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Research Report

Sound lateralization in subjects with callosotomy, callosal agenesis, or hemispherectomy

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Abstract

The question of whether there is a right-hemisphere dominance in the processing of auditory spatial information in human cortex as well as the role of the corpus callosum in spatial hearing functions is still a matter of debate. Here, we approached this issue by investigating two late-callosotomized subjects and one subject with agenesis of the corpus callosum, using a task of sound lateralization with variable interaural time differences. For comparison, three subjects with left or right hemispherectomy were also tested by employing identical methods. Besides a significant reduction in their acuity, subjects with total or partial section of the corpus callosum exhibited a considerable leftward bias of sound lateralization compared to normal controls. No such bias was found in the subject with callosal agenesis, but merely a marginal reduction of general acuity. Also, one subject with complete resection of the left cerebral cortex showed virtually normal performance, whereas another subject with left hemispherectomy and one subject with right hemispherectomy exhibited severe deficits, with almost total loss of sound-lateralization ability. The results obtained in subjects with callosotomy indicate that the integrity of the corpus callosum is not indispensable for preservation of sound-lateralization ability. On the other hand, transcallosal interhemispheric transfer of auditory information obviously plays a significant role in spatial hearing functions that depend on binaural cues. Moreover, these data are compatible with the general view of a dominance of the right cortical hemisphere in auditory space perception.
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Theme: Neural basis of behavior
Topic: Cognition

Keywords: Auditory localization; Spatial hearing; Hemispheric asymmetry; Corpus callosum; Space perception; Human

1. Introduction

Sound localization is mainly based on processing of interaural differences in time and sound-pressure level. The auditory system is thus organized bilaterally, with a large number of interconnections between the two halves of the brain, and sound stimuli originating in the left and right hemispaces are processed in the primary auditory cortices of both hemispheres. Despite this pronounced bilaterality of the auditory system, a preference exists, at least at

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Abbreviations: AMP, auditory median plane; ANOVA, analysis of variance; CAG, callosal agenesis; CC, corpus callosum; CTO, callosotomy; EEG, electroencephalography; ITD, interaural time difference; JND, just noticeable difference; LHE, left hemispherectomy; LI, laterality index; RHE, right hemispherectomy; SE, standard error of the mean

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cortical level, for processing of contralateral sound. In animals, neurons in primary auditory cortex are preferentially sensitive to contralateral sound, and unilateral lesions including the primary auditory cortex induce more severe deficits for sound localization in contralateral hemispace [22,30,46]. Also, neuroimaging studies have revealed increased activations of the human auditory cortex with contralateral monaural sound [60] or virtual spatial sound from contralateral hemispace [45]. Finally, less accurate auditory localization in contralesional hemispace has been obtained in patients with unilateral cortical damage [49,63].

In humans, this pattern of incomplete contralaterality seems to be asymmetrical, with a dominant role of the right cortical hemisphere. Sound localization seems to be more accurate in the left than in the right hemispace [7], and neuroimaging studies have shown several areas to be more strongly activated in the right cortical hemisphere during sound-localization or lateralization tasks [1,8,16,18,29, 31,39,44,58,64,66]. Also, deficits in sound-localization precision after lesions in the right hemisphere are generally reported to be more severe [53–55,61,62,65].

Auditory cortical areas of both hemispheres are interconnected via the fibers of the corpus callosum (CC). In cats, these fibers have been shown to convey auditory spatial information [27,28,50]. The question thus arises as to how much this interhemispheric transfer participates in the emergence of the asymmetric contralaterality pattern described above. Poirer et al. [48] and Lessard et al. [35] found almost normal performance in sound localization, measured through pointing, in six acallosal subjects and one early-callosotomized subject, without significant left/right asymmetries. These data need not imply functional insignificance of the CC in spatial hearing, however, but might instead indicate long-term compensatory plasticity. In order to further elucidate the role of the CC in auditory space perception, we tested two subjects with late callosotomy, using a simple task of sound lateralization that involved neither motor nor higher-order cognitive performance. For comparison, we also included one subject with callosal agenesis, three subjects with left or right hemispherectomy, and 20 healthy controls.

2. Materials and methods

2.1. Subjects with callosotomy

D.D.V. is a 40-year-old man who had his second operation, completing the full callosotomy for the relief of a generalized multifocal epilepsy, at the age of 30 years. Magnetic-resonance-imaging (MRI) scans of D.D.V., showing the extent of callosal resections, are available in Fabri et al. [15] (Fig. 2B, inset). Moreover, D.D.V. had a lesion in the first frontal circonvolution of the right hemisphere and a small lesion in the right medial parietal cortex, which probably resulted from the callosotomy surgery. Epileptogenic lesions in the left hemisphere were not detectable. D.D.V. is right-handed and has a Wechsler Adult Intelligence Scale III (WAIS III [57]) Full Scale IQ of 81. Previous experimental studies revealed that D.D.V. neglects visual stimuli in the left hemifield, which was manifest in line bisection [19] and reaction time to stimuli flashed in the left visual field [12]. These studies suggested a left-hemispheric control of attention restricted to the right side of space. A recent case study, however, described D.D.V.'s hemineglect as unusual, because his neglect was not evident when he responded by pointing to or touching the locations of the stimuli, probably because these responses were controlled by the dorsal rather than the ventral visual system [13]. Besides his manifestation of neglect, D.D.V. showed evidence of functional disconnection typical of split brain subjects, including prolonged interhemispheric transfer times, enhanced redundancy gain in simple reaction time to bilateral stimuli, and an inability to match visual stimuli across hemifields [13].

G.S. is a 44-year-old woman who has a complex partial epilepsy with secondary generalization, and a focal EEG in the right hemisphere. G.S. had undergone partial callosotomy when she was 26 years of age. The partial resection of the corpus callosum comprises the anterior 4/5, sparing the splenium. A computerized-tomography scan (CT) of G.S. is shown in Fig. 2A (inset). Moreover, CT scans in G.S. revealed a marked cranial asymmetry, indicating a larger left hemisphere. GS has a frontal lesion in the right hemisphere, which may be a result of the callosotomy surgery. She is right-handed and has an IQ in the normal range, with a WAIS III Full Scale IQ of 99 (Verbal IQ: 82; Performance IQ: 122). Both these subjects (with callosotomy) were chronically treated with antiepileptic medication. GS has not previously participated in experimental studies.

2.2. Subject with callosal agenesis

J.P. is a right-handed woman who was 37 years old at the time of testing. She was diagnosed by computerized-tomography scan with agenesis of the corpus callosum at the age of 31 years after presentation with major depression, recurrent migraines, and some left-sided weakness. No other abnormalities were found on this scan, and an electroencephalography (EEG) recording proved to be normal. An MRI scan taken a year later confirmed the diagnosis of callosal agenesis, and her anterior commissure was estimated from the scan to be 28 mm^2 in cross section (see [3]; Fig. 2C, inset). This is at least 3 times the normal area [2,14,41]. Her WAIS III scores were in the borderline-extremely low range, with Full Scale IQ of 66 (Verbal IQ: 66; Performance IQ: 74). Despite these low scores, she presented normally during experimental testing sessions, as in previous studies [3,4], and lives independently in the community with her husband of 10 years.

2.3. Subjects with hemispherectomy

S.F. is a 36-year-old man who was born with Sturge–Weber Syndrome. At about 6 months, it was noticed that he did not use his right arm and leg as much as the left, and at 6.5 months, he had his first seizure. These continued with variable frequency of none to seven seizures per day. Additionally, he showed a progressive right hemiparesis. At the age of 8 months, he had a severe right hemiplegia. Movements of the right leg were normal but still more limited than those of the left leg, and reflexes were abnormally brisk. At the age of 10 months, a hemispherectomy was recommended and carried out. The cortex of the left hemisphere was found to have some degree of atrophy. The whole left cortex was removed leaving the thalamus and basal ganglia intact. Postoperative recovery was good. S.F.'s seizures ceased entirely until the age of 5 when he had some petit mal attacks, and was put on anticonvulsive medication. When he was 17, his Full Scale IQ was 64–75, his Verbal IQ was 74–82, and his Performance IQ was 60–70. Currently, S.F. has been seizure-free for over 15 years and EEG recording in 1995 showed normal right-sided background activity during walking and attenuation of all left-sided frequencies.

M.J. is a 43-year-old woman who was admitted to surgery at the age of 8 years because of intractable epilepsy. She was diagnosed with hemiplegia at 8 months and, throughout childhood, her seizures continued despite frequent changes of anticonvulsant medication. Psychological assessments during this period revealed progressive mental and behavioral deterioration. Air encephalography revealed gross atrophy of the left cerebral hemisphere with midline displacement. Occlusion of the middle cerebral artery was considered to be the original source of the damage. The entire left cerebral cortex was removed during the procedure, including the temporal structures and hippocampus. At 2 months follow up, her physical condition was good and her behavior had improved significantly. The intellectual decline was halted and almost 2 years after the operation, her Verbal IQ was 79, Performance IQ 65, and Full Scale IQ 70. When she was 30 years old, M.J. had further assessment for possible return of petit mal seizures. EEG recordings showed frequent epileptiform activity in the left central region as well as a disturbance of background activity in the same region. M.J. was put on anticonvulsive medication with good results. Both absences and tonic spasms disappeared, and there was an improvement in memory and thinking.

B.P. is a 45-year-old man who was born with Sturge–Weber Syndrome. Left hemiplegia was apparent directly after birth, and from the age of 2 months, he began having mild convulsions, which were medically well controlled. Grand mal seizures began when he was 5 or 6 years old and were not controlled by medication. An air encephalogram was performed when he was 7 years and revealed atrophy of the right hemisphere. A hemispherectomy was performed when he was 9 years old. Pathology revealed atrophy of the cortex and angiomatosis of the surface of the brain. Following the operation, he was seizure-free for 5 years and since then he has had some petit mal attacks which are well controlled by medication. He still has occasional mild seizures that are triggered by stress. He has no use of his left hand and has no vision in his right eye because the retina is affected by the increased vascularization of the Sturge–Weber Syndrome.

Further details on these three subjects with hemispherectomy are available in Hausmann et al. [20].

2.4. Normal controls

Twenty right-handed subjects (10 females and 10 males), ranging in age from 34 to 49 years (mean 41.3 years, SE 4.4 years), participated in the study as normal controls. These control subjects were recruited and tested at the Faculty of Psychology, University of Bochum, and at the Leibniz Research Centre for Working Environment and Human Factors, Dortmund.

2.5. Procedure

Prior to the beginning of the main experiment, all subjects were tested for hearing loss. For this purpose, monaural pure-tone stimuli (duration 100 ms) with a frequency of 1 kHz (which was the stimulus frequency used in the main experiment) were delivered to the subjects' ears at various sound-pressure levels (range 10–80 dB re 20 μPa; equipment as described below). The hearing thresholds for each ear of each of the subjects with callosotomy (CTO), callosal agenesis (CAG), left hemispherectomy (LHE), and right hemispherectomy (RHE) did not differ from those in normal controls ($F_{1,19} < 2.406$, $P > 0.137$).

In the main experiment, sound lateralization was tested using tone bursts (frequency 1 kHz) with triangular envelopes (duration 20 ms; rise/fall time 10 ms). The stimuli were presented to the subject via supra-aural headphones (TDH-39P, Telephonics, Farmingdale, NY). The peak sound-pressure level was calibrated to 80 dB re 20 μPa. Interaural time differences (ITDs) for the sound stimuli were varied between trials following a quasi-random order over a range from −362.8 μs (sound leading in time at the left ear) to +362.8 μs (leading at the right ear), in steps of 45.4 μs. These stimuli usually evoke an intracranial sound image, along the line joining the ears [6], and shifts of the sound image with respect to the median plane of the head can be easily detected by normal subjects, even if the changes of interaural differences are very small (see Section 3.1.; e.g., [38]). Under conditions of an acoustic free field, the maximum ITDs presented here occur at sound azimuths of about 30° to the left or right of the median plane [6]. Subjects were instructed to make a two-alternative ("left" or "right") choice on the perceived position of the sound with respect to the median plane of the head. Immediately after presentation of each stimulus, the CTO, CAG, LHE, and RHE subjects reported their judgments verbally. The subjects' responses were recorded by the experimenter. To make sure that verbal responses coincided with the corresponding side, CTO, CAG, LHE, and RHE subjects were asked (after completion of about 50 trials) to simultaneously point with their preferred hand to the side where the sound appeared. Because of their hemiplegia, hemispherectomized subjects used the hand ipsilateral to the removed cortical hemisphere. In no case did we observe inconsistencies between the two types of response, and none of the subjects had any difficulty in performing this task. In the vast majority of the trials, all subjects responded immediately after stimulus presentation. All subjects were asked to indicate when they were uncertain with their response, and when they did so the trial was repeated. This procedure was conducted in order to prevent any tendency of the subject to prefer either "left" or "right"' judgments.

Since the sound-lateralization task is quite easy to perform by healthy subjects, one modification was introduced for the control group: subjects indicated their judgments without a verbal response, by merely pressing a "left" or "right" key, and responses were recorded automatically by a custom-written computer program. There was no time pressure to respond. A minimum of 20 practice trials was conducted prior to data collection. The experimental session was composed of 136 trials (8 presentations of each ITD) and lasted about 15–20 min. Experiments were conducted in illuminated rooms.

2.6. Data analysis

As in previous studies [38], the subjects' judgments were determined as a function of ITD and data were fitted to the sigmoid equation

$$f = 100\Big/\left(1 + e^{-k(\mathrm{ITD}-\mathrm{AMP})}\right)$$

where f is the frequency of judgments "right", given as a percentage; the AMP (auditory median plane) is that ITD where f is 50%; k is the slope of the function at 50%; e the base of the natural logarithm. The maximum-likelihood fit was performed using standard software (SigmaPlot 2001, SPSS Inc., Chicago, IL). Various parameters, derived from the fit, were used to describe different aspects of the subjects' performance. (1) The AMP value was used as a measure for systematic shifts in sound lateralization. Negative AMPs indicate the tendency that a sound presented without interaural difference (ITD = 0) appeared to the right of the median plane, positive AMPs indicate a bias to the left. (2) The ITD required for subjects to judge the correct laterality of the stimulus in 75% of the trials (that is, half the difference between the ITDs with 25% and 75% of the judgments "right" [42]) was defined as the just noticeable difference (JND). The JND can be regarded as a measure for the subjects' acuity of sound lateralization. It was calculated from the slope (k) of the sigmoid function by using the equation JND = $1.099/k$, which is a simplified derivation from the sigmoid equation shown above. (3) The coefficient of determination (R^2), indicating the goodness of the fit, was used as a measure of the precision of the subjects' judgments. (4) Finally, the overall numbers of correct responses were analyzed separately for negative (correct response "left") and positive ITDs (correct response "right"). From these data, a laterality index (LI) was calculated by using the equation

$$\mathrm{LI} = (N_\mathrm{R} - N_\mathrm{L})/0.5(N_\mathrm{R} + N_\mathrm{L})$$

where N_L is the number of correct responses obtained with negative ITDs and N_R the number of correct responses obtained with positive ITDs (judgments on stimuli with ITD = 0 were not considered in this analysis). A positive value of LI thus indicates more accurate performance with sounds leading at the right ear, and a negative LI indicates higher accuracy with sounds leading at the left ear (cf., e.g., [36]).

In order to compare data obtained in the CTO, CAG, LHE, or RHE subjects with those of the normal control group, we treated each of these six subjects as a separate group, with error terms taken from analysis of the 20 controls. Statistical comparisons were made separately for each of the parameters mentioned above, using one-factor analyses of variance (ANOVA) with group as factor.

This study conformed to the Code of Ethics of the World Medical Association (Declaration of Helsinki), printed in the British Medical Journal (18 July 1964). All subjects gave their informed consent to participate in the study, which was approved by the Ethical Committee of the University Medical School and General Hospital of Ancona and by the Human Participants Ethics Committee of the University of Auckland.

3. Results

3.1. Normal controls

The judgments of each of the control subjects could be perfectly fitted to a sigmoidal function (mean R^2 = 0.990, range 0.953–1.000; Fig. 1). The mean JND was 27.2 μs (SE 3.0 μs), which approximately equals the JND observed previously using the same stimulus in a sample of younger normal subjects [38]. The mean AMP exhibited only an insignificant tendency to be shifted to the left (−8.6 μs, SE 7.7 μs; t_{19} = 1.111, P = 0.28). In accordance with that, the mean percentage of correct responses to negative ITDs (95.3%, SE 0.9%) did not differ from that to positive ITDs (97.0%, SE 0.8%; t_{19} = 1.188, P = 0.25), with a mean LI that was virtually zero (0.018, SE 0.015).

3.2. Subjects with callosotomy

For each of the two subjects with CTO (G.S., D.D.V.), the fit of the data to a sigmoidal function was highly significant ($P < 0.0001$), indicating a general ability to lateralize sounds

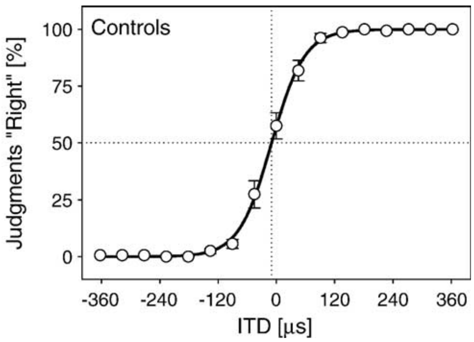

Fig. 1. Sound lateralization in normal control subjects. The frequency of the judgments "right" is plotted as a function of the interaural time difference (ITD) of the acoustic stimulus. The mean values across subjects (symbols, ±SE) were fitted to a sigmoid equation (solid line; $R^2 = 1.000$, $P < 0.0001$). The ITD at the 50% level of the fitted function (indicated by the intersection of the dotted lines) was defined as the auditory median plane. Negative values of ITD indicate sound stimuli leading in time at the left ear, positive values stimuli leading at the right ear.

(Figs. 2A, B). The coefficients of determination for the fit were, on the other hand, significantly lower than in the control group (G.S.: $R^2 = 0.835$, $F_{1,19} = 174.10$, $P < 0.0001$; D.D.V.: $R^2 = 0.874$, $F_{1,19} = 97.53$, $P < 0.0001$), thus suggesting reduced precision of judgment. Also, in both of the CTO subjects, the JNDs for the detection of ITDs were significantly larger than those found in the controls (G.S.: 90.3 µs, $F_{1,19} = 21.80$, $P < 0.0001$; D.D.V.: 101.8 µs, $F_{1,19} = 30.40$, $P < 0.0001$; Fig. 4A).

In addition to this general reduction of the acuity of sound lateralization, in both CTO subjects, we found a considerable systematic error of ITD perception to the left: the AMP was shifted to the right by +81.2 µs in G.S. and +144.6 µs in D.D.V., and these deviations differed significantly from those in the control group (G.S.: $F_{1,19} = 6.44$, $P = 0.020$; D.D.V.: $F_{1,19} = 18.76$, $P = 0.0004$; Fig. 4B). The percentage of correct responses to negative ITDs did not differ from that of normal controls (G.S.: 96.9%, $F_{1,19} = 0.13$, $P = 0.72$; D.D.V.: 100.0%, $F_{1,19} = 1.20$, $P = 0.29$), whereas positive ITDs were judged significantly less accurately (G.S.: 73.4%, $F_{1,19} = 44.90$, $P < 0.0001$; D.D.V.: 60.9%, $F_{1,19} = 105.20$, $P < 0.0001$; Fig. 5A). The resulting LIs showed a significant bias to the left relative to those in the controls (G.S.: −0.274, $F_{1,19} = 17.49$, $P = 0.0005$; D.D.V.: −0.481, $F_{1,19} = 51.52$, $P < 0.0001$; Fig. 5B), as was already evident from the analysis of the AMP described above.

3.3. Subject with callosal agenesis

As in the subjects with CTO, the fit of the data of the subject with CAG (J.P.) to a sigmoid function was highly significant ($P < 0.0001$; Fig. 2C). The coefficient of determination for the fit was only slightly, but still significantly, reduced compared with the control group ($R^2 = 0.929$, $F_{1,19} = 26.99$, $P < 0.0001$). Moreover, the JND of J.P. significantly exceeded those of controls (66.7 µs, $F_{1,19} = 8.52$, $P = 0.008$), indicating lower general acuity of sound localization (Fig. 4A). AMP (+12.4 µs, $F_{1,19} = 0.353$, $P = 0.56$), numbers of correct responses to negative (90.6%, $F_{1,19} = 1.20$, $P = 0.29$) and positive ITDs (90.6%,

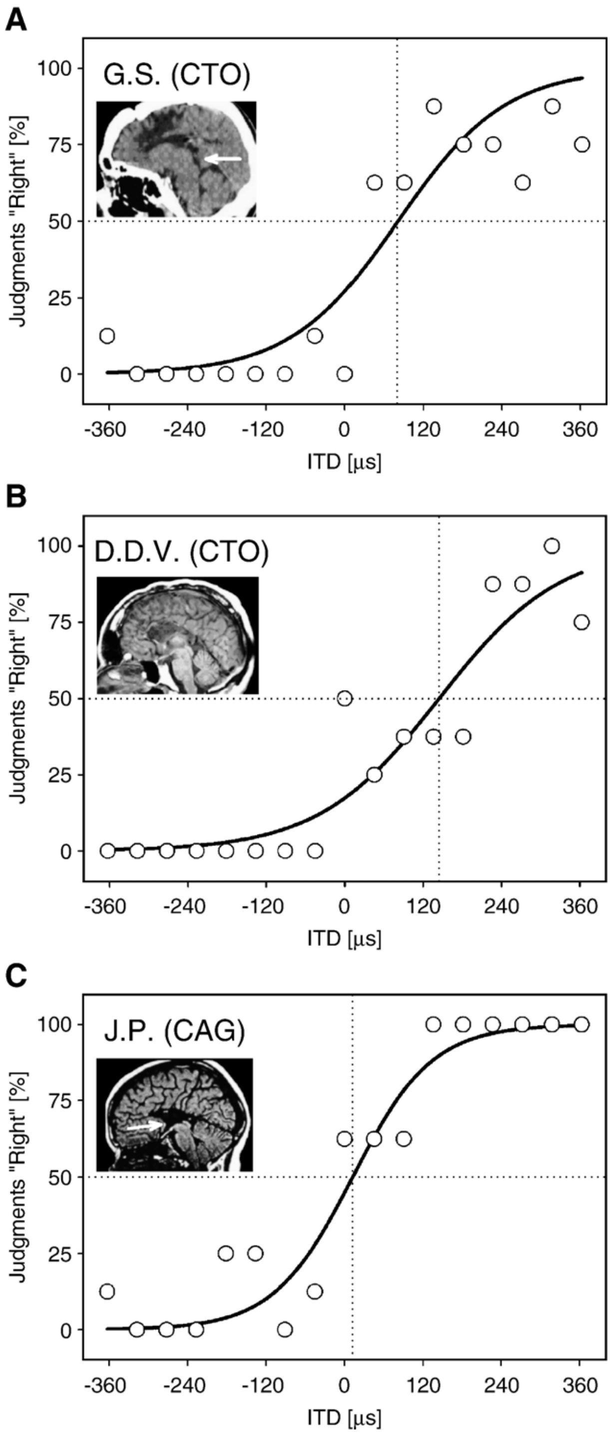

Fig. 2. Sound lateralization in subjects with callosotomy (CTO; A, B) and agenesis of the corpus callosum (CAG; C). Parameters and conventions are as in Fig. 1. Insets show computerized-tomography (A) or MRI scans (B, C) of the subjects. The arrow in panel A indicates the preserved posterior part of the corpus callosum of subject G.S. The arrow in panel C indicates the anterior commissure of subject J.P.

$F_{1,19} = 3.31$, $P = 0.085$), and LI of J.P. (0.000, $F_{1,19} = 0.07$, $P = 0.80$) did not differ from those obtained in normal controls (Figs. 4B and 5A, B).

3.4. Subjects with left hemispherectomy

The results of one subject with LHE (S.F.) differed only marginally from those of the control group (Fig. 3A). The goodness of the fit of the data to a sigmoidal function ($P <$ 0.0001) was as high as in the controls ($R^2 = 0.993$; $F_{1,19} = 0.06$, $P < 0.80$), and the same held true for the JND (24.9 µs, $F_{1,19} = 0.03$, $P = 0.87$; Fig. 4A). As can be seen in Figs. 3A and 4B, there was a shift of the AMP to the right, which remained only slightly below the level of statistical significance when compared with control data (+60.9 µs, $F_{1,19} = 3.87$, $P = 0.064$). However, the number of correct responses to positive ITDs was significantly lower than in controls (89.1%, $F_{1,19} = 5.13$, $P = 0.035$), while no difference was obtained for negative ITDs (98.4%, $F_{1,19} = 0.53$, $P = 0.47$; Fig. 5A). As with the AMP, the resulting LI indicated, on the other hand, a nonsignificant tendency to the left (−0.099; $F_{1,19} = 2.84$, $P = 0.11$; Fig. 5B).

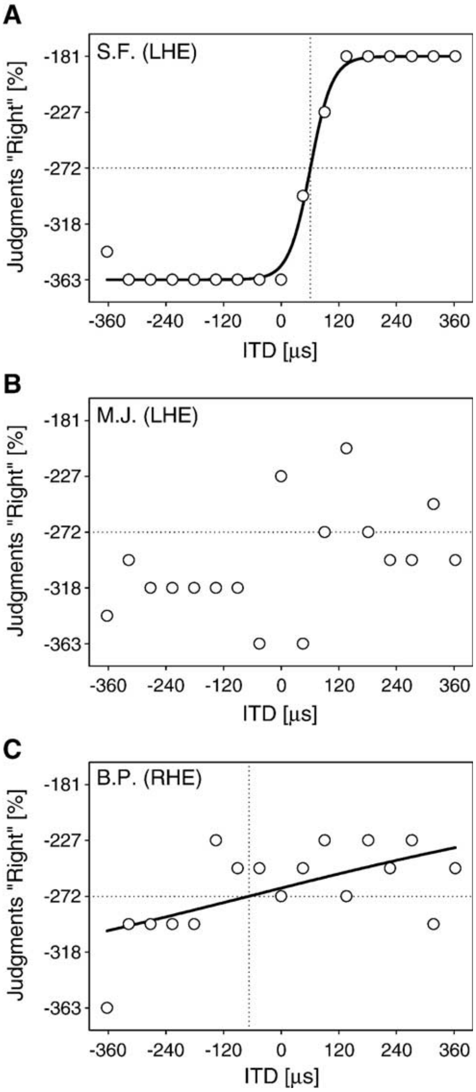

Fig. 3. Sound lateralization in subjects with left (LHE; A, B) and right hemispherectomy (RHE; C). Parameters and conventions are as in Fig. 1. In subject M.J., the fit of the data to a sigmoid equation was nonsignificant.

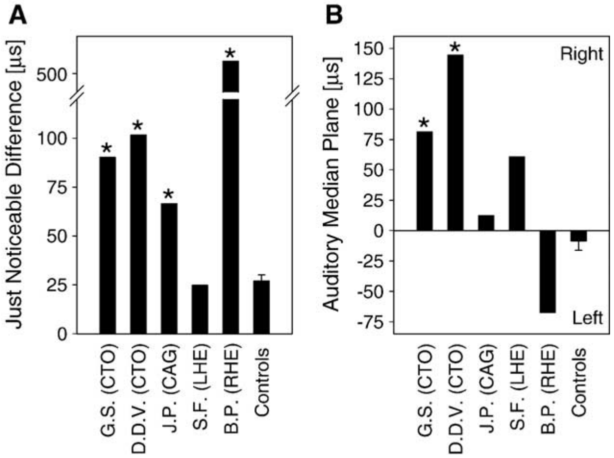

Fig. 4. Just noticeable differences in interaural time (A) and positions of the auditory median plane (B). Individual data for subjects with CTO, CAG, LHE, and RHE (as derived from the sigmoidal functions plotted in Figs. 1 and 2) are shown in comparison with the mean values (±SE) of the control group. Asterisks indicate significant differences from data of controls. Results of M.J. are not shown, since the fit of the data to a sigmoid equation was nonsignificant in this subject.

Unlike all other subjects, the second subject with LHE (M.J.) showed an almost total loss of sound-lateralization ability (Fig. 3B). Her data could not be fitted to a sigmoidal function ($P = 0.22$), and the coefficient of determination was thus significantly below those of controls ($R^2 = 0.196$, $F_{1,19} >$ 1000, $P < 0.0001$). There was merely a weak, but still significant, correlation of the number of judgments and ITD, indicating some residual performance (Spearman rank correlation analysis; $R_s^2 = 0.300$, $P = 0.023$). Both the percentages of correct judgments on negative (78.1%, $F_{1,19} = 16.10$, $P < 0.0001$) and positive ITDs (45.3%, $F_{1,19} = 215.96$, $P < 0.0001$) were significantly lower than those of controls (Fig. 5A). The LI indicated a significant bias to the left with reference to the control group (−0.470; $F_{1,19} = 61.60$, $P <$ 0.0001; Fig. 5B).

3.5. Subject with right hemispherectomy

The subject with RHE (B.P.) showed significant, but substantially reduced, performance in sound lateralization. The statistical significance of the fit of his judgments to a sigmoidal function ($P = 0.049$) was so weak that reliable conclusions based on the AMP (−67.4 µs) and JND values (506.7 µs), derived from the resulting equation, cannot be drawn (Figs. 4A, B). The coefficient of determination for the fit was considerably below those of controls ($R^2 = 0.351$, $F_{1,19} > 1000$, $P < 0.0001$). As is already clear from this analysis, both the percentages of correct responses to negative (56.3%, $F_{1,19} = 83.16$, $P < 0.0001$) and positive

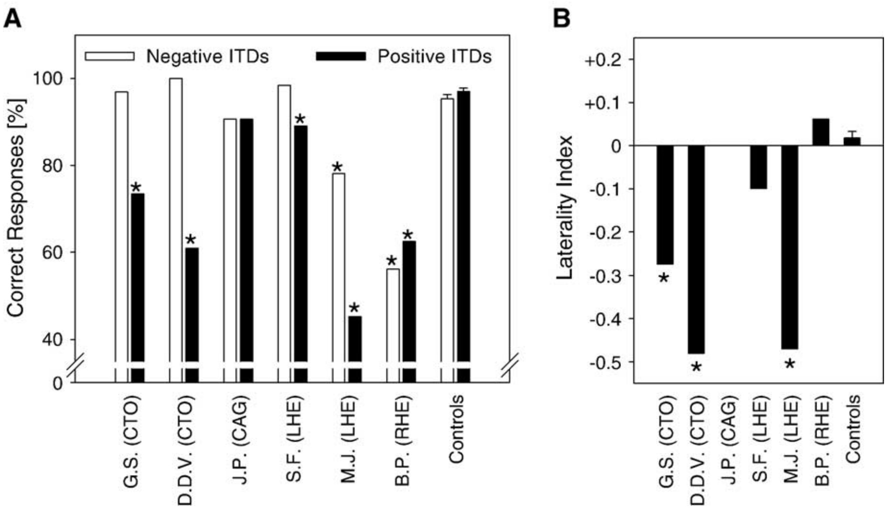

Fig. 5. (A) Percentages of correct judgments on sounds leading in time at the left (negative ITDs; open bars) and right ear (positive ITDs; closed bars). (B) Laterality indices (LIs) derived from the data shown in panel A. Negative LIs indicate a higher percentage of correct judgments on negative than positive ITDs, positive LIs indicate a higher percentage of correct judgments on positive than negative ITDs. Individual results for subjects with CTO, CAG, LHE, and RHE are shown in comparison with the mean values (±SE) of the control group. Asterisks indicate significant differences from controls.

ITDs (62.5%, $F_{1,19} = 96.27$, $P < 0.0001$) lay significantly below the levels found in normal control subjects (Fig. 5A). The LI of B.P., which did not indicate any bias to the left or right, was within the range of controls (+0.062; $F_{1,19} = 1.53$, $P = 0.23$; Fig. 5B).

4. Discussion

The results obtained in the two subjects with CTO demonstrated, besides a significant reduction of precision compared to normal controls, a considerable leftward bias of sound lateralization: sound leading in time at the right ear (positive ITD) was heard in the median plane (Figs. 2A, B), resulting in a rightward shift of AMP. The preserved sound-lateralization ability of these subjects indicates, on the one hand, that the integrity of the CC is not an indispensable prerequisite for spatial hearing. On the other hand, the clear deficits shown suggest that in the normal brain transcallosal transfer of auditory information plays a significant role, at least in the fine-tuning of auditory space perception. Both callosotomized subjects showed a leftward bias in sound lateralization (rightward shift of AMP) that was of similar amplitude, though slightly stronger in D.D.V. Thus, the splenium, which has been spared in G.S., but not in D.D.V., seems to be less relevant in sound lateralization. This is in accordance with the finding that the auditory cortices are interconnected primarily via the posterior midbody [59]. Although topographical correspondence between cortex and CC seems to be rough (e.g., [9]), callosal axons originating in the auditory fields were found in the posterior two thirds of the CC, i.e., in its body and splenium [9,43].

Only one subject with CTO has, to our knowledge, previously been tested for sound localization (S.D. in [35]). Using a task of pointing to sound sources, Lessard et al. [35] obtained merely a slightly reduced precision in sound localization in this subject. Inconsistencies between studies could at least partly be due to interindividual factors (e.g., IQ or lesion sites). However, the obvious discrepancy from the results of our CTO subjects (G.S., D.D.V.), who showed both more severe deficits and clear asymmetry in ITD perception, is likely to be due to the fact that CTO was conducted at an age when these subjects were adult (26 and 30 years), whereas the subject S.D. of Lessard et al. [35] was operated at the age of 6 years. It is likely that processes of compensatory plasticity occurred to a lesser degree in our late-callosotomized subjects than after early CTO. This assumption is also supported by our finding that performance of the subject with CAG (J.P.) was only slightly worse than that of controls, and judgments on ITDs were approximately symmetrical with reference to the median plane. Only slight deviations from normal sound-localization performance have been also found in six subjects with CAG who were tested in two earlier studies by Poirer et al. [48] and Lessard et al. [35]. The latter study [35] even reported some improvements of acallosal subjects in monaural sound localization relative to normal controls. As with early CTO, congenital absence of the CC may result in processes of neural plasticity that compensate for the reduced transfer of auditory spatial information between the cortical hemispheres. Even though cortical re-arrangements after late CTO cannot be ruled out, the present data suggest that occurrence of compensatory plasticity is possible only to a restricted extent when section of the CC is conducted in adulthood.

The most interesting finding obtained in CTO subjects is the clear leftward bias in ITD perception, corresponding to a rightward shift in AMP. Since the ITD is a main cue for sound azimuth, the auditory shifts measured (81.2 and 144.6 μs) may correspond to azimuthal shifts of a free-field sound source by about 6–10° [33]. Whether this substantial bias was the result of a genuine systematic error (i.e., a shift of the psychometric function towards more positive ITDs) or a lower accuracy with judgments on positive ITDs remains open since the slopes of the psychometric function were quite flat compared to the range of ITDs presented to the subjects. From the analyses shown in Figs. 2A, B and 5A, the latter possibility seems, however, more likely; that is, there may be a specific impairment in the perception of sounds to the right of the veridical median plane.

When one considers the contralaterality proposed for auditory processing [45,60], these results suggest an impairment of the left hemisphere with absence or reduction of transcallosal interhemispheric transfer. It thus seems that, in the normal brain, this interhemispheric transfer may be asymmetric, with the left hemisphere (processing right hemispace) receiving more intense auditory spatial input from the right hemisphere than the right hemisphere receives from the left. That is, while the right hemisphere may quite accurately process contralateral spatial information without transcallosal input from the left hemisphere, the accurate processing of information in right hemispace by the left hemisphere may critically depend on transcallosal input from the right hemisphere. This finding provides further support for the view of a right-hemisphere dominance in spatial hearing, as has already been suggested by neuroimaging studies in healthy subjects [1,8,16,18,29,31, 39,44,58,64,66] or by psychophysical studies in brain-damaged patients [53–55,61,62,65]. In particular, the majority of previous studies on structural correlates of human spatial hearing assumed the right posterior parietal cortex to have a key position in the cortical processing of auditory spatial information (e.g., [1,8,37,39,58,64,66]). On the basis of single-unit recordings in the monkey, the human parietal cortex has been suggested to be part of a dorsolateral "where" stream for auditory spatial functions, which originates in the caudal superior temporal gyrus and projects to the dorsolateral prefrontal cortex [1,10,39,51,52,56]. In this context, the existence of homotopic and heterotopic interhemispheric projections of the parietal cortex [21] leads to the speculation that the apparent right-hemisphere dominance of the human parietal cortex in spatial hearing is related to the asymmetry of transcallosal transfer hypothesized above on the basis of our findings. This will need to be substantiated, however, by future research.

At first glance, the view of a right-hemisphere dominance in spatial hearing seems to be compatible also with the accurate performance obtained in subject S.F. with LHE, thus suggesting that the presence of the left hemisphere is not necessary for development of normal spatial hearing functions. It has to be noted, however, that S.F. was operated quite early in life (at the age of 10 months). As a consequence, our data may reflect the impressive capacity of the human brain to compensate for the loss of left-hemispheric auditory areas, rather than the superiority of the right hemisphere. In accordance with this claim, subject M.J., whose left hemisphere was removed at the age of 8 years, was unable to perform the sound-lateralization task, as was also subject B.P., whose right hemisphere was removed at the age of 9 years. However, this total inability of B.P. and M.J. in ITD perception apparently contrasts with previous investigations on sound localization in hemispherectomized subjects. Poirier et al. [49], Zatorre et al. [63], and Lessard et al. [34] all found preserved localization ability in subjects who had undergone left or right unilateral cerebral hemispherectomy, with some individual subjects even performing at normal or near-normal levels. Possibly, the seeming contradiction with the results of our subjects B.P. and M.J. is based on differences in the subjects' IQ or methodology used. With respect to methodology, we tested lateralization of pure-tone ITDs, which depends exclusively on *binaural* processing. In contrast, broad-band stimuli presented in a free sound field, as used in the studies cited above, may allow the evaluation of *monaural* spectral-pinna cues for sound localization in addition to the binaural cues (cf. [6]). As proposed by Lessard et al. [34], hemispherectomized subjects may compensate for impairments in binaural processing by more effective utilization of monaural cues, a possibility that was excluded in the present experimental condition.

The results of subjects B.P. and M.J. are, on the other hand, in agreement with earlier findings that total inability of sound localization or lateralization can occur in individual patients with left-hemispheric lesions and those with right-hemispheric lesions, even though severe deficits are usually observed more frequently in the latter group [5,53–55,61,62,65]. Thus, in the normal brain, both right- and left-hemispheric auditory areas seem to play significant roles in spatial hearing. That the general view of a right-hemisphere dominance in spatial hearing is rather simplistic has been also suggested by studies using functional magnetic resonance imaging, positron emission tomography, magnetoencephalography, and transcranial magnetic stimulation. These investigations have generally indicated stronger involvement of several cortical areas in the right than in the left hemisphere during various tasks of sound localization or lateralization, namely, parietal cortex (Brodmann area, BA 7, 40), superior temporal gyrus (BA 22/42), and inferior temporal gyrus (BA 20) [8,16,18,29,31,37,44,58,64,66]. Neuroimaging studies have, however, also revealed some areas, such as middle temporal cortex (BA 37) and insula, that were found to be activated in the left hemisphere [39,66]. The specific functions of these left- and right-hemispheric areas in spatial hearing are, at present, still unclear. As suggested by our results, transcallosal transfer may significantly contribute to the coordination of the processing of auditory spatial information within this complex bilateral network of homotopic and heterotopic cortical areas.

Although we employed a quite simple task of sound lateralization, our results may be also interpretable in terms of a supramodal hemispheric asymmetry in allocation of attention. That is, the contralaterality of sensory processing, either auditory or visual, could be superimposed on a superiority of the right hemisphere in spatial attention.

Based on studies focusing on the integration of the left and right visual hemispaces, it has been hypothesized that the left hemisphere is concerned almost exclusively with attention to the right side of egocentric space, whereas the right hemisphere is capable of directing attention to both sides of space [24,25,40]. This might be compatible with our findings of almost normal performance following left hemispherectomy and substantial deficits in sound lateralization following right hemispherectomy. However, as shown here, a disconnection of transcallosal networks subserving spatial attention does not result in a failure of sound lateralization (even though acuity is reduced), but rather in a strong leftward shift in perceived sound positions. Thus, it is conceivable that a lack of interhemispheric communication impairs the general ability to allocate attention to the right hemispace, which is under control of both the left and the right hemisphere.

The hypothesis of a supramodal hemispheric asymmetry in spatial attention is supported by previous studies, which showed that D.D.V. neglects stimuli in the left visual field. This was manifested in visual line bisection [19] and reaction time to stimuli flashed in the left visual field [12]. Similarly, Heilman and Adams [23] investigated a 32-year-old women, who neglects stimuli on the left side as a result of CTO due to multifocal epilepsia at age of 31 years. Although she had damage to right frontal, parietal, and occipital regions and the left temporal region at age of 14 years, no signs of left hemineglect were present before CTO. Thus, lesions in the right hemisphere in the CTO subjects of Heilman and Adams [23] and of the present study (D.D.V. and G.S.) are not necessarily related to any attentional bias. Although we cannot unequivocally conclude that a general attentional bias is exclusively due to a lack of interhemispheric communication, this hypothesis is supported (at least in the visual modality) by other split-brained subjects without lateralized lesions (e.g., [11,17,26,32,47]). Hence, despite several limitations, the present findings in combination with those previous studies point to a supramodal hemispheric asymmetry in the control of spatial attention, and provide further clues as to the relevance of interhemispheric communication in allocation of attention.

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