericentral (P-C) and right) in the binaural condition using a stationary sound source.
The individual results were pooled according to the trajectories and the distances covered by the moving sound. Figure 3 reports these results for the control subjects and for the acallosal subjects. Their mean error scores were submitted to ANOVA with group (control subjects and acallosal subjects) as the between-subjects variable and position (left, pericentral, right) and distance (10°, 32°, 52°) as within-subject variables. The analysis revealed a main effect of group \( F(1,189) = 16.62, P < 0.0001 \); overall, the acallosal subjects were less accurate than the control subjects. A main effect of position was also revealed \( F(2,189) = 33.98, P < 0.0001 \); all subjects were more efficient in the pericentral field than in the periphery. Furthermore, a main effect of distance was revealed \( F(2,189) = 26.66, P < 0.0001 \); all subjects performed better with sounds travelling over shorter distances.

The mean trajectories of acallosal subjects, the callosotomized subject and the control subjects in the binaural moving sound condition are illustrated in Fig. 4. The total estimated trajectory was examined to determine whether the subjects manifested hypo- or hypermetric performance as well as expansion or constriction of the trajectory. The mean trajectory of the control subjects was relatively accurate. There was only a slight expansion for the shortest trajectories in both the pericentral and lateral fields (Fig. 4A). Inspection of Fig. 4B shows that the acallosal subjects had a tendency to localize the lateral trajectories near the central field compared with the callosotomized subject and the control subjects. Moreover, as shown in Table 1, the callosotomized subject was more variable in his performance than the control subjects, especially in the lateral fields.

Monaural listening

**Fixed sound source condition.** The pooled error scores of each group are shown in Fig. 5 for each position and listening condition (LEO or REO). These scores were submitted to ANOVA with group (acallosal subjects and control subjects) as the between-subjects variable and condition (LEO and REO) and position (left, pericentral, right) as the within-subject variable. The analysis yielded a main effect of position \( F(2,126) = 15.61, P < 0.0001 \) for all conditions,
revealing that all subjects localized the sound sources more accurately in the field ipsilateral to the unplugged ear than in the pericentral field, and more accurately in the pericentral field than in the field contralateral to the functional ear. The analysis further showed a significant group x position x condition interaction \([F(2,126) = 14.73, P < 0.0001]\). Post hoc comparisons revealed that the performance of the acallosal subjects was superior to that of the control subjects in the pericentral field in the LEO condition \((F = 5.441, P < 0.05)\) and in the REO condition \((F = 10, P < 0.01)\). Furthermore, acallosal subjects performed more accurately than control subjects for positions contralateral to the functional ear in the LEO condition \((F = 22.962, P < 0.001)\) and in the REO condition \((F = 39.896, P < 0.01)\).

Figure 6 illustrates how control subjects and acallosal subjects localized the sound sources. Of particular interest is their performance in localizing the sounds coming from the field contralateral to the functional ear. It can be noted that both control subjects and acallosal subjects showed a positional bias in favour of the unobstructed ear when localizing a sound presented on the side of the obstructed ear (Fig. 6A–D). However, the acallosal subjects were more accurate than the control subjects in localizing sounds on the side of the functional ear. The callosotomized subject showed no systematic directional bias, as he pointed to the appropriate side even when the sound was delivered in the field ipsilateral to the obstructed ear.

Figure 6 also shows the variability of performance for all groups (bars at data points). As shown in this figure, the acallosal subjects showed greater variability, particularly when they localized sounds in the field contralateral to the functional ear. This pattern is attributable to the fact that, unlike control subjects, some acallosal subjects did not consistently show a directional bias towards the functional ear. The performance of two acallosal subjects (S.Pe. and S.Po.) was remarkable. This is shown in Fig. 7, which illustrates that these subjects localized the sounds on the appropriate side even when they were presented on the side of the obstructed ear. The early-callosotomized subject (E.-C.) was also able to perceive the sound arriving from the side of the obstructed ear, although less accurately in the hemifield contralateral to his epileptic focus, i.e. when the right ear was obstructed.

Moving sound source condition. As in the binaural experiment, the mean error scores were submitted to ANOVA with group (control subjects and acallosal subjects) as the between-subjects variable and condition (LEO and REO), position (left, right and pericentral fields) and distance \((10^\circ, 32^\circ, 52^\circ)\) as within-subject variables. The analysis yielded a significant triple group x position x condition interaction \([F(2,378) = 52.39, P < 0.0001]\). Post hoc comparisons revealed that the performance of the control subjects decreased significantly when the moving sound was presented in the pericentral field rather the side ipsilateral to the functional ear. This was true for both conditions, namely LEO \((F = 136.15, P < 0.001)\) and REO \((F = 153.78, P < 0.001)\). By contrast, acallosal subjects performed better than control subjects with presentations in the pericentral field (LEO, \(F = 13.33, P < 0.001\); REO, \(F = 25.76, P < 0.001\)) and in the hemifields ipsilateral to the plugged ear in both the LEO and the REO condition (LEO, \(F = 73.76, P < 0.001\); REO,
Figure 8 illustrates the mean performance of the control subjects, the acallosal subjects and the early-callosotomized subject in the two monaural conditions. In the lateral positions, the control subjects showed a directional bias towards the hemifield ipsilateral to the functional ear for the trajectories presented contralaterally to this ear. This was also true for the acallosal subjects but the directional bias was less marked (Fig. 9A–D). The early-callosotomized subject did not show a directional bias. As in the fixed sound source experiment, however, his performance was less accurate in the hemispace contralateral to his epileptic focus when the right ear was obstructed. In the pericentral field, both the acallosal and the early-callosotomized subjects had better performance than control subjects, showing little directional bias in both listening presentations (Fig. 9C–F).

The variability of the acallosal subjects’ responses is shown in Table 2. This table indicates that the acallosal subjects generally showed more variability than the control subjects in the field ipsilateral to the occluded ear. Again, this pattern can be explained by the fact that, unlike control subjects, the acallosal subjects did not consistently show a directional bias towards the functional ear. The early-callosotomized subject did not show much variability except in the REO condition, especially when he had to localize sounds in the field contralateral to his epileptic focus.

This variability also masks how well the acallosal subjects S.Pe. and S.Po. and the early-callosotomized subject S.D. (E.-C.), who showed no systematic directional bias in the fixed sound source condition (Fig. 7), performed in the moving sound condition. If, instead of presenting the averaged absolute error of the beginning and ending of the trajectory, as shown in Fig. 9, one shows only the proportion of trials in which the subjects pointed for at least one of these end-points to the correct side, including that of the obstructed ear when the sound extended or began in this field, some quite remarkable results are obtained. These are presented in Fig. 10. They demonstrate that these three subjects, unlike the three other acallosal subjects and the control subjects, almost always pointed to the side of the obstructed ear when the sound was presented to this side for at least one of the endpoints.

Discussion
Overall, our results confirm that, in the binaural listening condition, subjects lacking the corpus callosum were as accurate as neurologically intact subjects when localizing fixed sound sources but were less precise when the trajectories of moving sounds had to be localized. Under the monaural listening condition, on the other hand, the performance of the acallosal subjects was superior to that of the control subjects, confirming the hypothesis that reduced access to cortical interaural comparisons, caused by the absence of the corpus callosum, results in more efficient use of monaural cues.

In the baseline binaural experiment, all subjects were more accurate when fixed or moving stimuli were presented centrally than when they were presented in the lateral fields. This finding is in agreement with previous studies in free-field conditions (Oldfield and Parker, 1986; Makous and Middlebrooks, 1990; Poirier et al., 1993).

Generally, the acallosal subjects and the early-callosotomized subject were as accurate as control subjects when they

Table 1

<table>
<thead>
<tr>
<th>Subject group</th>
<th>Position</th>
<th>Left hemifield</th>
<th>Pericentral field</th>
<th>Right hemifield</th>
</tr>
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<tbody>
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<td></td>
<td></td>
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<td>10° 32° 52°</td>
<td>10° 32° 52°</td>
</tr>
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<td>3 2 12</td>
<td>5 6 6</td>
<td>9 5 5</td>
</tr>
<tr>
<td>E.-C.</td>
<td></td>
<td>10 13 12</td>
<td>5 9 13</td>
<td>16 7 23</td>
</tr>
<tr>
<td>Control</td>
<td></td>
<td>7 5 8</td>
<td>5 4 5</td>
<td>9 6 10</td>
</tr>
</tbody>
</table>

E.-C. = early-callosotomized subject.

Fig. 5 Mean error scores of the experimental group (acallosals) and control group in each field [left, pericentral (P-C) and right] and for each condition (LEO = left ear obstructed, REO = right ear obstructed) in the monaural listening conditions with a fixed sound source.
localized a fixed sound source throughout the auditory field. However, this applied only to the localization of a stationary sound source. With moving sound sources, the acallosal subjects and the early-callosotomized subject were less efficient than the control subjects in both the lateral and pericentral fields. The difficulty of the acallosal subjects and the early-callosotomized subject in localizing a moving sound source may reside, in part, in the fact that detecting the location of a stationary source is easier than identifying the trajectories of moving sounds because the latter requires a more detailed analysis of the dynamic interaural differences (e.g. Middlebrooks and Green, 1991) and presumably the
contribution of a cortical component. After studying the localization performance of hemispherectomized subjects, Poirier et al. (1994) suggested that the processing of moving sounds is affected more by the cortical lesion than by the processing of stationary auditory targets. Since the lack of the corpus callosum prevents the interhemispheric integration of cortical interaural cues, a finer analysis of sound cues, such as modulation in amplitude and frequency, may not be possible. This, in turn, could explain why the deficits were greater with a moving than with a fixed sound source. Finally, the poorer performance of acallosal subjects in their lateral and pericentral fields, found both in our study and that of Poirier et al. (1993), suggests that the role of the corpus callosum is not confined to the fusion of the two auditory spaces but that fibres of the corpus callosum may subserve the fine tuning of audiospatial discrimination processes throughout auditory space.

In contrast to the results of some electrophysiological studies carried out in animals, which suggest a preponderant role of the corpus callosum in midline representation (Imig et al., 1986), agenesis of the corpus callosum in our human listeners did not specifically affect sound localization in the central auditory field. This observation may be explained by the fact that the acallosal and the early-callosotomized brain had the possibility early in life of benefiting from cerebral plasticity. Thus, the subjects with early absence of the corpus callosum may have developed compensatory mechanisms involving alternative secondary interhemispheric pathways that may assume the midline representation. The anterior commissure is a likely candidate for this function. The anatomical studies of Pandya and Seltzer (1986) have shown that, in the primate, the superior temporal region sends fibres to the opposite hemisphere through both the anterior commissure and the corpus callosum. However, one of the acallosal subjects (S.Pe.) does not have an anterior commissure, yet his localization abilities in the pericentral field were as good as those of the control subjects. Another potential compensatory mechanism would involve the increased use of ipsilateral pathways, either by anatomical or by functional

![Fig. 7](image_url) Percentage of trials in which the sounds were lateralized correctly in the binaural condition and in each of the monaural conditions when the sound was presented ipsilaterally to the obstructed ear. The subjects of the control group and three acallosal subjects (L.G., M.G. and S.G.) localized the sound with a positional bias; two acallosal subjects (S.Pe. and S.Po.) and the early-callosotomized subject S.D (E.-C.) did not show a systematic directional bias. LEO = left ear obstructed; REO = right ear obstructed.

![Fig. 8](image_url) Mean error scores of the experimental and control groups in each field (left, pericentral (PC) and right) and for each condition (LEO = left ear obstructed; REO = right ear obstructed) in the monaural listening condition using a moving sound source.
accentuation (Dennis, 1976; Jeeves, 1994). In the auditory system, this possibility is even more likely, since there are numerous cross-over points at various subcortical levels.

In the monaural listening condition, the acallosal subjects and the early-callosotomized subject were, on average, more accurate than the control subjects in the pericentral field and in the hemifield contralateral to the functional ear. The pattern of performance was essentially the same whether they localized a fixed or a moving sound source. In fact, the control subjects systematically localized the sounds on the side of the obstructed ear. This result is congruent with previous psychophysical studies that have shown that the introduction of a unilateral earplug in normal subjects results in a prominent lateral displacement of an average of 30.9° towards the side of the open ear (Slattery and Middlebrooks, 1994). However, it was also demonstrated that subjects can learn to increase the precision of their location judgement under monaural listening (Butler, 1987). Javer and Schwarz

Fig. 9 Monaural sound localization performance of the control subjects with the left ear occluded (A) and the right ear occluded (B). Sound localization performance of the acallosal subjects and the early-callosotomized subject when the left ear (C and E, respectively) or the right ear (D and F, respectively) was occluded. Symbols representing estimated trajectories are explained in the caption of Fig. 4.
have investigated whether subjects can adapt their directional hearing in azimuth by altering the interaural time delays. They showed that an introduction of a delay in one ear led to immediate displacement of the perceived sound location towards the opposite side. Within hours of exposure, the displacement was reduced, and further normalization of the perceived localization occurred over several days. Learning and/or brain reorganization may also occur in sensory-handicapped individuals. Thus, three of the five deaf subjects studied by Slattery and Middlebrooks (1994) showed little or no localization bias towards the functional ear. The fact that they were able to localize sounds over a much greater range of azimuth implies the development of strategies for monaural sound localization. Similar results have been obtained from some blind human subjects (Lessard et al., 1998). They, too, were able to localize sound sources on the side of the plugged ear without showing a directional bias.

A similar pattern of performance was seen in our sample of acallosal subjects. It is thus possible that the acallosal subjects and the early-callosotomized subject have compensated for the reduction of interaural disparities of the two hemispheres by developing greater efficiency in using monaural cues. This pattern of performance was not observed in normal subjects, presumably because they use predominantly interaural com-

### Table 2

<table>
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<tr>
<th>Subject group</th>
<th>Position</th>
<th>Left hemiﬁeld</th>
<th>10°</th>
<th>32°</th>
<th>52°</th>
<th>Pericentral ﬁeld</th>
<th>10°</th>
<th>32°</th>
<th>52°</th>
<th>Right hemiﬁeld</th>
<th>10°</th>
<th>32°</th>
<th>52°</th>
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<tr>
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<td></td>
<td>95 92 85</td>
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<td>16</td>
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<td>12</td>
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<td>10</td>
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<tr>
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<td></td>
<td>14 9 9</td>
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<td>18</td>
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<tr>
<td>REO Acallosal</td>
<td></td>
<td>7  17 7</td>
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<tr>
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LEO = left ear obstructed; REO = right ear obstructed; E.-C. = early-callosotomized subject.

### Fig. 10

Percentage of trials in which the sounds were lateralized in the appropriate hemiﬁeld for at least one of the end-points of the trajectories in the binaural condition and in each of the monaural conditions when the sound was presented ipsilaterally to the obstructed ear. The subjects of the control group and three acallosal subjects (L.G., M.G. and S.G.) localized the sounds with a positional bias. Two acallosal subjects (S.Pe. and S.Po.) and the early-callosotomized subject S.D. (E.-C.) did not show a systematic directional bias in that they localized at least one of the end-points in the correct hemiﬁeld.
parisons for interaural time delay and interval intensity difference, including the additional binaural integration provided by the corpus callosum. As several authors have pointed out, in normal subjects, monaural cues for sound localization in the horizontal plane have retained their subordinate role (Searle et al., 1976; Butler and Flannery, 1980; Flannery and Butler, 1981; Martin and Webster, 1987; Humanski and Butler, 1988; Musicant et al., 1990), thereby creating a systematic directional error towards the functional ear for positions situated on the side of the plugged ear. Our data suggest that the absence of the corpus callosum increases the capacity of each hemisphere to analyse those monaural cues, perhaps through the accrued contribution of the ipsilateral pathway. In fact, two of the five acallosal subjects and the early-callosotomized subject were quite exceptional as they localized the sounds on the appropriate side even when they were presented on the side of the obstructed ear. The independence of each hemisphere in the absence of the corpus callosum could increase their capacity to use monaural spectral cues more effectively.

The auditory system has numerous cross-over points at various subcortical levels, and sound localization cues are partially processed at these levels (Altman, 1968; Altman et al., 1970; Sovijärvi and Hyvärinen, 1974; Bechterev et al., 1975; Rauschecker and Harris, 1989; Spitzer and Semple, 1991; Stumpf et al., 1992; Toronchuk et al., 1992). Such subcortical crossings include the collicular and thalamic commissures, which are known to be involved in the analysis of spectral cues. Indeed, several free-field studies in animals have demonstrated that auditory space is represented within the deep layers of the superior colliculus (Gordon, 1973; Updyke, 1974; Dräger and Hubel, 1975; Tiao and Blakemore, 1976; Chalupa and Rhoades, 1977; Harris et al., 1980). Furthermore, King (1993) and Middlebrooks and Knudsen (1984) have shown that, consistent with a monaural map of auditory space, cells of the superior colliculus are more sensitive to stimuli with a spectral composition. It is conceivable that the congenital absence of the corpus callosum results in increased interaction between subcortical and cortical structures to allow maximal use of spectral information, thus providing better localization abilities under monaural listening conditions.

Although an increased contribution of subcortical input may be invoked to account for the compensation observed in the acallosal subject and the early-callosotomized subjects, the contribution of a cortical component cannot be entirely ruled out. Indeed, cortical involvement in monaural processing is suggested by the incidental finding of poorer localization performance in the hemifield contralateral to the epileptic focus in the split-brain subject. The early-callosotomized subject S.D., whose epileptic focus is clearly lateralized to the left hemisphere, displayed a more erratic performance in the right hemispace when the left hemisphere did not receive a direct contralateral stimulation from the right ear. These findings attest to the important role played by individual experience in developing strategies to localize a sound source through reinforcement of the available pathways in the sensory-deprived or brain-lesioned individual.

In conclusion, our findings suggest that acallosal and early-callosotomized subjects compensate for reduced access to cortical binaural comparisons by making increased use of monaural cues. As several authors (Lassonde et al., 1991; Jeeves, 1994) have pointed out, acallosal subjects, as well as patients who have undergone callosotomy early in life, seem to have access to a number of compensatory mechanisms, the effectiveness of which depends on the extent to which they are used. The results of the present study indicate that monaural cues can provide useful information for sound localization in the horizontal plane, and that the use of these cues can be enhanced functionally or/and anatomically by individuals who do not benefit from interhemispheric integration due to callosal pathology.

Acknowledgements

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