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Authors: Duffour-Nikolov C, Tardif E, Maeder P, Thiran AB, Bloch J, Frischknecht R, Clarke S

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Auditory spatial deficits following hemispheric lesions: Dissociation of explicit and implicit processing

Catherine Duffour-Nikolov [1], Eric Tardif [1], Philippe Maeder[2], Anne Bellmann Thiran[1], Jocelyne Bloch[3], Rolf Frischknecht[1] and Stephanie Clarke[1]

[1] Service de Neuropsychologie et de Neuroréhabilitation, CHUV, 1011 Lausanne, Switzerland

[2] Service de Radiodiagnostic et Radiologie Interventionnelle, CHUV, Lausanne, Switzerland

[3] Service de Neurochirurgie, CHUV, Lausanne, Switzerland

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Corresponding author :
Prof. S. Clarke
Service de Neuropsychologie et de Neuroréhabilitation, CHUV, 1011 Lausanne, Switzerland
Telephone +41'21'314'13’09
Fax +41'21'314'13'19
E-mail: Stephanie.Clarke@chuv.ch

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Abbreviations

IID = interaural intensity difference
ITD = interaural time difference
SRM = spatial release from masking

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Abstract

Auditory spatial deficits occur frequently after hemispheric damage; a previous case report suggested that the explicit awareness of sound positions, as in sound localization, can be impaired while the implicit use of auditory cues for the segregation of sound objects in noisy environments remains preserved. By assessing systematically patients with a first hemispheric lesion, we have shown that i) explicit and/or implicit use can be disturbed; ii) impaired explicit vs preserved implicit use dissociations occur rather frequently; and iii) different types of sound localization deficits can be associated with preserved implicit use. Conceptually, the dissociation between the explicit and implicit use may reflect the dual-stream dichotomy of auditory processing. Our results speak in favour of systematic assessments of auditory spatial functions in clinical settings, especially when adaptation to auditory environment is at stake. Further, systematic studies are needed to link deficits of explicit vs implicit use to disability in everyday activities, to design appropriate rehabilitation strategies, and to ascertain how far the explicit and implicit use of spatial cues can be retrained following brain damage.

INTRODUCTION

Auditory spatial deficits occur frequently after brain damage; in rehabilitation settings it is very likely that over 50% of patients with right and over 30% with left hemispheric lesions are deficient in sound localization and/or sound motion perception (Bellmann, Clarke, & Assal, 2001; Clarke, Bellmann Thiran, Maeder, Adriani, Vernet et al., 2002; Spierer, Bellmann-Thiran, Maeder, Murray, & Clarke, 2009). The proportion is considerably higher in the acute stage (Adriani, Maeder, Meuli, Thiran, Frischknecht et al., 2003) and progressive recovery is often witnessed throughout the subacute and chronic stages (Rey et al. 2007). Although chronic auditory spatial deficits occur after purely unilateral lesion within the right (Altman, Balonov, & Deglin, 1979; Clarke, et al., 2002; Griffiths, Rees, Witton, Shakir, Henning et al., 1996; Haeske-Dewick, Canavan, & Homberg, 1996; Pavani, Meneghello, & Ladavas, 2001; Poirier, Lassonde, Villemure, Geoffroy, & Lepore, 1994; Ruff, Hersh, & Pribram, 1981; Zatorre & Penhune, 2001) or left hemisphere (Clarke, Bellmann, Meuli, Assal, & Steck, 2000; Pinek, Duhamel, Cave, & Brouchon, 1989; Sanchez-Longo & Forster, 1958), current evidence suggests a bihemispheric contribution to low level spatial processing and a right hemispheric dominance in the building up of global auditory spatial representations (Lewald, Foltys, & Topper, 2002; Spierer, Bellmann-Thiran, et al., 2009).

Auditory spatial cues fulfil two ecologically important roles. First, they contribute to overt sound localization, which allows us to identify explicitly the position of a sound source, to point to it (Makous & Middlebrooks, 1990) or to discriminate two successive sound positions (Mills, 1958). Patients who are unable to localize explicitly sounds report typically difficulties in crossing the street; they fail to follow the position of vehicles by auditory cues and compensate often by repeated visual checking (Thiran & Clarke, 2003). Another frequently reported difficulty resides in identifying the speaker within a group of unknown people; unable to determine where the voice comes from, patients proceed then by checking whose lips are moving. Second, auditory spatial cues contribute to sound object segregation (Bregman, 1990; Carlyon, 2004; Cherry, 1953; Darwin, 1997; Drennan, Gatehouse, & Lever, 2003; Yost, 1991). A well known example is our capacity to follow speech in noisy surroundings (Bregman, 1990; Carlyon, 2004; Cherry, 1953; Darwin, 1997; Drennan, et al., 2003; Yost, 1991); this capacity is often disturbed in brain-damaged patients, who then report for example not to be able to attend a gathering or to work in a factory or a supermarket. In normal subjects, the role of spatial cues in segregating sound objects has been demonstrated by the phenomenon of spatial release from masking (SRM). A target sound (e.g. speech), which has been made unrecognizable by a simultaneous masking sound, became intelligible with increasing spatial separation between the speech source and the masking noise (Carhart, Tillman, & Johnson, 1967). The use of spatial cues for parsing the sound mixture, such as demonstrated with SRM tasks, can occur implicitly, i. e. without the explicit awareness of the positions of the target and masker. This was reported in two patients, one with a right inferior collicular lesion (Litovsky, Fligor, & Tramo, 2002) and the other with a large right hemispheric lesion (Thiran & Clarke, 2003). The latter patient, MN, presented spatial deafness, being totally unable to localize sounds or to compare their positions in free-field or in tasks using interaural time (ITD) or intensity differences (IID); despite her profound inability to use explicitly auditory spatial information, she did it implicitly, benefiting fully from spatial cues in SRM tasks.

The case of MN demonstrated a striking dissociation between the completely abolished explicit and the preserved implicit use of auditory spatial cues, raising three issues which we addressed in this study. By assessing systematically patients with a first hemispheric lesion, we have shown that i) explicit and/or implicit use can be disturbed; ii) impaired explicit vs preserved implicit use dissociations occur rather frequently; and iii) different types of sound localization deficits can be associated with preserved implicit use.

METHODS

We report here on 13 patients with a first hemispheric lesion, but no brainstem lesion, who entered consecutively our diagnostic and rehabilitation programme and fulfilled the following criteria: (i) no prior neurological or psychiatric illness; (ii) absence of brain stem lesions; (iii) normal hearing thresholds in tonal audiometry; (iv) absence of major behavioural troubles, ataxia or comprehension deficits; and (v) normal performance in sound object recognition (Table 1). The latter was assessed with a previously published test of 50 samples of environmental sounds (normative data in Table 2; no significant differences between age groups; (Clarke, Bellmann, De Ribaupierre, & Assal, 1996); only patients with z score >-2.0 were included in the study.

All patients but three (LR, DB, Eld) were right-handed. All patients had MRI and/or CT scan, which were analyzed for the site and extent of the lesion, and all had a comprehensive neuropsychological evaluation. The auditory testing reported here was administered between 12 and 145 days after the lesion occurred and spanned on average over 9.8 days, including audiogram, sound object recognition, sound lateralization using ITD cues, SRM, sound lateralization using IID. The study was approved by the Ethics Committee of the Faculty of Biology and Medicine, University of Lausanne.

Auditory spatial abilities were assessed using sound lateralization paradigms with ITD (as in (Altman, et al., 1979; Anne Bellmann, et al., 2001; Clarke, Adriani, & Bellmann, 1998; Clarke, et al., 2000; Cusack, Carlyon & Robertson, 2001; Clarke, et al., 2002; Griffiths, et al., 1996; Rey, Frischknecht, Maeder, & Clarke, 2007; Spierer, Bellmann-Thiran, et al., 2009; Spierer, Meuli, & Clarke, 2007; Tanaka, Hachisuka, & Ogata, 1999; Thiran & Clarke, 2003) or IID (as in (Bisiach, Rusconi, Peretti, & Vallar, 1994; Spierer, Bellmann-Thiran, et al., 2009; Sterzi, Piacentini, Polimeni, Liverani, & Bisiach, 1996). For each test, the volume was set at a level judged comfortable by the subject (75-85 dB SPL; CESVA SC-L; www.cesva.com).

Explicit use of ITD cues: sound lateralization

The capacity to discriminate sound positions has been assessed with a task simulating five azimuthal positions with ITD and is referred hereafter as sound lateralization (Anne Bellmann, et al., 2001; Clarke, et al., 2000; Clarke, et al., 2002; Spierer, Bourquin, Tardif, Murray, & Clarke, 2009). Sixty 2 s broadband "bumblebee" sounds (20-16000 Hz, with 2 dominant bands at 20-1000 Hz and 3000-5000 Hz; “Sound Effects, volume 14, DOM) were presented to the subject, shaped with 100 ms rising and falling times, in 5 azimuthal positions (LL: extreme left, L: intermediate left, Ce: centre, R: intermediate right and RR: extreme right) simulated by ITD (intermediate lateral positions with 300 μs; extreme lateral positions with 1 ms; and the central position with 0μs). Subjects pointed with their ipsilesional hand to the perceived position on a head-fixed graduated half circle (as in Altman, et al., 1979; Bisiach, Cornacchia, Sterzi, & Vallar, 1984). Normative data were obtained from 60 normal subjects (30 male and 30 female, aged between 20 and 85 years; 20 subjects aged 20-34 years; 20 aged 35-49 years; 20 aged 50 or more years; overall mean age = 42.5 years, S.D. = 14.3 years); none of the measures reported below differed significantly between age groups

(Anne Bellmann, et al., 2001; A. Bellmann, Meuli, & Clarke, 2001; Spierer, Bellmann-Thiran, et al., 2009). The average angular values of the perceived extreme positions were LL=-60.1° (S.D. = 13.0°) and RR=62.9° (S.D. = 12.5°); for the intermediate positions L=-37.8° (S.D. = 13.8°) and R=40.5° (S.D. = 14.2°); and Ce=-0.1° (S.D. = 4.5°). Five measures of performance were calculated (Table 2). First, the relative locations attributed to two consecutive stimuli (Rel loc) counted the number of correct responses when a stimulus was correctly placed to the left or the right of the previous stimulus in correspondence with the difference in ITD or within ±10° of the previous location for identical ITD. Second, the position attributed to the central stimulus (i.e., stimulus with ITD = 0) was assessed (Center). Third, the index of left vs right (Index L/R) corresponded to the number of pointings to the left minus to the right in response to the 48 lateralized stimuli, irrespective of the correctness of the replies. Fourth, symmetry of positions attributed to stimuli with the same absolute value of ITD but different leading ear was evaluated by comparing the means of the angular values attributed to simulations with left vs right ear leading for the two extreme positions (Sym LL-RR) and the two intermediate positions (Sym L-R). Fifth, the consistency with which a location was attributed to a specific value of ITD was assessed by the magnitude of the standard deviation for this measure (Consistency). The performance of patients has been transformed into z scores relative to the mean and S.D. of the control population. For Rel loc and for the five Consistency measures deficient performance corresponded to $z < -2.0$. Centre, Index L/R, Sym LL-RR, Sym L-R assessed deviations that could be towards the left or right hemispace (i. e. positive or negative values); hence deficient performance corresponded to $z<-2.0$ for right-ward or to $z>2.0$ for left-ward deviations.

Implicit use of ITD cues: spatial release from masking

The SRM effect is also present when the spatial removal of the masking noise is lateralized by interaural time difference (ITD), each ear receiving the same frequencies at a same intensity level (i. e., the signal-to-noise ration remains constant within each ear; (Carhart, et al., 1967). We have adopted this approach to our testing procedure. In the SRM paradigm the target was an 800 ms long cry of a tawny owl (20–5000 Hz, centered between 350 and 900 Hz; “All Birds of Europe”, Delachaux & Niestlé) and was always presented at the central position (ITD = 0). The masker consisted of a 2.5 s broadband helicopter sound (20–5500 Hz, the frequency region containing the dominant sound energy was around 700 Hz; Nathan Sound Loto) and was presented at one of 11 possible spatial positions lateralized with ITD (400, 320, 240, 160, 80 μs favouring either the left or right ear, or 0 ITD). Sixty-six items (plus 10 which were not included in the analysis, see after) were presented to the subject, of which 22 were masker alone and 44 target and masker. In the latter the target began 1 s after the onset of the masker. In order to avoid expectation of the target at a constant interval, 10 other trials (distractors) were added to the test but not included in the result analysis. In 5 of them, the target began 500 ms after the masking sound and in 5 others, 1500 ms after. Three versions of the test were constructed in which the intensity of the target sound was varied while the intensity of the masking sound was kept constant. In the “easy” standard version of the test, the masker was 79dB and the target 44dB (referred to as the 0dB version in Table 3 and in Figs 1-3); in the “intermediate” version the target was attenuated by 2dB (-2dB version); and in the “difficult” version by 4 dB (-4dB version) as compared to the standard version. Subjects were instructed to respond by raising one hand or through visual contact whether the target was present or not. The maximum target detection per position of the masker was 4. In our paradigm, SRM is present if i) the centrally located target fails to be detected when the masker is located also centrally; and ii) the same centrally located target is detected when the masker is located at the periphery. Normative data for the 3 versions of the test were obtained from 60 normal subjects (mean age 41.8 years, S.D. 15.9 years; (Thiran & Clarke, 2003). In the “easy” version of the test, i. e. when the owl cry was relatively loud, all subjects detected the target in 3-4 out of the 4 presentations when the masker was presented in the periphery (lateralized with ITD of 240, 320 or 400 μs to the left or to the right). When the masker was presented centrally or near the midsagittal plane (lateralized with ITD of 80 μs to the left or to the right), the individual performance of the subjects varied: over 60 % of the control subjects failed completely to detect the target; others detected it less often; and a small number of control subjects detected the target as often as when the masker was in the periphery. On average, normal subjects detected the target less often when the masker was in central than in peripheral positions; the number of detections in function of the laterality of the masker was a U-shaped curve (see Fig. 3 in Thiran and Clarke, 2003). The few subjects who did not have a U-shaped curve in the “easy” version of the test, presented this profile in at least one of the other two versions. In all three test versions, normal subjects gave consistent replies, without false detection, and did not present zig-zaging inflections in the detection curve. In the normal population, the SRM effect is indeed present as a less frequent detection of the target when the masker is in central as compared to peripheral positions. For the absence of the SRM effect two conditions need thus to be satisfied: i) the subject is sensitive to different levels of masking, i. e., the target is more frequently detected in the easy than in the more difficult versions of the test; ii) the rate of target detection is independent of the position of the masker, i. e. the target is not more frequently detected when the masker is in peripheral than in central positions. In addition the magnitude of the SRM effect in a given subject was expressed as the difference in target detection when the masker was in the central and intermediate positions (ITD = 0, 80, 160, 240, 320, -80, -160, -240, -320 μs) as compared to the two lateral ones (ITD = 400, -400 μs); the SRM score was calculated as the sum, for the central and intermediate positions, of the differences between the mean target detection at the two lateral positions and the target detection at the central and the intermediate positions.

Additional tests of explicit use of spatial cues

Sound lateralization has been also assessed with a task simulating five azimuthal positions with IID (Clarke, et al., 2000; Spierer, Bourquin, et al., 2009). The test and its analysis were identical to those of the above described ITD sound lateralization test, with the exception that the 5 azimuthal positions were simulated by varying the intensity ratio: 50:50 for the central; 75:25 for intermediate; and 95:5 for extreme lateral positions. Normative data from 60 normal subjects were published previously and did not differ significantly between age groups (Spierer, Bellmann-Thiran, et al., 2009). The average angular values for the perceived extreme positions were LL=-66.6° (S.D. = 13.5°) and RR=70.2° (S.D. = 13.2°); for the intermediate positions L=-32.1° (S.D. = 14.7°) and R=32.7° (S.D. = 15.4°); for the center Ce= 0.1° (S.D. = 5.1°). The normal scores on the relative positioning of 2 consecutive stimuli are listed in Table 2.

Sound motion perception was assessed with a test simulating azimuthal sound motion by means of ITD, as described previously (Clarke, et al., 2000). Six different motions of a motorcycle sound were simulated: LL-RR and the vice-versa; LL-Ce and vice-versa; and RR-Ce and vice-versa. Subjects indicated the perceived motion direction on their head; their performance was assessed by the number of replies that were correct for motion direction. Normative data were obtained from 60 normal subjects; none of the measures reported below differed significantly between age groups (Anne Bellmann, et al., 2001). Mean score and standard deviation is listed in Table 2.

Patients with right hemispheric lesions may present directional hypokinesia (Heilman, Bowers, Coslett, et al. 1985; Cusack, Carlyon & Robertson 2001) or premotor type of neglect (Sterzi, Piacentini, Polimeni, et al. 1996), which could be at the original of the spatial bias which we observed in several of our patients. We know this not to be the case, because additional testing involving verbal responses and same-different discrimination in a sound lateralization task revealed a very similar type of deficit.

RESULTS

Three patients (MC, MB, ILR) had normal performance in sound lateralization (ITD and IID) and sound motion perception, two other patients had a very mild deficit in sound lateralization ITD (DB) or normal ITD but deficient IID lateralization (RN). Eight patients (LC, LR, ELd, ELz, LBA, KJ, BL, DO) had deficient performance in ITD sound lateralization, often associated with deficits in IID lateralization and/or sound motion perception. The SRM effect was present in nine (MC, MB, RN, DB, LC, LR, ELd, ELz, LBA) and absent in four patients (ILR, KJ, BL, DO; Table 3).

Preserved sound lateralization and SRM effect

Two patients had normal performance in all evaluations of sound lateralization and sound motion perception and presented a U-shaped curve for the SRM effect (MC, MB; Table 3; Fig. 1 top).

Deficient sound lateralization and preserved SRM effect

Seven patients presented the SRM effect, but had a minor (RN, DB) or major deficit in sound lateralization (Table 3; Fig. 2). The type of sound lateralization deficits varied between the latter. LC and LR had a pervasive auditory spatial deficit, which involved sound lateralization with ITD and IID cues and sound motion perception with ITD cues. LC's performance at sound lateralization using ITD cues could be interpreted as disturbed global auditory representation: the relative lateralization was severely deficient, the consistency in attributing the same positions to same cues was deficient for all 5 positions, and the right half of the space was overinvested. LR appeared to have a roughly preserved global representation of the auditory space: his relative lateralization was only moderately deficient, and the space was invested symmetrically. He was, however, unable to use the ITD cues for precisely ordered auditory representation: the consistency within the left hemispace was deficient. ELd, ELz and LBA had a more discrete auditory spatial deficit. Their global auditory representation appeared preserved: the relative lateralization was within normal limits. Their precise appreciation of auditory coordinates was, however, disturbed: the consistency within parts of the auditory space was deficient.

Absent SRM effect

Four patients were unable to perform the SRM task correctly (Table 3; Fig. 3). They were sensitive to different levels of masking– they detected the target more often in the easy than in the difficult versions of the test - but they were not sensitive to the SRM effect, since they did not detect the target differently when the masker was presented in peripheral vs central positions. Patients BL tended to detect the target in almost all trials for all masker positions in an easy version of the test, the target being most likely well above masking level in all positions. Unlike normal subjects BL did not present a U-shaped curve in the more difficult test version; although she had difficulties to detect the relatively faint target in the more difficult version, the decrease of detection level occurred independently of the masker position. The performance of patients ILR, KJ and DO was characterized by numerous false alarms; the tendency to respond positively increased most likely the noisiness of the results.

One of these patients had normal performance in sound lateralization (ILR). His profile – preserved sound localization with putatively disturbed SRM effect – may constitute a double dissociation to the above described profile of deficient sound localization and preserved SRM effect.

The 3 other patients (KJ, BL, DO) had sound lateralization deficits of varying severity. KJ had a severe auditory spatial deficit, which can be interpreted as disturbed global auditory representation: the relative lateralization was severely deficient, the peripheral positions were shifted towards the right and the centre towards the left, the consistency in attributing the same positions to same cues was deficient for 3 out of 5 positions. BL had a less disturbed global representation of the auditory space: her relative lateralization was only moderately deficient, but the left hemispace tended to be overinvested and the centre was displaced towards the left. DO had a more discrete auditory spatial deficit. His global auditory representation appeared preserved: the relative lateralization was within normal limits. His precise appreciation of auditory coordinates was, however, disturbed, with a systematic bias towards the right.

Deficits in sound lateralization and/or absence of SRM effect

Further analysis of patients with deficits in sound lateralization and/or SRM suggested a dissociation between explicit and implicit uses of spatial cues. On the behavioural level, there was a negative correlation between performance in sound lateralization and the SRM score (R = 0.711, p = 0.037; Fig. 4). Lesion analysis of the four profiles defined by the respective performance in sound lateralization and in SRM (Fig. 5) speaks in favour of at least partially distinct networks. First, damage to fronto-parietal cortex tended to be associated with deficits in sound localization, in agreement with the previously described role of the auditory “Where” pathway (Clarke, et al., 2000; Clarke, et al., 2002; Rey, et al., 2007; Spierer, Bellmann-Thiran, et al., 2009). Second, temporal lobe damage appeared to play a major role in the absence of the SRM effect: i) it was present in all patients with absent SRM effect; ii) only 2 out of 6 patients with temporal damage had normal SRM effect; and iii) among the 9 patients with normal SRM effect only 2 had temporal damage. Third, lesions involving the frontal, parietal and temporal lobes were found in association with combined deficits of sound lateralization and SRM and never with an isolated or without any deficit.

DISCUSSION

The dissociation between explicit and implicit use of auditory spatial cues is of clinical and conceptual importance. Clinically, preserved use of spatial cues for sound object segregation is likely to be accompanied with a better adaptation to everyday-life situations and in particular to noisy surroundings. This has been clearly so in our single case study where, with a retrospective evaluation of 10 years, noisy surroundings were not a problem for the patient (Thiran & Clarke, 2003). Here we demonstrated that the dissociation between the explicit and implicit use of auditory spatial cues is not rare: In a population of patients with hemispheric lesions and major or minor sound lateralization deficits it is more likely to find the implicit use preserved (70%) than disturbed (30%). This was also the case in a previously published neglect population where a similar proportion of patients with sound lateralization deficits was found to make use implicitly of spatial cues in a diotic listening task (Spierer, et al., 2007).

The above described dissociation is reminiscent of a similar dissociation in the visual domain, where perception of object size, orientation and shape was shown to dissociate, in brain-damaged patients, from the control of goal-directed grasping (Goodale, Meenan, Bulthoff, Nicolle, Murphy et al., 1994; Jakobson, Archibald, Carey, & Goodale, 1991; Perenin & Vighetto, 1988).

Conceptually, our finding challenges the belief that the contribution of spatial cues to the explicit awareness of sound positions, as in sound localization, and to the implicit processing, as in sound object segregation, is processed by the same cortical spatial network. Converging evidence highlights the dual-stream model of auditory processing as possible underpinning of the explicit/implicit dichotomy. This is of potential relevance to the rehabilitation of brain-damaged patients, since it predicts that different approaches may be needed for the retraining of explicit vs implicit cues following brain damage.

Spared implicit use vs mild to severe explicit deficits

As indicated by electrophysiological, TMS and neuropsychological studies (Lewald, et al., 2002; Magezi & Krumbholz, 2010; Spierer, Bourquin, et al., 2009), two distinct cortical stages are likely to be involved in (explicit) sound localization: i) the precise computation of spatial coordinates allowing spatial comparison within the contralateral hemispace for the left hemisphere and the whole space for the right hemisphere; and ii) the building up of a global auditory spatial representation in the right temporo-parietal cortices. The disruption of either stage leads to localization deficits, which are clinically perceived as mild or severe, respectively, and which can be associated with preserved implicit use of spatial cues. Global spatial representation was clearly affected in MN (Thiran & Clarke, 2003) and in LC (here), whereas the precise computation of spatial coordinates was disturbed in LR, ELd, ELz and LBA and, to a much lesser degree, in RN and DB (here). The impairment of either stage of (explicit) sound localization can be, however, also associated with impaired implicit use of spatial cues, as shown here by the global spatial representation impairment in KJ and partially in BL, and the impairment of precise computation of spatial coordinates in DO.

Beyond the independence of the impairment severity, the explicit and implicit use of spatial cues may possibly double-dissociate, as suggested by the profile of ILR, who did not present the SRM effect, but had normal sound lateralization. However, more cases are needed before confirming this hypothesis.

Explicit vs implicit dichotomy in normal subjects

Several observations in normal subjects support an explicit vs implicit dichotomy. Spatial unmasking of speech is a well documented phenomenon, demonstrated in free-field condition (Drennan, et al., 2003; Saberi, Dostal, Sadralodabai, Bull, & Perrott, 1991), virtual auditory space (Hawley, Litovsky, & Culling, 2004), and simulation with ITD (Bronkhorst & Plomp, 1988; Darwin & Hukin, 1999; Edmonds & Culling, 2005). Spatial cues remain, however, relevant for sound object segregation also in the absence of proficient sound lateralization ability. Thus, the intelligibility of speech was shown to be improved by binaural manipulations which did not produce clear lateralization (Licklider, 1948). In another experiment, inverting the speech waveform - or the masking noise - at one ear, which gives a diffuse, non-ecologically relevant lateralization, caused a greater release-from-masking than when ITD cues were used (Carhart, Tillman, & Greetis, 1969a, 1969b; Carhart, et al., 1967; Carhart, Tillman, & Johnson, 1968; Levitt & Rabiner, 1967; Schubert, 1956; Schubert & Schultz, 1962).

The role of spatial cues in sound object segregation is similar to that of non-spatial cues and both are believed to share the same mechanisms in auditory streaming. Thus, concurrent introduction of fundamental frequency difference was shown to enhance the SRM effect on the identification of vowels (T. M. Shackleton & Meddis, 1992) and, in another paradigm, changes of simultaneous vs sequential grouping weakened it (Darwin & Hukin, 1999).

Explicit vs implicit use and the dual-stream model of auditory processing

The dual-stream model of auditory processing which posits a specialization for sound localization within the “Where” and for sound recognition within the “What” stream has been derived from work in non-human primates (Kaas & Hackett, 2000; Rauschecker & Tian, 2000) and from activation studies in normal subjects (Maeder et al. 2001; Arnott et al. 2004; De Santis et al. 2007). Neuropsychological studies have shown that sound localization, i. e., the explicit use of spatial cues, depends critically on the integrity of the auditory “Where” stream (Clarke, et al., 2000; Clarke, et al., 2002; Rey, et al., 2007; Spierer, Bellmann-Thiran, et al., 2009). Our current results suggest that the implicit use of auditory cues in sound object segregation may be linked to the “What” stream. A contribution of auditory spatial information to the “What” stream has been demonstrated recently at the level of the early-stage auditory areas (Rivier & Clarke, 1997; Wallace, Johnston, & Palmer, 2002). Two of these areas are considered to be part of the “What” pathway because of their specialization in sound recognition (Viceic, Fornari, Thiran, Maeder, Meuli et al., 2006); one of the two (ALA) was shown to carry also spatial information (Budd, Hall, Goncalves, Akeroyd, Foster et al., 2003; Hall, Barrett, Akeroyd, & Summerfield, 2005) and to be modulated by the position of sound objects (van der Zwaag, Gentile, Gruetter, Spierer, & Clarke, 2011).

Cortical vs subcortical processing

The relative contribution of cortical versus subcortical processing to the implicit use of auditory spatial cues is not entirely clear. Electrophysiological studies in animal models strongly suggest the involvement of inferior collicular neurons in the SRM effect (Caird, Palmer, & Rees, 1991; Jiang, McAlpine, & Palmer, 1997a, 1997b; Lane & Delgutte, 2005; McAlpine, Jiang, & Palmer, 1996), whereas human lesion studies stress the role of cortical structures. A single case study of a right inferior collicular lesion reported deficient sound localization and preserved use of spatial cues for sound object segregation; the latter was believed to be preserved because it depends primarily on cortical processing (Litovsky, et al., 2002). Our results support a hemispheric, possibly cortical contribution, since the implicit use of spatial cues can be disrupted after a hemispheric lesion, without damage to midbrain structures. However, an important subcortical contribution cannot be ruled out. Clinically, the preserved SRM effect was associated with well formulated complaints of impaired understanding of speech in noisy environment in the case of the collicular (Litovsky, et al., 2002) but not the hemispheric lesion (Thiran & Clarke, 2003). Combined evidence suggests that that both cortical and subcortical structures extract ITD for sound segregation in normal individuals and that the SRM contribution of subcortical structures may depend on cortico-subcortical projections (Rouiller, 1997).

Conclusion

Auditory spatial deficits occur frequently in brain damage and can be characterized by different involvement of explicit and implicit use of spatial cues. Specific impairments should be assessed systematically when issues of adaptation to the auditory environment are at stake. Conceptually, the dissociation between the explicit and implicit use relies at least partially on the dual-stream dichotomy of auditory processing. Further, systematic studies are needed to link deficits of explicit vs implicit use to disability in everyday activities, to design appropriate rehabilitation strategies, and to ascertain how far the explicit and implicit use of spatial cues can be retrained following brain damage.

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Figure 1

Performance of four patients with no (top two rows) or only minor deficit (bottom two rows) in sound lateralisation and a preserved SRM effect. Left column: Performance in sound lateralisation using ITD cues; the positions (y- axis; in degrees; error bars = S.D.) which the patient attributed to the 5 different ITD (x-axis) favouring the left (LL: extreme left for ITD = 1 ms, L: intermediate left for ITD = 300 μs) the right (R. intermediate right for ITD = 300 μs, RR: extreme right for ITD = 1ms) or none of the ears (Ce: centre for ITD = 0ms) are indicated within the right (positive values) and the left (negative values) auditory hemifields. Patient code and lesion side are indicated in top left corner. Right column(s): Performance in the SRM test; the number of correct target detections (y-axis; max = 4) which the patient did for each of the 11 lateralisation of the masking sound (x-axis; in μs; negative values for left ear lead). The level of attenuation of the target in comparison to the standard version of the test is indicated in bottom right corner, the number of false detection (F.D.) in bottom left corner of each graph. For details of performance see Table 3, for normative data on both tasks see Figures 2 and 3 in Thiran and Clarke (2003).

Figure 2

Performance of five patients with deficits in sound lateralisation and preserved SRM effect. Same conventions as Figure 1

Figure 3

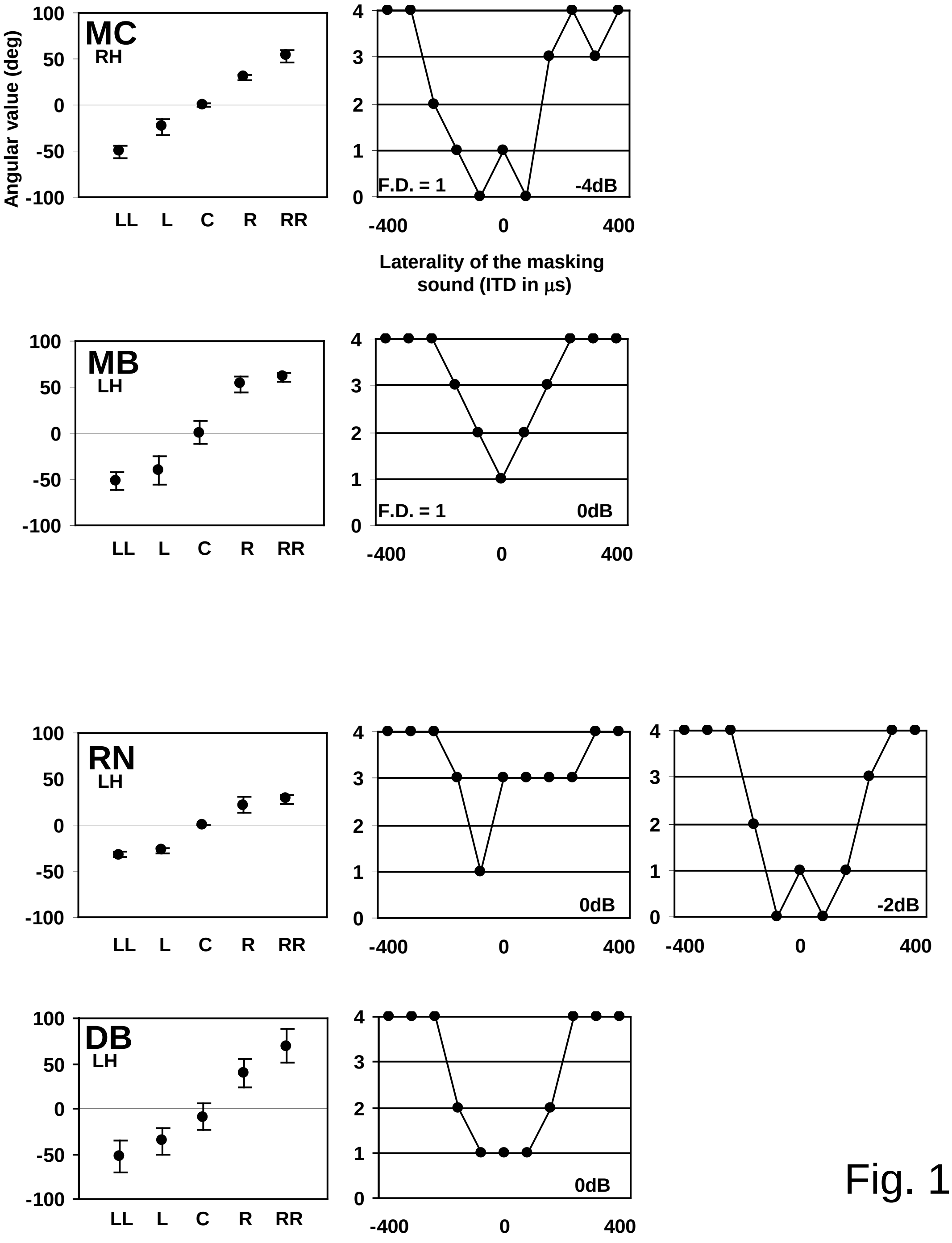
Performance of patients with absent SRM effect, of which one had normal (top row) and three deficient performance in sound lateralisation (bottom rows). Same conventions as in Figures 1 and 2. Abnormal number of false detection in the SRM task is marked by an asterisk.

Figure 4

Relationship between explicit and implicit use of auditory spatial cues in patient population with deficits in sound lateralization and/or SRM task. For definition of Rel. loc. and SRM score, see Methods.

Figure 5

Lesions associated with deficient explicit and implicit use of spatial cues (bold); deficient explicit and preserved implicit use (italics); preserved explicit and deficient implicit use (outlined); and preserved explicit and implicit use (grey). Patients are designated with their codes; position within a circle denotes the presence of a lesion within the corresponding lobe. F = frontal lobe; P = parietal lobe; T = temporal lobe.


MC
RH
Angular value (deg)
100
50
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-50
-100
LL
L
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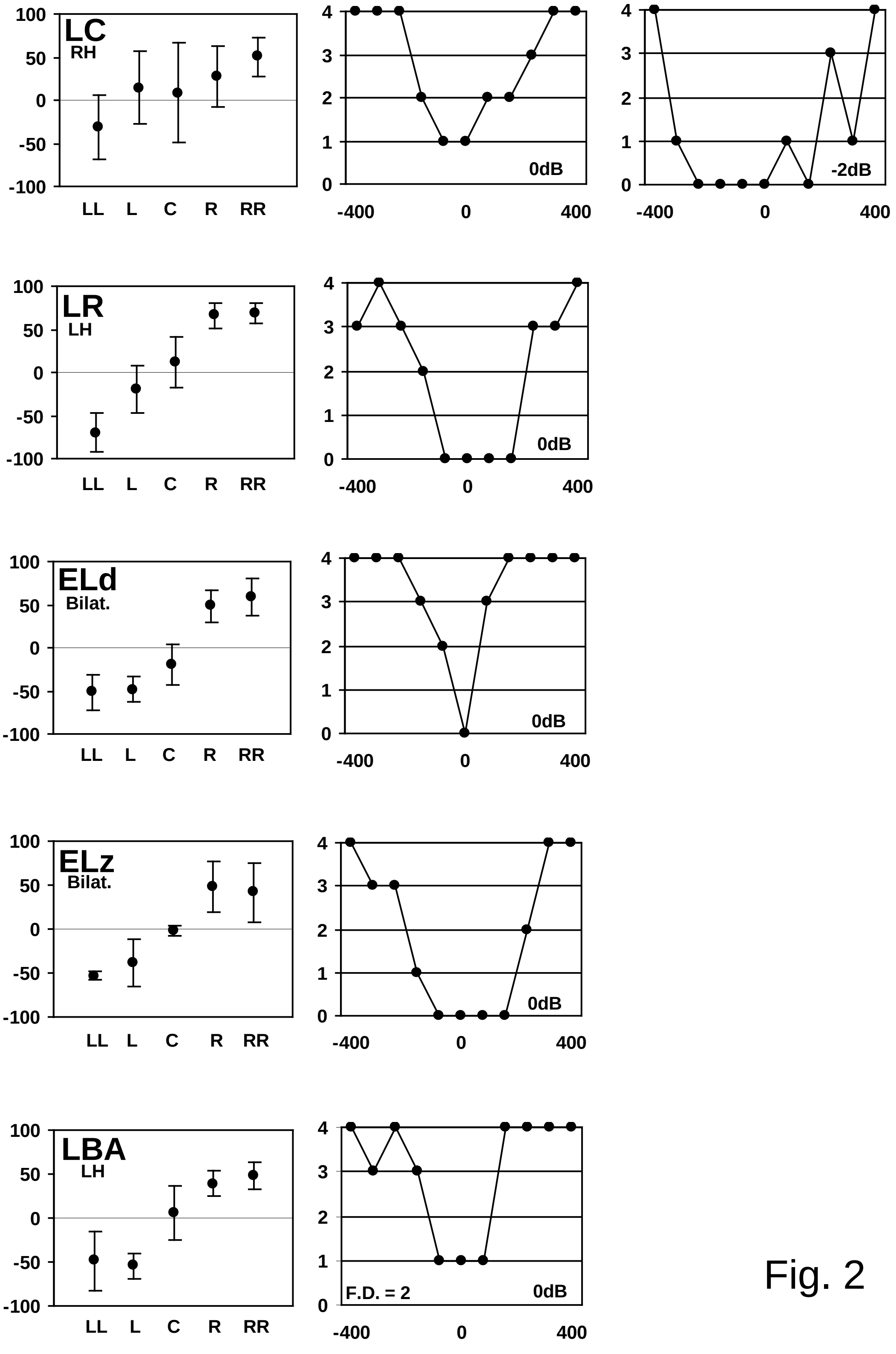
RR
4
3
2
1
0
F.D. = 1
-4dB
-400
0
400
Laterality of the masking sound (ITD in μs)
MB
LH
F.D. = 1
0dB
RN
LH
0dB
-2dB
DB
LH
0dB

Fig. 1


LC
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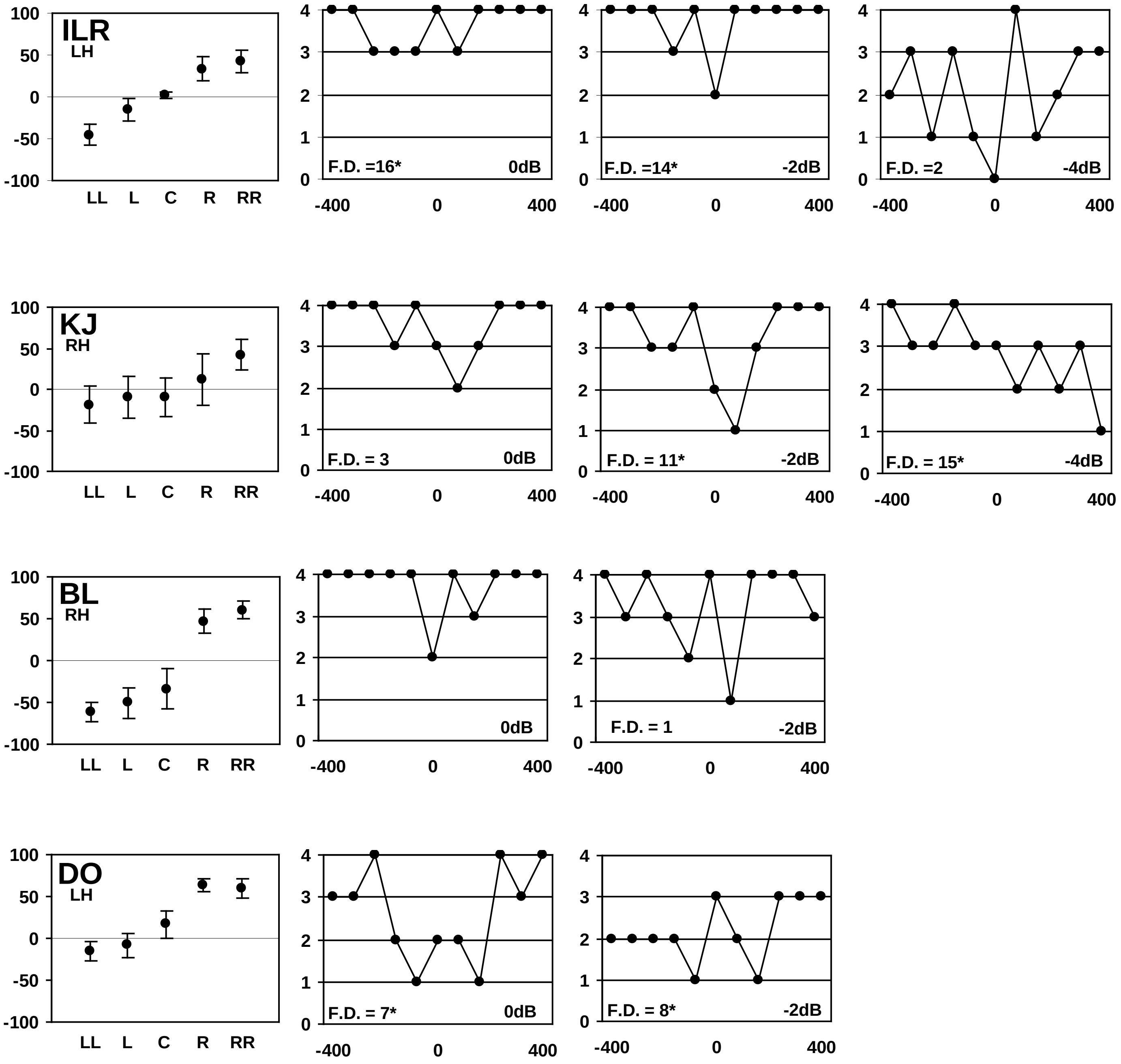
F.D. = 2

Fig. 2


ILR
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F.D. =16*
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F.D. =14*
-2dB
F.D. =2
-4dB
F.D. = 3
0dB
F.D. = 11*
-2dB
F.D. = 15*
-4dB
0dB
F.D. = 1
-2dB
F.D. = 7*
0dB
F.D. = 8*
-2dB

Fig. 3

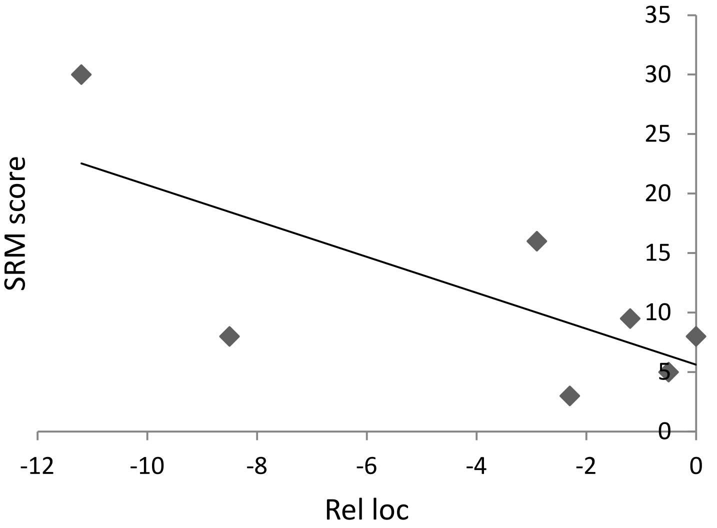

Fig. 4

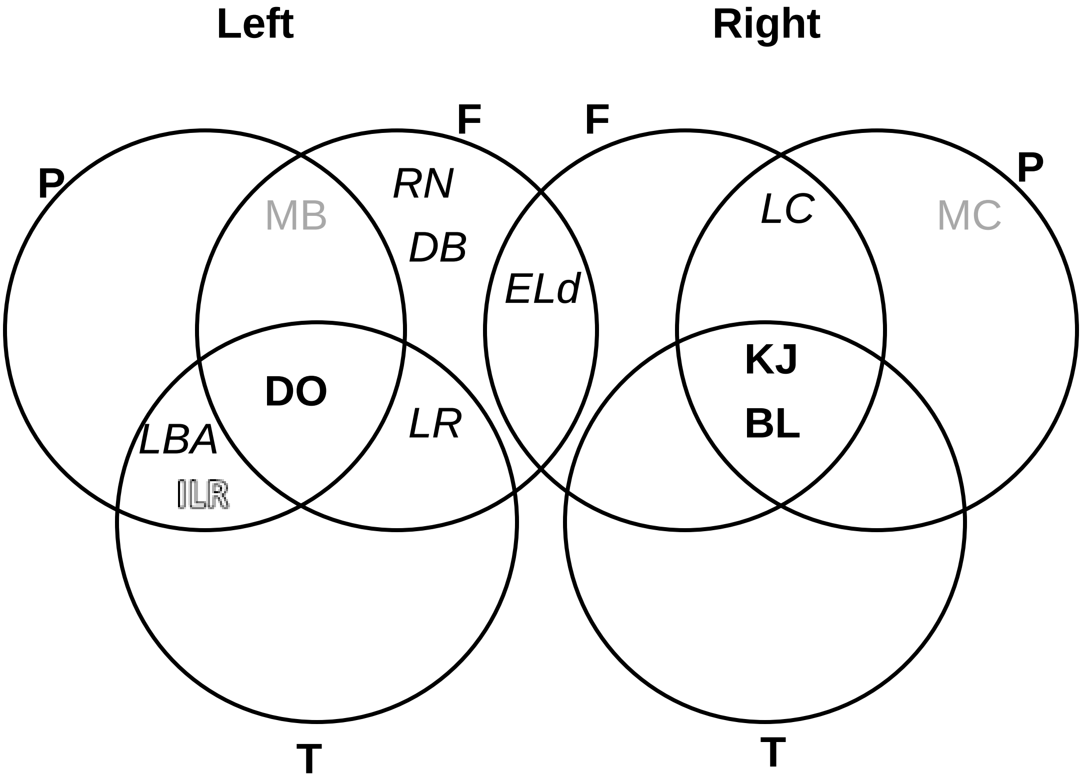

Fig. 5

Table 1. Patients who participated in this study, their age and sex, the site and the aetiology of their lesions, as well as time since lesion and the general neuropsychological status at the time point when the auditory cognitive testing reported here was carried out. All patients had normal performance in recognition of environmental sounds, as specified in inclusion criteria (the performance in the sound recognition test is indicated in z scores). Patient codes correspond to arbitrary string of letters.

Case	Age (years)	Sex	Lesion site	Aetiology	Time since lesion (days)	General neuropsychological status at the time of auditory testing	Sound recognition
MC	32	F	R parietal	Haemorrhage	17	Constructive apraxia	0.9
MB	17	F	L fronto-parietal	Cerebral empyema with partial veinous thrombosis	145	Word finding difficulties; sequellae of surface dysorthographia; discrete signs of constructive apraxia	-0.8
RN	55	F	L frontal	Haemorrhage	92	Minor executive disturbances	-0.4
DB	18	M	L frontal and thalamic, posterior corpus callosum, R cerebellar	Contusions; right cerebellar infarct; multiple diffuse white matter damage	46	Surface dysorthographia; minor difficulties in divided attention	0
LC	62	F	R fronto-parietal	Contusion, traumatic brain injury	12	Moderate executive dysfunction	-1.9
LR	36	M	L fronto-temporal	Intra-parenchymatous haematoma; temporal herniation; internal carotid artery aneurysma	101	Left hemineglect, partial anosognosia, executive dysfunction, minor signs of constructive apraxia, dyscalculia, visuo-spatial memory deficits, disturbed visuo-spatial reasoning	-0.8
ELd	22	M	Bilat. frontal	Traumatic brain injury	13	Word finding difficulties; moderate verbal memory deficit	-0.4
ELz	22	M	Bilat.; diffuse	Haemorrhage, traumatic brain injury	94	Severe verbal memory deficit, moderate executive dysfunction	-1.6
LBA	52	F	L temporo-parieto- occipital	Haemorrhage	19	Aphasia sequellae (word finding difficulties, paraphasias, paragraphia, alexia; but preserved comprension of simple and semi-complex orders), ideomotor and constructive apraxias, verbal memory deficit	-1.9
ILR	41	M	Left temporo-parietal (superficial)	Ischemic infarction	15	Conduction aphasia	-1.9
KJ	33	M	R fronto-parieto-temporal	Infarction; post-traumatic dissection of right internal carotid artery	111	Residual signs of left visuo-spatial neglect	0
BL	46	F	R fronto-parieto-temporal	Ischemic infarction	45	Left multimodal hemineglect, moderate executive dysfunction, dyscalculia	0.5
DO	46	M	L fronto-parieto-temporal	Ischemic infarction	111	Broca’s aphasia with agraphia (preserved comprension of simple orders)	-1.6

Table 2. Normative data for performance (means, standard deviation) in lateralization using ITD cues, as well as lateralization using IID cues and motion perception using ITD cues. For sound lateralization , the relative positions of two consecutive stimuli (Rel. loc.) are given here for both cues, further details only for lateralization ITD: the position attributed to stimuli with ITD = 0 ms (Centre); index of Left vs Right responses (Index L/R); index of response symmetry (Sym) for the extreme (LL-RR) and the near-centre positions (L-R); and the consistency with which a location was attributed to a specific value of ITD for the 5 positions (Consistency; LL, L, Ce, R, RR). For sound motion the perception of the direction of the moving sound was assessed.

60 normal subjects	Lateralization ITD										Lateralization IID	Motion ITD
	Rel loc	Centre	Index L/R	Sym LL-RR	Sym L-R	Consistency					Rel. loc.	
						LL	L	Ce	R	RR		
Mean	57.15	3.30°°	1.01	3.05	2.91	10.57°	11.42°	6.93°	11.42°	10.72°	56.95	52.42
Standard deviation	1.79	4.48°	1.183	9.52	12.10	4.41°	5.64°	11.32°°	5.64°	4.41°	1.84	8.93

Table 3. Patients who participated in the study and their performance (in z scores) in lateralization using ITD cues, SRM, as well as lateralization using IID cues and motion perception using ITD cues. For sound lateralization , the relative positions of two consecutive stimuli (Rel. loc.) are given here for both cues, further details only for lateralization ITD: the position attributed to stimuli with ITD = 0 ms (Centre); index of Left vs Right responses (Index L/R); index of response symmetry (Sym) for the extreme (LL-RR) and the near-centre positions (L-R); and the consistency with which a location was attributed to a specific value of ITD for the 5 positions (Consistency; LL, L, Ce, R, RR). For Rel loc and for the five Consistency measures deficient performance corresponded to z < -2.0. Centre, Index L/R, Sym LL-RR, Sym L-R assessed deviations that could be towards the right or left hemispace; hence deficient performance corresponded to z<-2.0 for right-ward or to z>2.0 for left-ward deviations. For sound motion the perception of the direction of the moving sound was assessed. For SRM three versions of the test were used, with different intensity differences between masked sound and masker (see Experimental procedure); the shape of the masking curve is described as U-shaped (U, i. e. as in normal controls) or non-U-shaped (NU); the number of false detections is indicated. Deficient performance is indicated in bold. NA = not assessed; other abbreviations as in the list. Four different profiles were observed: preserved SRM effect and preserved sound lateralization (MC, MB); preserved SRM effect and slightly (RN, DB) or more or less deeply deficient sound lateralization (LC, LR, ELd, ELz, LBA); absent SRM effect and preserved sound lateralization (ILR); and absent SRM effect and deficient sound lateralization (KJ, BL, DO).

Case	Lateralization ITD										SRM			Lateralization IID	Motion ITD
	Rel loc	Centre	Index L/R	Sym LL-RR	Sym L-R	Consistency					0dB	-2dB	-4dB	Rel. loc.	
						LL	L	Ce	R	RR					
MC	0.5	0	0.8	-0.4	0.4	-0.6	-0.4	0	0.6	-1.2	NA	NA	U; 1	0.6	0.5
MB	0	0.6	-0.6	0.6	-0.8	-0.3	0.7	0.5	-0.7	-1.4	U; 1	NA	NA	-0.5	0.5
RN	0.5	0.6	0.2	0.8	0.7	-1.6	-1.4	-0.6	-0.8	-1.3	U; 0	U; 0	NA	**-2.2**	0.3
DB	-1.2	**2.8**	0.6	-1.4	0.2	1.6	0.5	0.7	0.5	1.8	U; 0	NA	NA	-2.0	0.7
LC	**-11.2**	-1.2	**-2.3**	-1.6	-0.8	**-6.1**	**-5.5**	**-4.5**	**-4.1**	**-2.8**	U; 0	U; 0	NA	**-9.3**	**-2.6**
LR	**-2.9**	-1.9	-1.3	0.4	**-3.6**	**-2.7**	**-2.9**	-2.0	0.4	0.3	U; 0	NA	NA	**-5.4**	**-2.5**
ELd	0	**5.1**	1.6	-0.5	0.3	**-2.2**	0.5	1.4	1.1	**-2.4**	U; 0	NA	NA	**-6.0**	-1.5
ELz	0.5	-1.2	0.7	1.2	-0.7	-1.3	**-2.8**	0	**-3.0**	**-5.1**	U; 0	NA	NA	1.1	-1.1
LBA	0.5	-0.6	0	1.3	1.3	**-2.8**	0	**-2.1**	0.4	1.0	U; 2	NA	NA	0.5	-1.1
ILR	-0.5	0.4	-0.6	0.6	-1.2	0.4	0.7	-0.3	0.4	0.8	**NU; 16**	**NU; 14**	**NU**; 2	-1.8	0.4
KJ	**-8.5**	**3.1**	0.2	**-2.1**	0	**-2.9**	**-2.4**	1.4	**-3.4**	1.6	**NU**; 3	**NU; 11**	**NU; 15**	**-2.7**	-1.1
BL	**-2.3**	**8.3**	**2.5**	0.6	0.6	0.2	1.2	1.5	0.5	-0.1	**NU**; 0	**NU**; 1	NA	NA	-0.2
DO	-1.2	**-3.0**	**-3.1**	**-4.4**	**-4.3**	0.2	0.5	0.8	-0.8	0.2	**NU; 7**	**NU; 8**	NA	0	**-2.4**