

Cortical Motion Deafness

Case Study

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Summary

The extent to which the auditory system, like the visual system, processes spatial stimulus characteristics such as location and motion in separate specialized neuronal modules or in one homogeneously distributed network is unresolved. Here we present a patient with a selective deficit for the perception and discrimination of auditory motion following resection of the right anterior temporal lobe and the right posterior superior temporal gyrus (STG). Analysis of stimulus identity and location within the auditory scene remained intact. In addition, intracranial auditory evoked potentials, recorded preoperatively, revealed motion-specific responses selectively over the resected right posterior STG, and electrical cortical stimulation of this region was experienced by the patient as incoming moving sounds. Collectively, these data present a patient with cortical motion deafness, providing evidence that cortical processing of auditory motion is performed in a specialized module within the posterior STG.

Introduction

Perceiving dynamic aspects of our environment is an important function of our sensory systems. For humans, detecting and tracking the movement of objects is no longer a matter of survival as it is still for animals, but it allows us to gain information about the future path of objects and to react consequently. Yet, whereas the cerebral mechanisms that contribute to motion processing in the visual modality are well documented, much less is known about the auditory modality. Particularly, the existence of an auditory analog to area V5/MT that is specialized for visual motion (Dubner and Zeki, 1971; Griffiths et al., 1994) remains a challenging question (Griffiths et al., 1998; Kaas and Hackett, 1999; Romanski et al., 2000; Ducommun et al., 2002).

Despite recent evidence supporting the notion of segregated processing of auditory information into a ventral

“what” pathway mediating sound object recognition and a dorsal “where” pathway mediating auditory spatial processing (Rauschecker, 1998; Romanski et al., 1999; Rauschecker and Tian, 2000; Maeder et al., 2001), it remains unclear whether the discrimination of moving sound sources is independent from mechanisms that contribute to the localization of static sound sources (i.e., Middlebrooks and Green, 1991). Interestingly, a similar discussion had been carried out with respect to visual motion and location processing (Nakayama, 1985; Zeki, 1991). As argued by Nakayama (1985), three pieces of evidence were essential for the demonstration that dynamic visual signals are processed independently from static visual signals: (1) the demonstration of selective visual motion illusions such as the motion aftereffect (Wade et al., 1996), (2) the clinical syndrome of cortical motion blindness (Zihl et al., 1983), and (3) the existence of selective neural responses to visual motion (Dubner and Zeki, 1971).

In the auditory modality, studies in humans on the minimal audible movement angle (Perrott and Marlborough, 1989) and on the motion after-effect (Shu et al., 1993; Grantham, 1998) support the existence of a motion-specific analysis system. However, despite these psychophysical evidences, clinical and neurophysiological data do not unequivocally suggest the existence of neural correlates specific for this system. Although auditory motion processing can be impaired in patients with focal brain damage, these patients also presented deficits for auditory localization (Clarke et al., 2000; Griffiths et al., 1997b; Thiran and Clarke, 2003) or for fixed auditory lateralization (Griffiths et al., 1996, 1997a). Recently, a patient with a selective deficit for auditory motion has been described, yet brain damage was restricted to subcortical structures (Adriani et al., 2003). Thus, to our knowledge, there has been no description of a patient with focal cortical brain damage with a pure deficit for the processing of moving sounds. In animals, some electrophysiological evidence suggests that auditory motion and location information are processed by distinct neural substrates in both the cat’s primary auditory cortex (A1; Toronchuk et al., 1992) and the monkey’s lateral belt (Tian et al., 2001). Yet other evidence shows that neurons in monkey’s A1 (Ahissar et al., 1992) and in cat’s anterior ectosylvian sulcus (Jiang et al., 2000) are sensitive to cues for both auditory motion and location.

Data from neuroimaging studies are likewise contrasted since most of the brain areas reported as being selectively activated by moving sounds in some studies were also shown as being responsive to static sounds in other studies. These discrepancies are likely to result from methodological differences across studies (i.e., passive listening or active discrimination tasks; for discussion, see Zatorre and Penhune, 2001; Warren et al., 2002; Ducommun et al., 2002) and illustrate more generally the difficulty to compare findings from studies interested in one or the other subtype of auditory spatial processes with no direct comparison between those subtypes (e.g., Bushara et al., 1999; Lewis et al., 2000; Kaiser et al., 2000). Recent findings from studies directly

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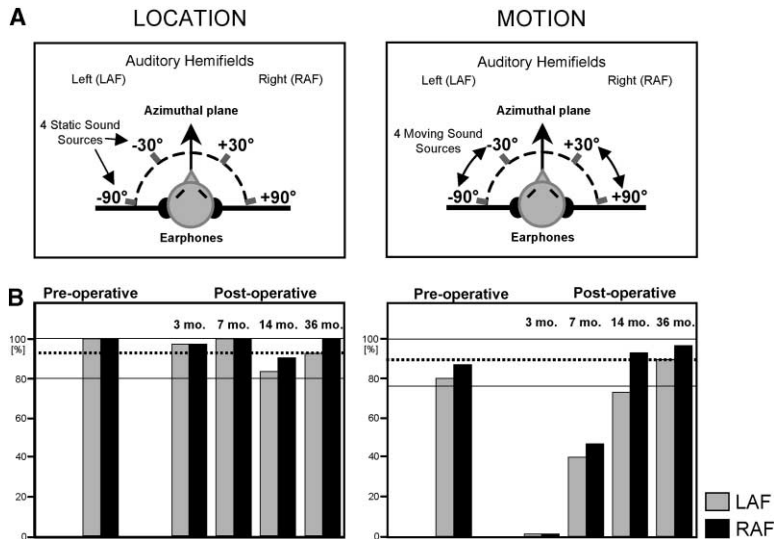


Figure 1. Spatial Auditory Tasks 1

(A) Stimuli were presented through earphones. Interaural time difference (ITD) was used to simulate sounds located at four different azimuthal positions (location task; left) or sounds moving between the four azimuthal positions (motion task; right). Two samples of sound were used within each hemifield, such that stationary stimuli were perceived as either “near” or “far” from midline (corresponding to the $\pm 30^\circ$ and $\pm 70^\circ$ azimuthal positions). Moving stimuli were perceived as going toward (from $\pm 70^\circ$ to $\pm 30^\circ$) or away from (from $\pm 30^\circ$ to $\pm 70^\circ$) midline. Location and motion discrimination were each tested separately within the LAF and the RAF. For further details, see text.

(B) Performance is given according to the AF of presentation. In the location task (left), the patient’s performance was normal in the LAF (gray bars) and RAF (black bars) at all test dates (preoperatively and postoperatively [3, 7, 14, and 36 months]). Performance was normal for the entire AF (see text and Table 1A).

In the motion task, preoperative performance was normal in the LAF (gray bars) and RAF (black bars). Postoperatively, at 3 and 7 months, the patient’s performance was severely deficient in both AFs. At 14 months, performance was mildly deficient in the LAF, but normal in the RAF. At 36 months, performance was normal in both AFs. For both spatial conditions, the 99% confidence interval and mean of the healthy control subjects is plotted.

comparing auditory motion and location processes with active or passive tasks suggest that differential brain activation mediates both processes. Using PET and fMRI in conjunction, Warren et al. (2002) showed bilateral activation both in the planum temporale (PT) and in the parieto-temporal operculum (PTO) in contrasts between sounds rotating around the head and stationary sounds located in front of the head. Similarly, Pavani et al. (2002) reported the selective activation of the PT, the superior parietal lobule, and the prefrontal cortex when contrasting vertical and horizontal sound movements with stationary sounds. Using electrical neuroimaging, we have shown that discriminating the direction of sounds moving randomly in opposite directions with respect to the discrimination of stationary sounds located at different positions yielded two critical time periods during which moving sounds activated the right postero-inferior parietal and inferior frontal cortex (Ducommun et al., 2002).

Collectively, these results support the idea that the processing of auditory motion is carried out by a network of brain areas (Warren et al., 2002) with no direct evidence for the existence of one anatomically distinct module specialized in auditory motion processing. Although some of the aforementioned findings underline the necessary role played by the posterior STG (including PT) and PTO (Warren et al., 2002; Pavani et al., 2002) in auditory motion processing, they do not suggest that these structures would be sufficient to process auditory motion. To that aim, further behavioral evidence from brain-damaged human subjects showing a motion-selective deficit, as it has been shown following damage to area V5/MT in the visual domain (Zihl et al., 1983), would be needed.

Here we describe a patient who developed a selective deficit in the perception and the discrimination of the direction of moving sounds (cortical motion deafness) following subtotal resection of the anterior temporal lobe

and additional focal cortectomy of the posterior STG. This neuropsychological finding is corroborated by preoperative neuroimaging evidence for auditory motion, suggesting that the right posterior STG contains a module specialized for the analysis of auditory motion.

Results

Behavior

Auditory functions were tested during invasive epilepsy monitoring (six days prior to the operation) and at four different times after the operation (3, 7, 14, and 36 months). Auditory testing included the discrimination of different spatial locations (Figure 1A), the discrimination of different directions of motion (Figure 1A), and the identification of nonverbal environmental sounds. In addition, we tested auditory motion and location processing at 36 months with more sensitive paradigms (Figure 2).

In Figure 1B, the patient’s mean accuracy rate (percentage of correct responses) is illustrated for spatial condition (location; motion), hemifield (left auditory hemifield, LAF; right auditory hemifield, RAF), and testing date (preoperatively; 3, 7, 14, and 36 months postoperatively) separately. Prior to right temporal lobe resection, auditory scene analysis (motion, location, and identification) was normal with respect to the applied test paradigms if compared to a group of healthy control subjects. The patient discriminated correctly the location (100% correct), motion (83% correct; Figure 1B), and identity (83% correct) of the auditory stimuli (Table 1A). No differences were observed between LAF and RAF.

Three months after the operation, performance on the sound motion task was at zero percent, since the patient was incapable of performing the motion direction discrimination task and could not be convinced to respond to our test stimuli. She stated, “I do not perceive the sounds as moving at all, but rather as being completely

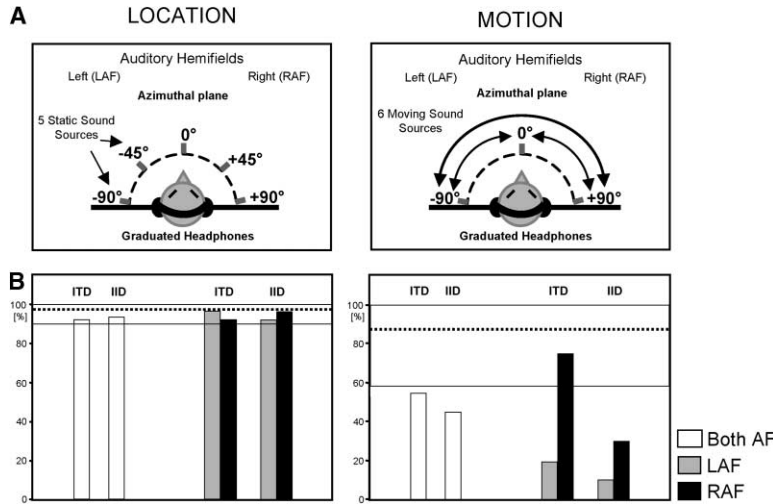


Figure 2. Spatial Auditory Tasks 2

(A) Two similar versions of the tasks were created accordingly to the parameter used (ITD or IID) to simulate different locations or different displacements of motion in the azimuthal plane. For the location task (left), one central and four lateral positions, two in each hemifield, were simulated. For the motion task (right), six different motions were simulated: extreme left to extreme right and the reverse; extreme left to midsagittal plane and the reverse; and extreme right to midsagittal plane and the reverse (see text for further details). (B) Performance is given according to AF of presentation and to sound parameter (ITD-IID). In the location task (left), performance was normal in all AFs and for each parameter. In the motion task, performance was severely deficient in the entire AF and for both ITD and IID cues (white bars). Note that hemifield analysis revealed normal performance in the RAF (black bar) but not the LAF (gray bar) for the IID parameter. For both spatial conditions, the 99% confidence interval and mean of the healthy control subjects is plotted.

stable.” She could not determine whether the targets moved toward or away from her. In contrast, discrimination of auditory location (97%; no hemifield differences) and auditory identity (80%) remained normal (Figure 1; Table 1A). Visual motion perception (Blanke et al., 2003) was tested in order to verify whether the patients’ motion deficit was a general motion impairment or specific for the auditory modality. The patient’s psychophysical performance was entirely normal for all directions with respect to age-matched healthy controls ($1.0\% \pm 0.4\%$ CM; mean \pm SD) and was tested preoperatively ($0.9\% \pm 0.3\%$ CM) and 3 months postoperatively ($1.2\% \pm 1.0\%$ CM).

Seven months after the operation, the patient was at chance level for auditory motion discrimination (43%) without important hemifield differences (LAF: 40%; RAF:

47%; Figure 1; Table 1A). Motion stimuli were still perceived as stable. Performance for both location (no hemifield differences) and identity tasks was flawless (100%).

Fourteen months after the operation, performance for the motion task was still deficient, but only in the contralesional hemifield (LAF: 73%; Figure 1B; Table 1A). Performance for the entire AF (83%) and ipsilesional hemifield (RAF: 93%) was normal. The patient did not perceive moving sound sources as stable any more but experienced them as moving. She considered the latter task more difficult than the location task, consistent with behavioral data in normal subjects (Middlebrooks and Green, 1991; Lessard et al., 1999). Location (87% correct; no significant hemifield differences) and identity (100% correct) tasks were still normal.

Table 1. Performance in Auditory Spatial Tasks

(A) ITD Condition ^a							
Examination	Months	Motion			Location		
		Total Score	LAF	RAF	Total Score	LAF	RAF
1 st	PreOp	83% (-1.31)	80% (-1.39)	87% (-0.66)	100% (1.45)	100% (1.01)	100% (1.20)
2 nd	3	0% (-14.92)	0% (-13.69)	0% (-15.02)	97% (0.97)	97% (0.63)	97% (0.60)
3 rd	7	43% (-7.87)	40% (-7.48)	47% (-7.26)	100% (1.45)	100% (1.01)	100% (1.20)
4 th	14	83% (-1.31)	73% (-2.46)	93% (0.33)	87% (-0.65)	83% (-1.13)	90% (-0.80)
5 th	36	93% (0.47)	90% (0.15)	97% (0.99)	97% (0.62)	93% (0.13)	100% (1.2)

(B) ITD-IID Conditions ^b							
Auditory Cues		Motion			Location		
		Total Score	LAF	RAF	Total Score	LAF	RAF
ITD		55% (-2.18)	20% (-2.04)	75% (-0.61)	92% (-1.76)	96% ^c	92% ^c
IID		45% (-3.15)	10% (-2.89)	30% (-2.95)	93% (-1.2)	92% ^c	96% ^c

Mean accuracy rate (%) and z-scores (in parentheses) are given; deficient performance, i.e., $z < 2$, is in bold.

^a The patient’s performance in auditory spatial tasks across the different preoperative and postoperative testing dates. Performance is compared to that of a control group.

^b The patient’s performance in auditory spatial tasks (at 36 months) with respect to both ITD and IID auditory cues. Performance is compared to that of a control group.

^c Mean accuracy rate per auditory hemifield not available for the control population.

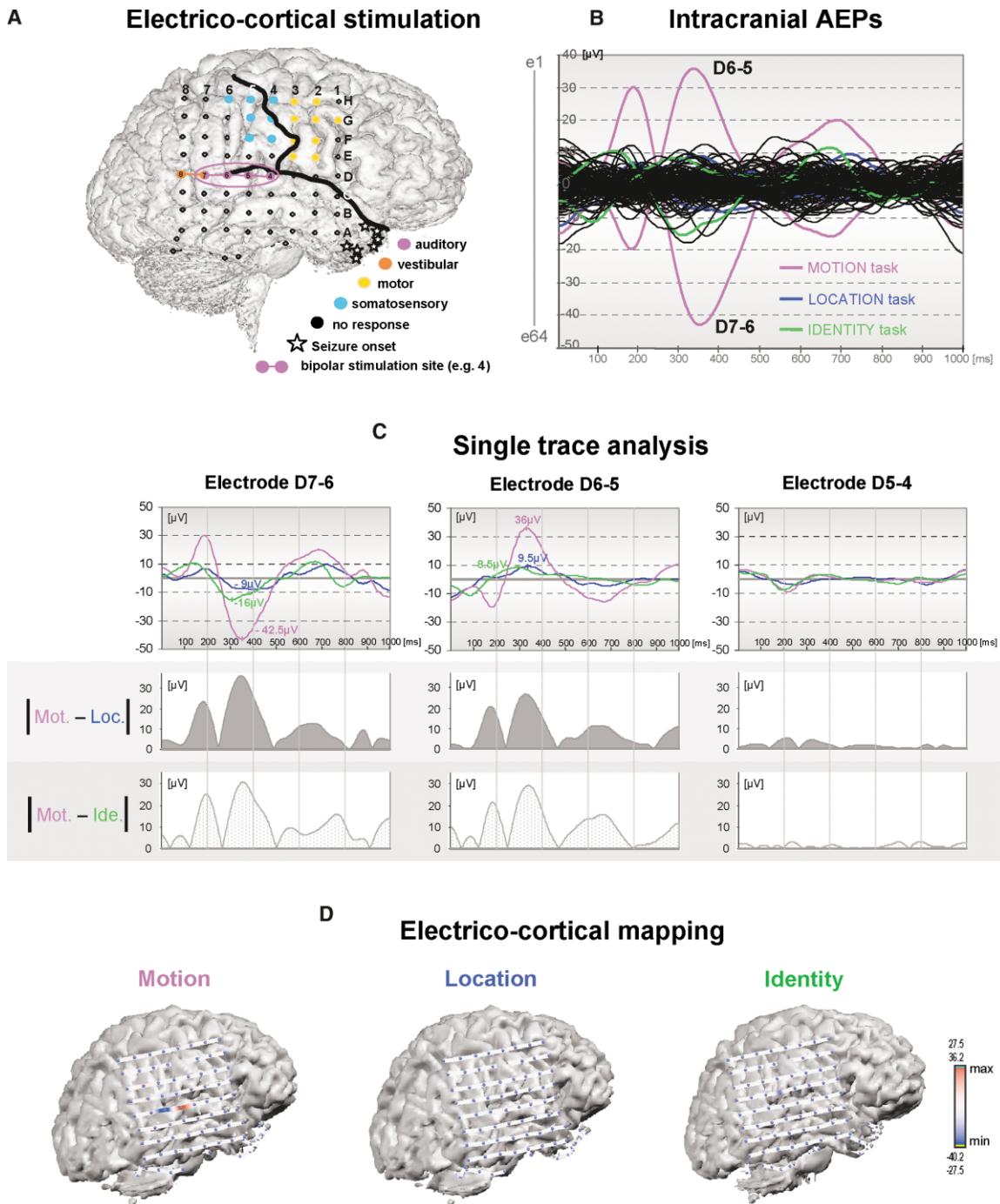


Figure 3. Anatomical Location of Electrode Sites Related to Auditory Motion

(A) 3D MRI surface reconstruction of the patient’s right hemisphere. The electrode sites where electrical stimulation (ES) evoked behavioral responses are given. Primary sensory (blue) and motor responses (yellow), as well as auditory (pink) and vestibular responses (orange) are indicated. Electrode sites where electrical stimulation induced auditory responses (experience of sounds approaching the patient’s face) are indicated in pink; see text for further details). Sylvian fissure and central sulcus are indicated by black lines. The epileptic focus is indicated by stars in the anterior and medial temporal lobe. Numbers and letters indicate the respective electrode positions on the 64-electrode grid (8 × 8). ES was carried out between adjacent electrodes within a row (i.e., D1-2, D2-3, D3-4, etc.).

(B) Intracranial AEPs for the lateral 64 electrode sites (8 × 8 grid) on the lateral convexity. Intracranial AEPs are shown for the auditory location (location AEPs, blue), motion (motion AEPs, pink), and identity (identity AEPs, green) tasks. Note the two electrode sites with the prominent motion AEPs components (pink) at 200 ms, 350 ms, and 700 ms. These motion AEPs were selective, since no other electrode site showed prominent responses in this condition. In addition, no AEPs were recorded in the two other conditions.

(C) The top of the figure shows the motion AEPs (pink lines) at these two electrode sites (left column, D6-7; middle column, D5-6) in more detail comparing them in the three auditory conditions. We also show electrode site D4-5 (right column), where electrical stimulation also induced the experience of auditory motion. Note that only sites D6-7 and D5-6 led to strong AEPs at 200 ms, at 350 ms, and at 700 ms in

Thirty-six months after the operation, the patient performed normally in the motion (93%), location (97%), and identity (93%) tasks. No hemifield differences were found in the location (LAF: 93%; RAF: 100%) or motion (LAF :90%; RAF: 97%; Table 1A; Figure 1B) tasks.

Testing with more sensitive paradigms at 36 months revealed that the patient's performance was deficient for the auditory motion task, but not the location task. Analysis of the entire auditory field (AF) showed 55% correct answers for motion tested by interaural intensity differences (IID) and 45% for motion tested by interaural time differences (ITD; Figure 2A). In addition, our patient made significantly more errors than controls with respect to the perception of the direction of auditory motion stimuli (i.e., rightward motion perceived as leftward motion or vice versa). She had eight such directional errors using the ITD stimuli and four using the IID stimuli. 83% of these 12 directional errors were found for stimuli moving in the ipsilesional (right) direction. If our patient's performance was analyzed for each hemifield separately, performance was deficient for both AFs (LAF, RAF) in the IID task (LAF: 10%, RAF: 30%), whereas performance in the ITD task was only deficient in the contralesional AF (LAF: 20%, RAF: 75%; Figure 2B; Table 1B). Performance in the location task was normal in the IID (93%) and ITD (92%) tasks (Figure 2B; Table 1B).

In conclusion, our patient presented impaired auditory processing that was selective for auditory stimulus class (motion versus location and identity) as well as sensory modality (auditory motion versus visual motion). Her auditory motion deficit predominated in the contralesional hemifield and for sound sources moving in the ipsilesional direction.

Intracranial Electrical Stimulation

Electrical stimulation (ES), carried out prior to resective surgery, suggested the implication of the right posterior STG in auditory motion processing. As can be seen in Figure 3A, ES of the electrode contacts on the posterior STG (bipolar stimulation site D4-5, D5-6, and D6-7) led at all three sites to auditory motion responses that were always experienced by the patient as if "there was a humming sound coming towards [her] face." The speed of motion was described as slow, continuous, and approaching her horizontally. Depending on the bipolar electrode position, the sound was perceived in different AFs. ES at site D4-5 was experienced as bilateral and symmetrical in intensity. ES at site D5-6 was also experienced as bilateral, but with a contralateral predominance. At site D6-7 the sound was experienced more weakly and only in the ipsilateral auditory field and was associated with vestibular responses. Other electrode sites on the parietal and temporal lobe did not induce

any overt auditory responses. Further responses are indicated in Figure 3A.

AEPs

Intracranial AEPs, carried out prior to resective surgery, were analyzed for all implanted electrodes separately during the auditory location, motion, and identity conditions. Overall, the strongest intracranial AEP responses were observed in the region of the posterior STG after the presentation of moving sounds (Figure 3B). Single trace inspection revealed that the motion AEP was characterized by three peaks, at ~200 ms, ~350 ms, and ~700 ms, with the highest response at 350 ms. The peak-to-peak amplitude (between the ~200 ms and ~350 ms peak) was 72.5 μ V at electrode site D6-7 and 56 μ V at electrode site D5-6. Note that only motion AEPs recorded from electrodes D6-7 and D5-6 led to strong AEPs (Figure 3C, left). No other prominent responses were obtained at nearby or more distant sites (i.e., electrodes D4-D5; Figures 3B and 3C). This selective response to auditory motion is further illustrated in Figure 3C, which compares the intracranial AEPs for motion (pink), location (blue), and identity (green) at electrodes D6-7 (left), D5-6 (middle), and D4-5 (right). We also plotted the absolute difference (in μ V) between the motion and location task (gray) and motion and identity task (white) for each of these electrode sites in order to highlight the differential motion responses at ~200 ms, ~350 ms, and ~700 ms. As can be seen in Figure 3A, the electrode sites that generated the motion-selective components (electrodes D6-7, D5-6) were immediately adjacent and localized on the posterior STG. Recall that ES of both sites induced the experience of auditory motion (Figure 3A). The three peaks of the motion AEP were characterized by a phase inversion between electrode site D6-7 and D5-6, particularly at 350 ms (Figures 3B and 3C), suggesting that the generator of the motion AEP component is localized at electrode D6. Figure 3D depicts the anatomical selectivity of the motion AEP and plots the intracranial AEP amplitude at 350 ms separately for all electrodes over the lateral convexity.

Concerning auditory location and identity conditions, we were surprised to find that intracranial auditory EPs to stationary sounds and nonverbal environmental sounds led to much smaller or no responses at all. Maximal responses (peak-to-peak amplitude) are indicated in Figures 3B and 3C and did not surpass ~26 μ V.

Resective Lesion

Lesion extent and location was documented and quantified on postoperative magnetic resonance imaging (MRI) scans. 160 contiguous 1 mm T1-weighted images were collected to construct the 3D MRI. The resection

the motion discrimination task. (Thus, auditory location and identity discrimination did not lead to AEPs at these two electrodes.) The maximal peak amplitude of the 350 ms peak is depicted for each auditory condition and each of the three electrode sites. The lower graphs show for each electrode site separately the amplitude differences over time (in μ V) between the motion AEP-location AEP (middle row, gray area) and between motion AEP-identity AEP (bottom, row white dashed area).

(D) This figure shows the intracranial AEP distribution over the cortex for the 64 lateral electrode sites at 350 ms for the auditory motion task (left), the auditory location task (middle), and the auditory identity task (right). Thus, the motion AEPs led to a strong focal electric field at electrode site D5 and D6, which was not observed for the location AEPs and identity AEPs. The amplitude of the intracranial AEP is shown in blue (negative values) and red (positive values) ranging from -27.5 to +27.5 μ V. The same scale is used for all three auditory tasks.

consisted of a subtotal anterior temporal lobe resection as well as a focal cortectomy of the posterior STG and lateral parts of PT and HG (see below). Cortectomy was performed because intracranial EEG recordings had shown spread of ictal activity to the posterior STG and middle temporal gyrus.

In detail, the resection extended from the anterior pole of the temporal lobe (including amygdala and uncus, but leaving the hippocampus except its most rostral parts intact) to the posterior third of the temporal lobe. In the posterior part of the temporal lobe, the resection did not include the fusiform or the inferior and middle temporal gyri (Figure 4). The resection included further the planum polare and the posterior part of the STG that bordered with the angular gyrus (gray arrow in Figures 4A–4C). Only the lateral aspects (approximately 4–5 mm) of PT (Figures 4A and 4B; white arrows) and Heschl's gyrus (HG; Figures 4A and 4B; dashed white arrows) were resected. PT and HG were undercut. Insula and parietal lobe remained intact (Figure 4A). In conclusion, the resection included the anterior temporal lobe and within the posterior temporal lobe the posterior STG, lateral PT, and lateral HG. The resection included the cortex where phenomenological (by electrical stimulation) and electrophysiological (AEPs) responses to auditory motion were observed (see Figure 3).

Discussion

Previous Neuropsychological Studies

Deficits for auditory motion processing have been previously described following cortical (Griffiths et al., 1996, 1997a; Clarke et al., 2000; Thiran and Clarke, 2003) or subcortical (Griffiths et al., 1997a, 1997b; Adriani et al., 2003) brain damage. However, in the studies of Griffiths et al. (1996, 1997a; patient HV), Clarke et al. (2000; patients CZ and MA), and Thiran and Clarke (2003; patient NM), all patients also performed pathologically on fixed auditory lateralization tasks (Griffiths et al., 1996, 1997a) or on auditory location discrimination tasks (Clarke et al., 2000; Thiran and Clarke, 2003). Moreover, even if a predominant deficit for auditory motion processing might suggest that the two spatial processes are dissociable (Griffiths et al., 1994; Poirier et al., 1994; Clarke et al., 2000; patient CZ), auditory location processing should ideally be normal, as is the case in motion blind patients for the localization of visual targets (Zihl et al., 1983). This is the case in the present patient: the auditory deficit was shown to be selective for moving sounds, with preserved processing of stationary and nonverbal environmental sounds (as in case 22 of Adriani et al., 2003, following subcortical brain damage). This dissociation was found with simplified paradigms (adapted to our patient's clinical condition and comparable to a previous study in healthy subjects; Ducommun et al., 2002) and was not present in a group of healthy control subjects. In addition, the dissociation was found with more sensitive paradigms independent of whether location and motion were simulated by IID or ITD. While we cannot exclude that our patient's performance differences between the more sensitive motion and location paradigms were due to differences in task difficulty, the severity and selectivity of her deficit in both the sensitive as well as the simplified paradigms would rather argue

against this deficit being only the result of task difficulty. Another point of concern might be that the present findings did not test auditory motion *per se* since the spatial percept (either static or moving) associated with ITD or IID modulation is considerably different from the natural condition in which both interaural cues as well as binaural cues can be used by the nervous system. Yet, it has been shown that auditory motion can be perceived and tested with even more impoverished stimuli than those used in the present study (Perrot and Strybel, 1997). In addition, Paavilainen et al. (1989) have found no electrophysiological differences between auditory locations produced either in the free-field or by using ITD or IID, suggesting that auditory processing in the free field or through headphones involves the same or similar neuronal mechanisms.

The motion deficit of our patient predominantly affected the contralesional LAF, which is consistent with animal (Altman and Kalmykova, 1986) and human (Poirier et al., 1994; Altman et al., 1987) lesion studies. The contralesional deficit was found with simplified and more sensitive (ITD) paradigms. Although our patient's performance was deficient in both AFs if tested with the more sensitive IID paradigm (Figure 2B), her performance was again lower in the contralesional AF. We note that despite the predominance of our patient's deficit in the contralesional AF, auditory motion processing was affected for the entire AF as reported with respect to the visual fields in patients with cortical motion blindness due to bilateral (Zihl et al., 1983) and unilateral (Barton et al., 1995) brain damage. A further observation allows us to link cortical motion deafness in our patient to cortical motion blindness: our patient had a predominant deficit for judging auditory motion in the ipsilesional direction (Barton et al., 1995; Vaina et al., 2001). Cortical motion deafness in our patient is thus characterized by deficient motion processing in the entire AF but predominates in the contralesional AF and for the ipsilesional direction of motion. These three characteristics have also been described in patients with cortical motion blindness with respect to moving visual stimuli (Barton et al., 1995; Vaina et al., 2001). Additionally, we were able to show by measuring auditory processing preoperatively that processing of auditory motion, location, and identity was normal and did not differ for the different auditory stimulus classes. This information is rarely available in neurological patients. Finally, the postoperative motion discrimination deficit of our patient was selective for the auditory modality, since visual motion discrimination was normal and unaffected by the operation. Together, these results extend previous neuropsychological findings following cortical (Griffiths et al., 1996, 1997a; Clarke et al., 2000) and subcortical (Griffiths et al., 1997a, 1997b; Adriani et al., 2003) brain damage as well as previous auditory psychophysical data suggesting the existence of a system specialized for the processing of auditory motion (Shu et al., 1993; Grantham, 1998). A question that might arise from our behavioral results is why the patient showed a strong motion impairment with more sensitive paradigms 36 months after the operation but performed normally with the easier paradigms. We suggest that her increased performance is related to functional recovery due to cortical plasticity changes (Adriani et al., 2003). Potential structures of recovery might have been medial aspects of right PT,

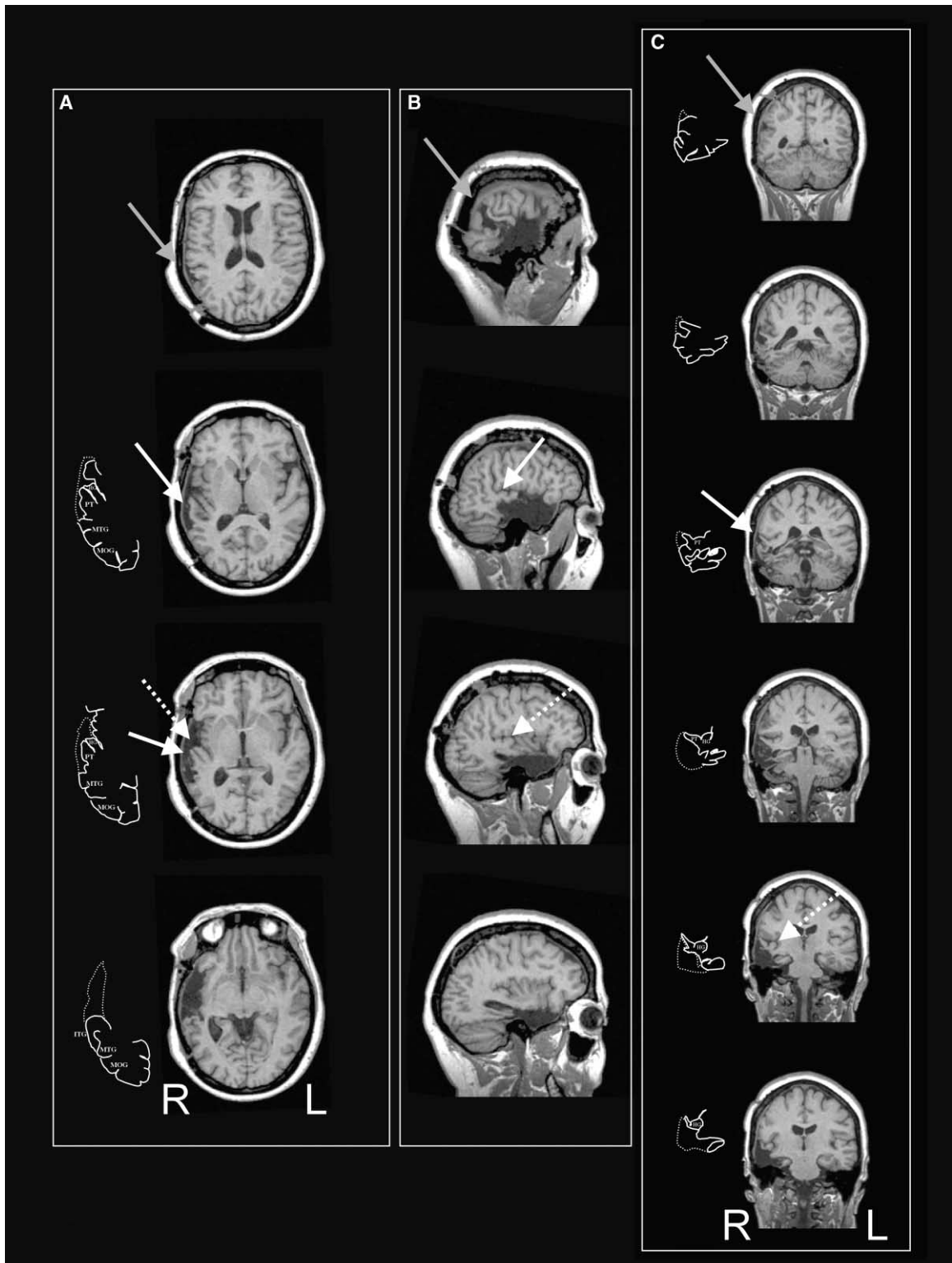


Figure 4. Postoperative MRI

MRI scans of the patient's postoperative lesion (shown in radiological coordinates; i.e., left [L]-right [R] reversal). Transverse (A), sagittal (B), and coronal (C) sections are given. To the left of several transverse and coronal MRI sections, a schematic drawing has been added in order to highlight the lesion. The resection consisted of a subtotal anterior temporal lobe resection that included amygdala and uncus as well as the anterior parts of the inferior, middle, and superior temporal gyri. The posterior parts of the middle and inferior temporal gyri were preserved. The resection in the posterolateral temporal lobe included the posterior STG (gray arrow indicates posterior resection end), the lateral 5 mm of the PT (white arrow), and the lateral HG (dashed white arrow). All panels show the preservation of medial HG and medial PT, whereas the planum polare has been resected. For further details see text. MOG, middle occipital gyrus.

right HG, and adjacent parts of the right parietal and temporal lobes, as well as contralesional structures. Additionally to our patient's deficit in discriminating moving sounds, the patient also experienced auditory phenomenological abnormalities during the experimental conditions, as reported by Griffiths et al. (1996) as the "absence or strongly diminished perception" of auditory motion. In our patient, sounds that were perceived as moving prior to the operation were no longer perceived as moving, allowing us to link a selective phenomenological abnormality (in an experimental paradigm) to a selective neuropsychological deficit as described previously in the visual modality as motion blindness (Zihl et al., 1983). In accordance, we propose to call our patient's clinical condition cortical motion deafness (MD).

With respect to the underlying neuroanatomy, impaired auditory motion processing has been observed following right hemispheric brain damage (Bellmann et al., 1998; Griffiths et al., 1996, 1997a; Clarke et al., 2000; Adriani et al., 2003; Thiran and Clarke, 2003) and/or left hemispheric brain damage (Bellmann et al., 1998; Adriani et al., 2003). In more detail, two studies proposed that vascular lesions at the parieto-temporal junction and the insula lead to impaired auditory motion processing (Griffiths et al., 1996, 1997a; Bellmann et al., 1998). The surgical lesion in our patient included in the right hemisphere the anterior temporal lobe, the posterior STG, as well as the lateral aspects of PT and HG, without damage to the insula and the inferior parietal cortex (see Figure 4). The present patient's surgical lesion is thus quite limited and confined to the right hemisphere when compared to previous studies that reported neurological patients with impaired auditory motion processing. Although we cannot exclude that resection of the anterior temporal lobe might be a necessary condition for MD, restricted resections of the anterior temporal lobe have not previously been associated with deficits in sound motion perception (Arnott et al., 2004). Moreover, based on the selectivity of the stimulation-induced responses and intracranial AEPs prior to the operation (see below) and the fact that medial aspects of PT and HG remained largely intact, our data suggest that damage to the right posterior STG, lateral PT, and lateral HG resulted in the clinical condition of MD. This extends and confirms previous neuroimaging work about the role of the parieto-temporal junction and the STG in auditory motion processing and is discussed below.

Functional Neuroanatomy of Auditory Motion Processing

Preoperative intracranial electrical stimulation and AEPs revealed selective phenomenological and electrophysiological responses to auditory motion on the right posterior STG. First, electrical stimulation of this region led to the auditory experience of external moving sounds that were approaching the face, concordant with observations by Mullan and Penfield (1959; i.e., case 32). Our patient did not experience static (external or internal) sounds as can also be induced by electrical stimulation of the STG (Mullan and Penfield, 1959; i.e., case 23). As in the visual system where electrical stimulation of striate and extrastriate cortex has been shown to evoke,

respectively, the experience of static and moving phosphenes (Brindley and Lewin, 1968; Girvin et al., 1979), these different phenomenological responses suggest differences of the functional properties of the underlying stimulated neuronal module(s). In our patient, the induction of the experience of moving sounds suggests that these underlying neuronal module(s) are involved in auditory motion processing.

This is further corroborated by the intracranial AEPs. Strongest motion AEPs were recorded from those sites on the right posterior STG, whose electrical stimulation resulted in the subjective experience of auditory motion. Even immediately adjacent temporal and parietal cortex did not show strong intracranial motion AEPs. This anatomico-functional convergence of a phenomenological response (the artificial induction of the experience of auditory motion by electrical stimulation) and electrophysiological responses to auditory motion (AEPs) provides evidence for similar functional properties of the underlying neuronal module(s) (Blanke et al., 1999, 2000). Intracranial AEPs at these three sites on the posterior STG not only were strongest, but also selective, for auditory motion, since AEPs to auditory location and identity evoked no signal or weaker signals at these sites. Given that auditory motion was simulated by ITDs (as for behavioral measures), we cannot exclude that motion AEPs were not evoked by motion per se, but rather by the detection of the component cues. However, the timing of the present AEP data shows that all AEP components appear when the phase shifts used to induce the sensation of sound motion have already been integrated to form an acoustic object. According to Yabe et al. (1999), there exists a ~ 200 ms window within which acoustic stimulus cues are integrated along the auditory ascending pathways and within the primary auditory cortex and treated as a single entity. Since the AEP components to our motion stimuli were observed after this ~ 200 ms window of integration, we suggest that our AEP responses rather reflect auditory motion processing than timing differences (although this has not been directly tested in the present study). This is also supported by previous AEP data showing two epochs after ~ 200 ms during which auditory motion as compared to auditory location induced a differential neural activity in the right temporo-parietal region (Duc-commun et al., 2002; Xiang et al., 2002).

An unexpected result of our study is the absence of phenomenological and neuropsychological responses to auditory location or identity. Although AEPs to location led to responses, these were much weaker than to motion. In view of clinical data showing that lesions of the right anterior temporal lobe were associated primarily with impaired auditory recognition (Clarke et al., 2000, 2002; Adriani et al., 2003), we would have expected corresponding deficits and/or more ample intracranial EPs to stationary and nonverbal environmental sounds over the temporal lobe. Several explanations may account for this. First, there is evidence that a fair degree of functional reorganization might occur in the early phase after lesion onset (Adriani et al., 2003). In addition, this functional reorganization might occur to different degrees for different auditory tasks (see also Adriani et al., 2003). Thus, we cannot exclude that our patient, who was tested 3 months after her operation, had already

recovered auditory location and identity functions. A second explanation may lie in the fact that the intracranial electrodes did not sample from all regions that were lesioned in the studies of Zatorre and Penhune (2001) and Clarke et al. (2000, 2002) or that sites coding auditory location might be localized at areas on the STG or within the sylvian fissure, which were not covered by electrodes (i.e., PT and HG). Finally, it has to be noted that the absence of ample intracranial EPs to auditory location in the present patient is consistent with previous electrophysiological (Ducommun et al., 2002; Xiang et al., 2002) as well as PET and fMRI (Warren et al., 2002) studies in which the direct comparison of moving versus stationary sounds yielded no location-specific responses in right temporo-parietal cortex.

Taken together, our results suggest that the processing of auditory motion is lateralized to the right hemisphere, consistent with several recent neuroimaging as well as clinical studies (Griffiths et al., 1996, 1997a; Baumgart et al., 1999; Ducommun et al., 2002). However, since recent evidence has shown that auditory motion analysis generates bilateral activation of the PT (Warren et al., 2002; Pavani et al., 2002) and the PTO (Warren et al., 2002), further investigations with left-sided or bilaterally implanted patients would be necessary to determine the anatomical lateralization of auditory motion processing.

A Specialized Module in Auditory Motion Processing?

Despite the convergence of our neuropsychological, phenomenological, and electrophysiological data providing evidence that the right posterior STG may be specialized for auditory motion analysis, it might be argued that our results cannot be applied to normal brain function, as the present study has been carried out in a patient with right temporal lobe epilepsy. However, even if early ictal discharges spread to the posterior temporal lobe, the patient's epileptic focus was found in the anterior medial temporal lobe and approximately 5 cm anterior with respect to the electrode sites that coded selectively for auditory motion. In addition, the location of sensory and motor functions did not suggest deviant brain organization with respect to anatomical representation of cortical functions. The selective implication of the right posterior STG in auditory motion processing is further supported by recent neuroimaging data revealing the differential activation of the parieto-temporal junction if moving sounds are compared to stationary sounds. With respect to gyral anatomy, these neuroimaging studies have revealed the selective activation of the PT either bilaterally (Warren et al., 2002; Pavani et al., 2002) or with a right lateralization (Baumgart et al., 1999) with additional differential activation of the PTO (Warren et al., 2002), the superior parietal lobule, and the prefrontal cortex (Pavani et al., 2002). The selective activation of the PT in response to moving sounds has led some authors to propose that the PT would act as a "computational module" (Warren et al., 2002) that continuously disentangles the intrinsic spectro-temporal features of a sound from the spectro-temporal effects due to its own movement. This computational stage would result in the subsequent formation of a spatial

percept at the PTO. According to our previous study, the next stage of this processing would be achieved at the level of the inferior parietal lobule (IPL) and the dorsolateral prefrontal cortex and would consist in the discrimination of the direction of displacement of the spatial percept (Ducommun et al., 2002). What is notable in the present study is that focal electrical cortical stimulation of the posterior STG (including the lateral PT) was sufficient to produce the perception of a "low humming *incoming* sound." Thus, the auditory object was not only perceived simply as moving, but also as moving in a certain direction, which would imply a high degree of functional specialization already at the level of the posterior STG, while we would have expected such properties either lying in a specific pattern of connectivity between PT, PTO, and IPL or appearing farther in the "motion pathway," at the level of either PTO or IPL. Though we cannot rule out the possibility that the propagation of the current induced by electrical cortical stimulation was not restricted to the posterior STG, electrical stimulation at the PTO or the IPL led neither to EPs to moving sounds nor to the experience of moving sounds, speaking against their direct implication in auditory motion processing. As the lateral part of HG has been resected in the present patient, we cannot exclude that a lesion of this structure is necessary for causing motion deafness. Yet, since previous neuroimaging studies have not implicated HG in auditory motion processing (Baumgart et al., 1999; Pavani et al., 2002; Warren et al., 2002) and since the extent of the posterior resection predominated on the PT and the posterior STG, we suggest that HG is not directly involved in auditory motion processing. This raises the possibility that a subregion within right posterior STG might constitute the auditory analog to area V5/MT in the visual modality. As we recorded motion-specific AEPs from the posterior STG and considering that medial parts of PT were not included in the resection, it may be the case that the critical region for auditory motion processing comprises the posterior STG and the lateral PT, with all the care due to uncertainty regarding anatomy of the PT (Westbury et al., 1999).

In conclusion, the present study linked parts of the right posterior STG to auditory motion processing by a convergence of electrophysiological, phenomenological, and neuropsychological data. Together, these data corroborate the involvement, in general, of the posterior STG in auditory spatial processing as part of a specialized postero-lateral pathway. Importantly, our data also provide evidence for the existence of an auditory motion module within the right posterior STG. By analogy with the V5/MT complex in the visual domain, we propose that the right posterior STG, including the lateral PT, may constitute the core region for auditory motion analysis.

Experimental Procedures

Patient

This 43-year-old right-handed female patient suffered from epilepsy since the age of 32 years. Her complex partial seizures started with an epigastric aura followed by the sensation of globally diminished hearing without lateralization. These manifestations were followed by staring, loss of consciousness, and bimanual automatisms. There were no secondary generalizations and no postictal aphasia.

Rarely, she had the dreamlike impression of flying and lightness and the distinct feeling that somebody was behind her (more frequently on the right side) although upon turning around there was nobody there. Her seizures were never accompanied by the perception of visual or auditory motion. She was addressed to noninvasive presurgical epilepsy evaluation for pharmacoresistant epilepsy, which consisted in ictal and interictal video EEG recordings, 3D MRI, interictal positron emission tomography, interictal and ictal single photon emission computer tomography, and interictal and postictal neuropsychological examinations. The neurological examination was normal. Based on these examinations, right temporal lobe epilepsy was diagnosed. However, since 3D MRI did not reveal any lesion, invasive monitoring was indicated to localize the seizure focus more precisely. Invasive EEG recordings confined the seizure onset to the right amygdala and immediately surrounding cortex (Figure 3A) followed by ictal propagation to more posterior contacts on the superior and middle posterior temporal lobe and the angular gyrus. Right anterior temporal lobectomy and focal cotectomy (see Results) was performed.

Stimuli and Apparatus 1

The spatial tasks have already been described elsewhere (Ducommun et al., 2002).

Spatial Tasks

Stimuli were binaural white noise bursts (500 Hz low-pass filtered, 500 ms duration), digitized on a Power Macintosh 8100 fitted with an Audiomedia cardII and running Sound DesignerII and Protocol Powermix software. Stimuli were played through earphones linked to the computer. The volume was adjusted for the patient at the beginning of the experiment (approximately 70–80 dB sound pressure level, SPL). The sensation of stationary and moving sound sources was created through ITDs. Two sound sources located at two different azimuthal positions and two sound sources moving between these two azimuthal positions (stimulus class) were presented to each auditory hemifield separately (stimulus placement), giving a total of four different stimuli for each task (Figure 1A). By introducing a constant phase lag between stimuli presented to each ear, we obtained sounds located either medially (ITD: 200 μ s) or laterally (ITD: 700 μ s) with respect to the midsagittal plane. Sound sources were perceived as being located at two different azimuthal positions within each hemifield ($\pm 90^\circ$ and $\pm 30^\circ$; 0° is directly ahead), with the azimuth on the frontal interaural plane (at zero elevation). The sensation of moving sound sources was created by linearly varying the phase lags from outer (ITD: 700 μ s) to inner (ITD: 200 μ s) position (giving the sensation of an inwardly moving sound) or from inner to outer position (outwardly moving sound). The perceived motion speed was approximately 120°/s. To ensure that the sound stimuli began and stopped exactly at the same time in each ear, the signals' onset and offset of the leading channel were cut. An additional 10 ms of fade-in and fade-out were introduced in both channels to avoid clipping. During both tasks, the patient fixated a centrally presented cross.

Identity Task

Stimuli consisted of environmental real recorded sounds of 500 ms duration, comprising the following categories: musical instruments (e.g., piano), animals (e.g., dog), nature sounds (e.g., water), human nonverbal sounds (e.g., sneezing), and machines sounds (e.g., saw). Stimuli presented frequency and amplitude modulations (e.g., animals) and included also impulsive sounds (e.g., hammer). Their amplitude has been normalized using Cool Edit Pro 2.0, sound editor software (Synthrilium), to ensure that all stimuli were perceived with the same intensity. They were presented centrally at the volume judged comfortable by the patient (approximately 70–80 dB SPL). Prior to inclusion in this study, each sound has been evaluated in a group of 20 healthy subjects in order to exclude ambiguous or nonfamiliar sounds. Only sounds identified correctly at >80% were included in the study.

Procedure 1

Spatial Tasks

The preoperative experiments were done at the bedside. The patient first completed a training session during which we explained the stimuli. A series of 10 trials of each stimulus class was presented,

with the instruction to silently perform the discrimination task. We then had the patient make overt responses, with accuracy feedback on each trial. This training session also served to define with the patient the most convenient way to respond by qualifying each of the sounds with an appropriate term. The patient decided to use the terms “near” and “far” (from the center) to qualify the 30° and 90° azimuthal positions of the stationary stimuli, respectively, and “leaving” and “approaching” to qualify the 30° to 90° azimuthal displacement and the 90° to 30° azimuthal displacement of the moving stimuli, respectively. As the patient wore a head bandage covering the implanted electrodes, it was not possible to collect her response by means of a graduated half-circle fixed on the headphones with the angular value of the different sound sources. Nor was it possible to test the patient under free-field condition or to convolve the acoustic signal at the earphones with a generalized head transfer function.

Auditory localization was tested by presenting the patient with 30 sound samples per AF. The patient's task was to judge the location of each sound. The same procedure was used for the auditory motion direction discrimination task (30 sound samples per auditory hemifield) except that the patient had to judge the direction of each sound. During the test, we were able to follow the answers of the patient. We should note that although the stimuli were presented in a lateralized fashion (such that the patient was aware that all stimuli of a given block of trials would be presented either on the left or right side), the task required the patient to discriminate the location or direction of motion *separately* for each AF, so that we could assess if the responses also varied as a function of the AF. This differs from classical studies where stimuli were randomly dispersed *between* both AFs (Grantham, 1986) and subjects discriminated between left- and right-sided presentations.

Identity Task

Semantic recognition, i.e., the ability to recognize an object by its sound, was tested by presenting the patient with 50 nonverbal meaningful environmental sounds. The patient's task was to identify each sound verbally.

Normative Data 1

15 right-handed subjects (7 female; mean age: 38 ± 4.7 years) without neurological or otological illnesses participated in the experiment and served as a control group for the present experiments. In the auditory motion task, subjects performed 90% correct (SD: $\pm 6.3\%$; LAF: $89\% \pm 6.5\%$; RAF: $91\% \pm 6.1\%$). In the auditory location task, subjects performed 93% correct (SD: $\pm 6.5\%$; LAF: $92\% \pm 7.9\%$; RAF: $94\% \pm 5.0\%$). In the auditory identity task, subjects performed 91% correct (SD: $\pm 6.2\%$). Performance of this group in the auditory motion and location task did not differ (t test for dependant samples; $df = 14$, $t = 1.58$, $p = 0.14$) and is shown in Figure 1B.

Stimuli and Apparatus 2

These tasks have been described elsewhere (Clarke et al., 2000).

Localization Task

The patient was presented with two versions of a localization task, accordingly to the parameter used to simulate different azimuthal positions (interaural time difference, ITD; interaural intensity difference, IID; Figure 2A). The stimulus was a 2 s broadband “bumblebee” sound from the sound library “Sound Effects,” vol. 14, shaped with 100 ms rising and falling times. The frequency distribution of the stimulus is characterized by two dominant frequency bands: a low-frequency band (20–1000 Hz) and a high-frequency band (3000–5000 Hz). The stimulus presented a low depth sine amplitude modulation. One central and four lateral positions, two in each hemifield, were simulated. In the ITD version of the test, the lateral positions were created by delaying the left or right channel by 0.3 ms or 1 ms. In the IID version of the test, the intensity ratio between the 2 channels was varied: 90 dB:10 dB (and 10 dB:90 dB) for the two most lateral positions, 75 dB:25 dB (and 25 dB:75 dB) for the two intermediate positions, and 50 dB:50 dB for the central position. Sixty items, 12 in each position, were presented in pseudorandom order in each version of the test.

Motion Task

For motion we also used two versions. Auditory motion detection was tested by creating an illusion of sound motion in the azimuthal

plane by changing ITD or IID progressively (Figure 2B). Six different motions were simulated: extreme left to extreme right and the reverse; extreme left to midsagittal plane and the reverse; and extreme right to midsagittal plane and the reverse. In the ITD version, motion from an extreme lateral position was created using an initial interaural time difference of 1 ms and progressive changes by 100 ms for each 50 ms of stimulus duration until both channels were in phase (for motion stopping at the midsagittal plane) or until the reverse balance was reached (for motion between the extreme lateral positions). In the IID version, motion from an extreme lateral position to the other was simulated by an initial interaural intensity difference (intensity ratio; 90 dB:10 dB or 10 dB:90 dB) lasting 700 ms and followed by a 900 ms interval where a linear transition was created until the reverse ratio was reached during the last 700 ms. Motion stopping at or starting from the midsagittal plane was simulated by an initial 700 ms period where the intensity ratio was equal to 90 dB:10 dB or 10 dB:90 dB (if the sound started from an extreme lateral position) or to 50 dB:50 dB (if the sound started from the midsagittal plane) followed by a 450 ms transition period and a 700 ms final period where the intensity ratio simulated the arrival position. Sixty items, 10 for each lateral sound movement, were presented in pseudorandom order in each test.

Procedure 2

In the location task, the patient was asked to indicate the perceived position on her head with her right hand (as in Altman et al., 1979; Bisiach et al., 1984). A graduated half-circle fixed on the headphones was used to determine the angular value of the position (from 0° at the vertex to 90° at each ear). As a measure of the overall performance, the relative positions attributed to two consecutive stimuli were compared (max, 59); a response was counted as correct when a stimulus was correctly placed to the left or the right of the previous stimulus accordingly to the interaural discrepancy or within $\pm 15^\circ$ of the previous location for identical interaural values. Alloacousis (perception of stimuli as shifted to the other side of the mediosagittal plane) were also recorded. The patients' individual scores were converted into z-scores relative to mean and SD of the control population (ITD version: mean = 57.2, SD = 1.8; IID version: mean = 57.0, SD = 1.8); the limit of normal performance was set 2 SD below the mean. Normative data on 60 control subjects have been reported elsewhere (Clarke et al., 2000).

As in the localization tasks, the patient wore headphones with a graduated half-circle (Figure 2A). The hand used for the indication of perceived sound motion was as described above. A response was counted as correct when the direction and the duration/length of a stimulus were both correct without alloacousis. The patients' individual scores were converted into z-scores relative to the control population (ITD version: mean = 52.4, SD = 8.9; IID version: mean = 51.9, SD = 7.9); the limit of normal performance was set 2 SD below the mean.

Normative Data 2

The control population consisted of 60 subjects aged between 20 and 65 years, of whom 30 were aged 20 ± 3.5 years and 30 aged 50 ± 6.5 years. The performance of young and old subjects did not show significant performance differences (see Clarke et al., 2000). The performance of the patient was compared to that of the control population by means of z-scores (Table 1B).

Visual Motion Perception

Visual motion perception (direction discrimination task) was tested by using a random dot display on a computer screen as described previously (Blanke et al., 2003). A five-alternative forced choice discrimination task was applied. Coherent motion stimuli were presented on a 20 inch computer monitor (frame rate: 70 Hz; 640×480 pixels) in black and white. Viewing distance was 100 cm ($12^\circ \times 12^\circ$ in the central visual field). The dots had a random duration and were randomly positioned. A percentage of the dots was programmed to be displaced with a velocity of $2^\circ/s$ in the tested direction (signal dots). The percentage of coherence motion (% CM) was defined as the number of signal dots divided by the total number of dots and multiplied by 100. Direction performance was determined

separately for all four cardinal directions. Visual motion perception was tested prior to and 3 months following the operation.

Intracranial Auditory Evoked Potential Tasks

The patient's task was to silently judge the position ("near" versus "far"), the direction ("toward" versus "away" from midline), or the meaning of the preceding sound. Stimuli were presented in a block design, according to the class of stimulus (location, motion, identity) and their placement for the spatial stimuli (LAF, RAF). For the spatial tasks, each block consisted of 100 trials (750 ms ISI) with equal probability of both possible responses (i.e., near and far in the case of blocks of trials with stationary stimuli, and toward and away in the case of blocks of trials with moving stimuli). A total of 200 trials was obtained per task. To obtain the same number of trials for the identity task, the stimuli were repeated four times in a pseudo-random order. To minimize eye movements, the patient was asked to fixate a centrally presented cross during auditory presentations.

Invasive Recordings and Electrical Cortical Stimulation

Subdural grid electrodes (Ad-Tech Corp.) were implanted to record seizures and ES was performed to plan the surgical resection. Informed written consent was obtained and ES and intracranial AEPs were conducted in conformity with the Declaration of Helsinki. Subdural grid electrodes were 3 mm diameter stainless steel electrodes with a center-to-center distance of 8 mm. Electrode location was determined by intraoperative photographs and 3D MRI of the brain with the implanted electrodes (Blanke et al., 2000). 88 subdural grid electrodes were placed over the right hemisphere covering the lateral and basal temporal lobe, the parietal lobe, and the frontal lobe (Figure 3A; not all basal temporal and anterior temporal electrodes are shown). ES was performed with a Grass Stimulator S12 (Grass Instruments) and permitted to localize primary motor and somatosensory cortex as well as auditory and vestibular cortices (Figure 3A). Constant current ES (3 mA, 0.3 ms duration, biphasic regular pulses) below the threshold of after-discharges was applied at 50 Hz in a bipolar fashion through adjacent contacts. Intracranial local field potentials were recorded continuously with a sampling rate of 200 Hz, bandpass 0.1–70 Hz, in a bipolar montage from all implanted electrodes. EEG was analyzed offline and all trials with epileptic activity were excluded from analysis.

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