Functional Anatomy of Human Auditory Attention Studied with PET[1]

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Positron emission tomography was used to investigate the functional anatomy of selective auditory attention in 17 right-handed male volunteers who submitted to different tasks: silent rest (REST), listening to frequent low- or rare high-pitched tones (LIS) delivered randomly to the right or the left ear, selective auditory attention where subjects had to attend to deviants in one ear, right (ATTR) or left (ATTL). Six subjects had the series REST, LIS, ATTR twice, eight subjects the series REST, LIS, ATTL, and the last three subjects the series REST, ATTR, ATTL. Event-related potentials were simultaneously recorded with PET and showed significant task and electrode site effects on the N100 amplitude. When compared to REST, LIS elicited bilateral temporal activations of the Heschl's gyri and the *planum temporale,* with a significant rightward asymmetry, and of the posterior part of the superior temporal gyrus. Significant right precentral and anterior cingulate gyri normalized regional cerebral blood flow increases were observed in the frontal lobe. Both the ATTR and the ATTL conditions, compared to LIS, activated the supplementary motor area, bilateral precentral, and left postcentral cortices without any temporal cortex activation. In addition, the ATTL condition resulted in a right prefrontal cortex activation. Pooling the 14 subjects revealed an asymmetry in the superior temporal gyrus favoring the cortex contralateral to the attended ear. Two major networks seem thus to be involved during selective auditory attention: (1) a local temporal network, on which selective attention produces a modulation of the functional lateralization, and (2) a frontal network that could mediate the temporal cortex modulation by attention.

INTRODUCTION

Although a lot of functional imaging research has been devoted to sound and auditory language processing, the function of the different cytoarchitectonic areas of the human auditory cortex remains to be investigated. Indeed, apart from the tonotopic representation of sounds in the temporal transverse gyri koniocortex that had been confirmed with PET (Lauter *et al.,* 1985) and magnetoencephalography (MEG) (Romani *et al.,* 1982) and the bilateral representation of sounds that was established with auditory evoked potentials of the exposed cortex (Celesia *et al.,* 1968) and further confirmed with PET (Mazziotta *et al.,* 1982), we lack information on the functional anatomy of the auditory cortex, in particular regarding the human auditory attention.

In fact, most of our knowledge on the neural bases of auditory selective attention in human has been provided by event-related potential (ERP) studies using two main experimental paradigms: the oddball and the selective attention paradigms.

In the oddball paradigm the subject is presented with a sequence of repetitive "standard" stimuli mixed with low probability "deviant" stimuli and is asked either to ignore (or to passively listen) or to detect the deviant stimuli. The oddball paradigm has allowed the identification of an electrical signature of the automatic processing of the physical characteristics of sounds: the mismatch negativity (MMN), a wave selectively elicited by deviants (Näätänen, 1990). Since very small change of the deviants' physical characteristics results in the appearance of a MMN, it corresponds to a full, although not conscious, processing of the stimuli characteristics (Alho, 1992).

The selective attention paradigm developed by Hillyard (Hillyard *et al.,* 1973) has allowed the uncovering of effects specific to attention and independent from the physical characteristics of the stimuli. In this experimental situation the subject has to detect the deviants occurring in a specified ear while ignoring the incoming stimuli in the other one. Under this experimental condition, the processing of the attended stimuli elicits

an enhancement of the N100 wave called the N1 attentional effect reflecting the early processing of sounds. This conclusion was challenged by Näätänen who described (with a slightly different paradigm) the processing negativity (PN), a slow endogenous negative wave obtained by subtracting unattended from attended sounds: for this author, the PN wave must not be considered a modulation of N1, but rather a new component emerging from selective attention with both temporal and frontal generators. This PN wave is very close to the negative difference wave, called Nd, obtained by subtracting from attended the unattended stimuli and which is made of an early component overlapping the N1 and a later component that may persist for 100 ms (for review see Näätänen, 1990; Hillyard *et al.,* 1995). The Nd early part can be confounded with the N1 effect, with a supratemporal plane origin, while its later part includes frontal components. These results were at the origin of a debate concerning the information processing during auditory selective attention: (1) early processing of the sounds demonstrated by the N1 effect, in the vicinity of the primary auditory areas, with a very limited processing of the unattended stimuli (Woldorff *et al.,* 1993), or (2) the bringing into play of a larger network including frontal regions, reflected by the prolonged negative wave observed by Näätänen, which compares each of the stimuli to an attentional trace in order to select the relevant stimulus.

It seems very likely that both types of processing may be involved in auditory selective attention, in a way similar to visual attention where both modality-specific and supramodal frontal networks appear to be implicated in selective attention tasks. Indeed, studies on visual selective and divided attention have shown a modulation of the visual cortex activity with the target features to be detected. For example, the regions known to be involved in form or velocity processing showed specific normalized regional cerebral blood flow (NrCBF) increases during selective attention to form or velocity (Corbetta *et al.,* 1990, 1991b). This phenomenon seems to be correlated with the P1 attentional effect (the equivalent of the N1 for the visual modality) as was recently demonstrated by a combined ERP–PET study showing that the fusiform gyri activation observed during selective visual attention matched the location of the P1 dipole generated during this task (Heinze *et al.,* 1995). It should be noted that these extrastriate attentional activations corresponding to the local amplification of cortical activity effects described by Posner (Posner and Dehaene, 1994) co-occurred with extravisual activations, in particular in the frontal lobe (Corbetta *et al.,* 1991a; Heinze *et al.,* 1995). These results, matched with the Posner model of attentional networks, would indicate that the fusiform amplification effect is mediated by these frontal areas (Posner and Dehaene, 1994).

In order to assess whether a local amplification due to selective attention would be observed in the auditory cortices, as was the case in the visual cortex, and to better characterize the functional anatomy of auditory cortex, we have adapted the selective auditory attention paradigm to the PET methodology. The same subjects were monitored simultaneously with ERP and PET, with rCBF measurements obtained during both passive listening and auditory selective attention to tones. Moreover, to uncover a possible effect of the lateralization of the attended stimulus, we varied the attending ear in the selective attention condition.

MATERIALS AND METHODS

Subjects

Seventeen right-handed French male medical students (age 24 ± 2.5 years, mean ± SD) participated in the study. All were right-handed as assessed by the Edinburgh's questionnaire (Oldfield, 1971) and were free of brain abnormalities as judged on their MRI brain scan. The study was approved by the French Atomic Energy Commission Ethic Committee, and all subjects gave their written informed consent.

Tasks

Three different tasks were used in this study. The first task was the standard control condition used in our laboratory that consists in resting silently, eyes closed, with no particular instruction except to relax (REST). In the second task, a simple listening condition (LIS), subjects listened to a series of pure tones delivered randomly to their right or left ear through earphones, which included 80% standard low-pitched (750 Hz) and 20% high-pitched deviant tones (1790 Hz). The tones lasted for 150 ms, and the interstimulus interval randomly varied from 400 to 800 ms. The third task was a selective attention task (ATT) during which the subjects listened to the same series of stimuli as during the LIS condition but were instructed to attend to the stimuli in one of their ears, to detect the deviant ones, and then to press a button with their right index finger. Auditory stimulations were started 75 s before ^{15}O-labeled water injection, and all measures were performed in darkness.

Groups

From the 17 subjects of the study, we made three groups of 6, 8, and 3 subjects, respectively. In the first two groups, the subjects underwent the same first and second tasks, namely REST and LIS, but had to perform different selective attention tasks: subjects 1 to 6 had to detect right ear deviants (attend to right, ATTR), and subjects 7 to 14 left ear deviants (attend to

left, ATTL). The 3 subjects of the third group were submitted to a paradigm that also included three different conditions: REST, ATTR, and ATTL conditions. The stimuli series were the same as the ones used for the ATTR and ATTL tasks performed by the subjects of groups 1 and 2, respectively.

Imaging Procedure: MRI

Prior to the PET experiment, each subject was submitted to a magnetic resonance imaging (MRI) T1-acquisition of 3-mm-thick contiguous axial slices covering the whole brain, together with 5-mm-thick orthogonal sagittal slices. This MRI examination was used (1) to check the absence of brain abnormalities, (2) to optimize the positioning of the subject's head in the PET (which was necessary because of the small axial field of view of the camera), and (3) to provide the images requested for a detailed analysis of the neuroanatomy of each subject (see Image Analysis below).

Imaging Procedure: PET

In the first 14 subjects, NrCBF was monitored by PET and oxygen-15-labeled water ($H_2^{15}O$) six times in each subject, replicating each of the three conditions in the following order: REST, REST, LIS, LIS, ATTx, ATTx (x = R for the first group and x = L for the second group) except for subjects 1 and 2, where the second REST occurred as the last condition. This was done in order to ensure that subjects would be naive with respect to the ATT task when performing the LIS task. The PET studies were conducted using a previously published procedure (Petit *et al.,* 1993). For each condition, seven brain slices were simultaneously acquired on a time-of-flight PET system (Mazoyer *et al.,* 1990), having a 7-mm transaxial resolution, a 9-mm slice thickness, and a 12-mm interslice distance. Following intravenous bolus injection of $H_2^{15}O$ (Herscovitch *et al.,* 1983) a single 80-s scan was acquired starting at the arrival of the radioactivity in the brain; images were reconstructed including a measured correction for radiation attenuation by the head. Between-scan interval was 15 min.

In the third group, the block of three conditions, REST, ATTR, ATTL, was replicated, the task order in each block being randomized. For each condition, 31 contiguous brain slices were simultaneously acquired on a 953B-ECAT system (Mazoyer *et al.,* 1991) having 5-mm transaxial resolution, and a 3.375-mm slice thickness. Image acquisition and reconstruction protocols were identical to those used for the first two groups.

ERP Recordings and Analysis

In the first two groups, task execution was controlled during each LIS and ATT condition by having ERP recorded using a coronal setup of five silver electrodes.

Recordings started with the beginning of the auditory tasks, 1 min before water bolus injection, and lasted for 8 min. After exclusion of artifacted trials, time locked to the stimulus ERP averaging was performed. N100 amplitude was computed for all stimuli, in each subject, as the amplitude of the wave in a 50-ms interval centered to the peak. A three-way (electrode, condition, trial) repeated measures ANOVA was conducted on the N100 amplitude variable.

Image Analysis

Our data analysis method has been detailed elsewhere (Mazoyer *et al.,* 1993). It is aimed at detecting increases of cerebral blood flow in cerebral structures having MRI-defined anatomical boundaries rather than detecting suprathreshold voxels in a between-subject averaged difference image as proposed by others (Fox *et al.,* 1989; Friston *et al.,* 1991). In our approach, the definition of the cerebral structures of interest is independent of the PET data. Rather, it is based on a parcellation of the brain similar to that proposed by others (Rademacher *et al.,* 1992). In a first step, a detailed analysis of each subject brain anatomy is performed by means of a dedicated software (Voxtool; General Electric). MRI slices are used to reconstruct a three-dimensional brain volume that is further segmented and allows the display of the external surfaces of both hemispheres, as well as brain sections in any incidence. The major sulci and gyri of each subject can then be identified and their limits marked onto the MRI axial slices. Using these anatomical landmarks, regions of interest corresponding to the intersection of the gyri with the MRI axial slices are delineated on each subject's MRI images. In this approach, anatomical volumes of interest (AVOI), such as gyri or gray nuclei, are defined as the union of their pieces on the different MRI axial slices. Beyond our usual set of about 80 AVOIs, a specific additional AVOI was defined for this protocol that encompasses the Heschl's gyrus and the *planum temporale* (HPT) that were defined, thanks to a slice passing by the supratemporal plane, following the method defined by Kulynych (Kulynych *et al.,* 1993). This AVOI was individualized because of the extensive literature on its possible role in auditory attention. Accordingly, the superior temporal gyrus AVOI (Sup Temp) was restricted to its lateral, posterior, and inferior part, corresponding to Wernicke's area in the left hemisphere.

To compute NrCBF, the seven PET slices acquired on each trial for the first 14 subjects were aligned with the individual high-resolution MRI images by visually matching three sets of isodensity contours automatically drawn on corresponding attenuation, blood flow, and MRI slices. For the third group, PET to PET and MRI to PET registrations were performed using the algorithms provided by the AIR package (Woods *et al.,*

TABLE 1

Summary of the NrCBF ANOVA

	AVOI								
Effect	SMA	Ant Cing	Post Cing	PRF	Precentral	Postcentral	HPT	Sup Temp	Temp Pole
Group (G)	0.20	0.61	0.52	0.17	0.14	0.98	0.56	0.93	0.37
Task (T)	<10^{-4}	**0.0076**	<10^{-4}	0.31	<10^{-4}	**0.048**	<10^{-4}	<10^{-4}	0.11
Group × task	0.39	0.99	0.68	**0.043**	0.47	0.15	0.71	0.75	0.19
Side (S)				**0.010**	0.20	0.57	**0.007**	0.55	0.070
Group × side				0.59	0.057	0.80	0.94	0.36	0.91
Task × side				0.090	0.66	**0.043**	0.23	0.81	0.48
G × T × S				**0.008**	0.56	0.82	0.21	0.47	**0.016**

Note. Main effects and interactions *P* values are given for all anatomical volumes of interest (AVOI) for which at least one *P* value was found below 0.05 ($N = 14$ subjects). Ant (Post) Cing, anterior (posterior) part of the cingulate and paracingulate gyri; SMA, supplementary motor area; PRF, prefrontal; HPT, Heschl gyrus and *planum temporale;* Sup Temp, superior temporal gyrus minus HTP and the temporal pole (Temp Pole); G, group factor (attend to left, attend to right); T, task factor (3 levels, rest, listening, attention); S, side factor (left hemisphere, right hemisphere).

1992, 1993). Within each AVOI, NrCBF during each condition was estimated as the ratio (in percentages) of the radioactivity concentration in the AVOI to that of the whole brain as measured either in the 7 or in the 31 PET slices, depending on the PET camera.

Statistical Analysis

For the first two groups, each AVOI NrCBF dataset was analyzed using a four-way repeated measures ANOVA with a three-level "task" factor (REST, LIS, ATT), a two-level "group" factor (group 1, ATTR; group 2, ATTL), a two-level AVOI hemisphere "side" factor (right, left), and a two-level "replication" factor, testing for factor main effects and interactions. In median AVOIs, namely the supplementary motor area (SMA) and anterior and posterior cingulum, the ANOVA did not include the side factor. Whenever the ANOVA global *F* test was found significant in an AVOI at the 0.05 level (two-tailed), pairs of NrCBF values during task and rest were compared with post hoc Student paired *t* tests. An additional feature of the AVOI method is that regional activation values are made available for each individual. These data will be present as bar charts under Results.

Considering the primary role assigned to the temporal cortex in the selective attention task by the ERP and MEG studies and since ERP studies have demonstrated a contralateral to the attended ear predominance of the N100 attentional effect (Näätänen and Picton, 1987), we pooled the three groups to try to uncover an attentional effect on the contralateral temporal regions. In order to do so we tested to zero the difference between "contralateral to the attending ear" and "ipsilateral to the attending ear" temporal AVOI NrCBF. This was done in order to match the PET data analysis with the classical "attend minus unattend"

ERP comparison that demonstrates the N1 effect and the Nd waves specific to selective auditory attention.

RESULTS

ERP Results

Similar to previous ERP studies on auditory attention, significant task ($P = 0.01$) and electrode site ($P < 0.001$) effects were observed corresponding to higher N100 amplitude values in the attention condition than in the passive listening condition, and to higher N100 values in the frontocentral electrodes compared to the temporal electrodes.

PET Results

Groups 1 and 2

ANOVA. Significant main effects and/or interactions were found by the ANOVA in nine brain structures (see Table 1), namely the SMA, the anterior cingulate cortex (Ant Cing), the precentral cortex, the dorsolateral prefrontal cortex (PRF), the postcentral cortex, the HPT, the Sup Temp, the posterior cingulate cortex, and the temporal poles.

Main effects. There was no overall group effect in any of these regions.

A significant task main effect was observed in seven of the AVOIs, excluding the PRF region and the temporal poles. Post hoc analyses (see Tables 2, 3, and 4) revealed that this task effect corresponded to NrCBF increases during the LIS and ATT conditions compared to the REST condition in six of these seven AVOIs and to NrCBF decreases in the posterior cingulum.

Significant side main effects were observed in the HPT and PRF regions due to significantly higher

TABLE 2

NrCBF Variations in Selected Regions of Interest during the Listening Condition Compared to Rest, in Subjects of Group 1 and Group 2

Region	ΔNrCBF	(SD) %	P value
	NrCBF variations		
SMA	−0.04	(3.01)	0.94
Anterior cingulum	1.87	(3.84)	0.015
Posterior cingulum	−2.00	(3.03)	0.0017
R PRF	−0.56	(2.60)	0.26
L	−0.54	(2.52)	0.26
R precentral	1.47	(2.71)	0.008
L	0.98	(2.68)	0.064
R postcentral	0.02	(1.79)	0.95
L	−0.11	(3.20)	0.86
R Heschl and *planum*	4.26	(4.19)	$<10^{-4}$
L	2.62	(3.60)	0.0007
R Sup Temp	3.13	(3.02)	$<10^{-4}$
L	2.91	(2.09)	$<10^{-4}$
R Temp Pole	−0.08	(3.73)	0.90
L	−0.14	(3.64)	0.84

Note. Cingulum, cingulate and paracingulate gyri; SMA, supplementary motor area; PRF, prefrontal cortex; R, right; L, left. *P* value is for the paired *t* test, $N = 28$, except for SMA where $N = 26$.

NrCBF values in the left HPT and in the right PRF when compared to their homologue in the contralateral hemisphere.

Interactions. A significant interaction between the group and the task factors was observed in one region only, namely PRF, and was characterized by a significant NrCBF increase in the attentive condition in the attend to left ear group only (group 2). There was no significant group by side interaction. A task by side interaction was noted in the left postcentral, this region showing an NrCBF increase in the left hemisphere during the attentive condition when compared either to REST or to LIS. This NrCBF increase in the postcentral gyrus is very likely to reflect the sensory motor response the subjects had to give when detecting a deviant by pressing a button with their right index (see Table 3). A very significant group by task by side interaction was observed in the dorsolateral prefrontal cortex ($P = 0.008$). In this region, the two groups exhibited very different NrCBF patterns during the selective attention condition (see Table 4): PRF was activated during the ATTL condition in group 2 only, bilaterally when compared to LIS, on the right side only when compared to REST. A triple interaction was also observed in the temporal poles, which consisted in a deactivation of the right temporal pole during the ATTL condition when compared to both REST and LIS, and in the left temporal pole during the ATTR condition when compared to LIS (see Table 4).

Finally, no interactions were noted in the Sup Temp, HPT, and precentral regions; in particular there was no task by side interaction. Post hoc *t* tests confirmed that these regions were activated during both the passive listening and the attention conditions in both groups, without any significant differences between groups, tasks or sides (see Tables 2 and 3).

Summary of the ANOVA results. To summarize, when compared to the silent rest condition, the passive listening and the attention conditions elicited similar activations in both groups in the bilateral superior temporal cortex, including the Heschl's gyrus and the *planum temporale.* In the precentral gyri and anterior cingulum, activations were present during both conditions but with a higher amplitude during the attend condition. In addition, the attention condition activated

TABLE 3

NrCBF Variations in Selected Regions of Interest Showing No Group Effect during the Attentive Listening Condition When Compared to the Reference Condition (REST) and to the Listening Condition

Region	Selective attention minus rest			Selective attention minus listening		
	(ΔNrCBF,	SD %,	P value)	(ΔNrCBF,	SD %,	P value)
SMA	3.81	(2.88)	$<10^{-4}$	3.85	(2.72)	$<10^{-4}$
Anterior cingulum	3.21	(4.61)	0.001	1.25	(3.56)	0.073
Posterior cingulum	−5.57	(4.73)	$<10^{-4}$	−3.50	(4.77)	0.0006
R precentral	2.76	(2.99)	$<10^{-4}$	1.29	(2.51)	0.011
L	3.08	(2.89)	$<10^{-4}$	2.10	(2.62)	0.0002
R postcentral	0.26	(2.06)	0.51	0.24	(2.51)	0.62
L	1.62	(3.09)	0.0097	1.73	(2.29)	0.0004
R Heschl and *planum*	4.65	(2.95)	$<10^{-4}$	0.39	(3.09)	0.51
L	3.61	(5.53)	0.0018	0.99	(4.85)	0.28
R Sup Temp	3.29	(3.39)	$<10^{-4}$	0.16	(2.99)	0.77
L	3.51	(2.41)	$<10^{-4}$	0.60	(2.57)	0.22

Note. LIS $N = 28$, SMA $N = 26$; cingulum, cingulate and paracingulate gyri; SMA, supplementary motor area; R, right; L, left.

TABLE 4

NrCBF Variations in the Regions of Interest Showing a G × T × S Interaction during the Attentive Listening Condition When Compared to the Reference Condition (REST) and to the Listening Condition

Region	Attend to right minus rest (ΔrCBF, SD %, P value, N = 12)			Attend to right minus listening (ΔrCBF, SD %, P value, N = 12)			Attend to left minus rest (ΔrCBF, SD %, P value, N = 16)			Attend to left minus listening (ΔrCBF, SD %, P value, N = 16)		
R PRF	−0.73	(2.68)	0.36	−0.62	(2.04)	0.31	1.54	(2.70)	0.037	2.44	(2.24)	0.0006
L	−0.67	(2.48)	0.37	−0.35	(1.85)	0.52	−0.37	(1.97)	0.46	1.40	(1.94)	0.011
R Temp Pole	−1.71	(6.42)	0.37	−0.15	(4.54)	0.91	−3.47	(3.27)	0.0007	−1.93	(2.17)	0.003
L	−2.01	(4.77)	0.17	−2.60	(3.01)	0.01	−1.99	(4.14)	0.073	−1.31	(3.39)	0.14

Note. P values are for the paired t tests; PRF, prefrontal cortex; R, right; L, left.

the SMA and the postcentral cortex in both groups. A deactivation of the posterior cingulate cortex was also noted in both conditions for both groups. Finally, the attention condition activated the right dorsolateral prefrontal cortex when subjects attended to deviants in their left ear only, and deactivations contralateral to the attending ear were observed in the temporal poles.

Individual Results

Individual NrCBF variations between the LIS and the REST conditions are given in Fig. 1. In the frontal lobe, NrCBF increases were found in 9 of the 14 subjects in the anterior cingulate AVOI and in 11 subjects in the right precentral gyrus. On the left side, there was a larger variability in the individual results: only half of the subjects depicted an NrCBF increase in the left precentral cortex. In the temporal lobe bilateral NrCBF increases were observed in all subjects but 1 in the right HPT, and all subjects but 3 in the left HPT, and in the right Sup Temp in all subjects but 1 on the left side and all but 2 on the right side.

The individual analysis of the ATT minus REST contrast (Fig. 2) showed SMA activation in all subjects. Blood flow in the anterior cingulate was also increased in all but 3 subjects, while in the precentral gyrus, all subjects but 1 exhibited a left precentral NrCBF increase. One should also note that 10 of the 14 subjects exhibited large NrCBF increases in the right precentral cortex. Very consistent temporal lobe activations were observed, similar to the listening condition, with NrCBF increases observed in all subjects in the superior temporal AVOI.

Attended–Unattended Contrast (All Subjects Pooled)

The results of the test to 0 of the difference between the temporal AVOIs contralateral to the attended ear and the homologue AVOI in the other hemisphere are given in Table 5, for the 17 subjects. No significant effect was found in the HPT region where the negative difference indicates an asymmetry in favor of the HPT ipsilateral to the attended ear. On the opposite, a close

to significant effect was observed in the Sup Temp, demonstrating the presence of a NrCBF asymmetry favoring the contralateral to the attending ear cortex. This result is illustrated in Fig. 3.

DISCUSSION

The Temporal Cortex Network for Auditory Attention

Passive Listening

The passive listening condition (LIS) used in the present study is very close to the ignore condition of an oddball paradigm (Näätänen, 1990), even if for obvious methodological reasons, namely the impossibility of stimulus targeting with PET, we did not ask the subjects to concurrently read a book or to perform another cognitive activity.

This LIS condition elicited superior temporal gyri activations extending from Heschl and the *planum temporale* to the posterior part of the gyri. The bilateral HPT activation observed in the temporal cortex was expected since the transverse superior temporal gyri are known to be auditory cortices (Liégeois-Chauvel *et al.,* 1991, 1994); it is consistent with temporal transverse gyri activations reported with functional imaging techniques: among others, the FDG PET study on nonauditory stimulations (Mazziotta *et al.,* 1983), the seminal PET study that demonstrated the tonotopic organization of auditory cortex in man (Lauter *et al.,* 1985), the pitch discrimination PET study of Zatorre (Zatorre *et al.,* 1992), and a recent functional MRI study on human auditory cortex (Binder *et al.,* 1994). Moreover, evoked potentials from auditory cortex had localized the generators of middle latency auditory-evoked potentials in Heschl's gyrus and the *planum temporale* (Liégeois-Chauvel *et al.,* 1994) and scalp ERP studies have located the exogenous N1 P2 and the MMN component generators in the supratemporal plane (for review see Näätänen and Picton, 1987; Näätänen, 1990). Finally, the presence of a significant asymmetry, favoring the right hemisphere, is consistent with the
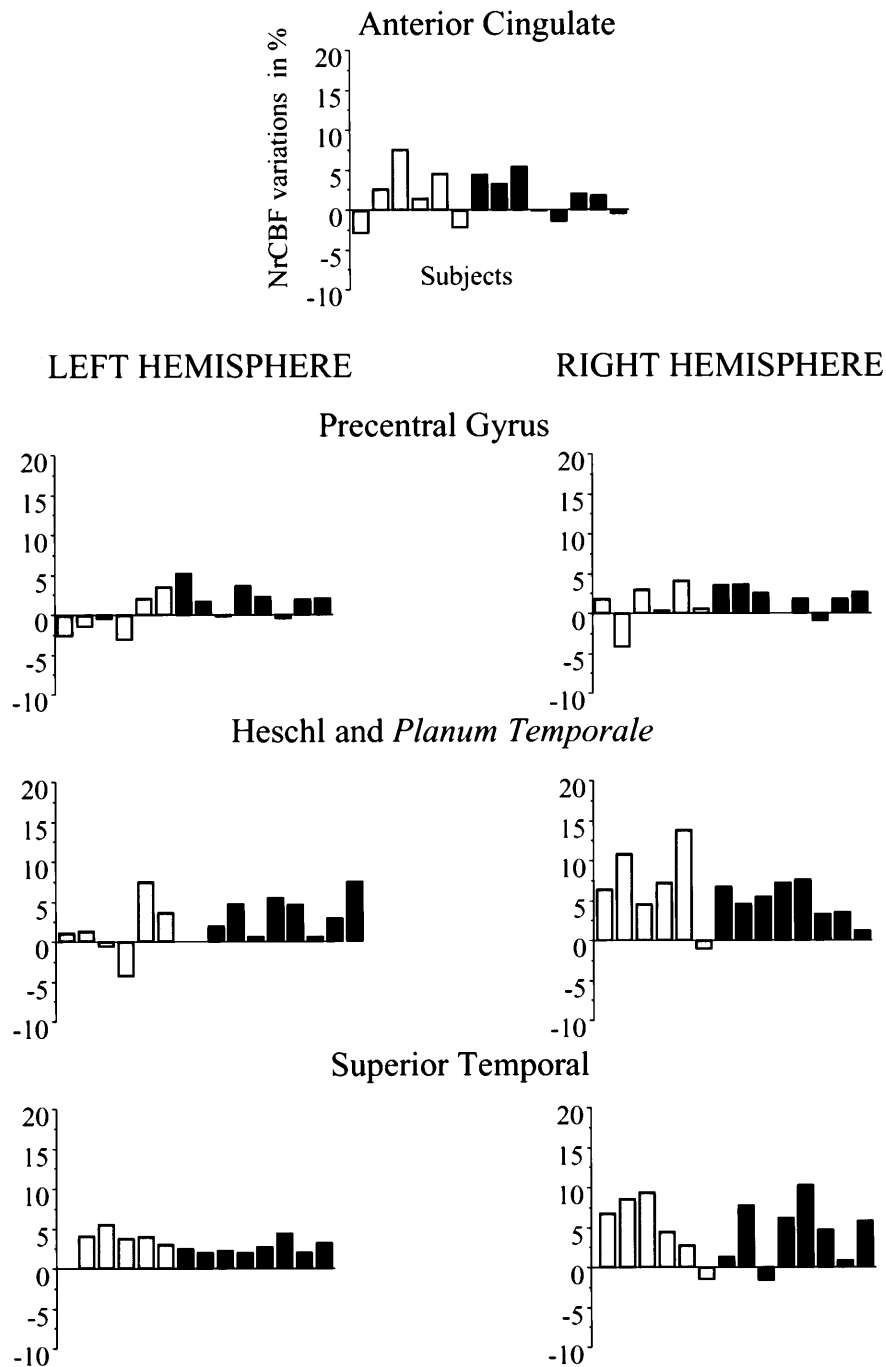
FIG. 1. Listening minus rest. Individual percentage variation of the NrCBF in selected regions of interest during LIS compared to REST. Hatched bars, subjects belonging to the attend to right protocol; closed bars, subjects belonging to the attend to left protocol.

left ear dominance for tone processing previously demonstrated with ERP (Tenke *et al.,* 1993) and PET (Zatorre *et al.,* 1992) for pitch discrimination and pitch perception of complex tones (Paquette *et al.,* 1996).

The major result observed in the temporal cortex during the LIS condition is the presence of a significant and reliable activation in the lateral and posterior part of the superior temporal gyri, clearly assessed thanks

to the MRI-guided volume of interest definition that allowed segregation of the primary and secondary auditory cortices into different AVOIs. Considering ERP data on tone processing, this activation could correspond to the activation of the generator first component of the N1 as described by Näätänen (Näätänen and Picton, 1987), the amplitude of which is proportional to the stimulus intensity and which is
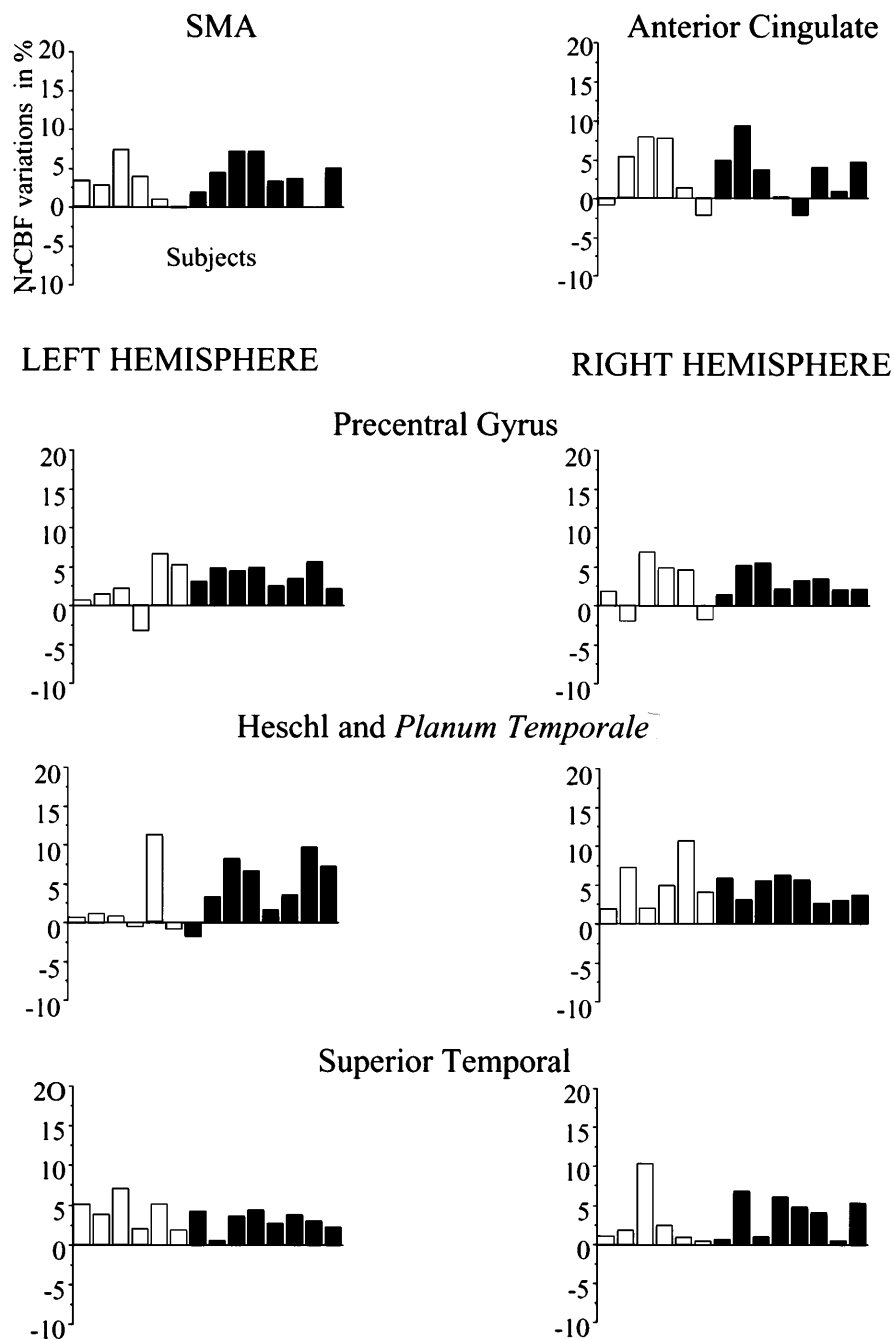
FIG. 2. Selective attention minus rest. Individual percentage variation of the NrCBF in selected regions of interest during ATT compared to REST. Hatched bars, subjects belonging to the ATTR protocol; closed bar, subjects belonging to the ATTL protocol.

generated in a region larger than the supratemporal plane since bilateral lesions of the temporal lobe must extend into the temporoparietal region before it is abolished (Woods *et al.,* 1987). In the left hemisphere, the superior temporal region, as defined in our study, corresponds to Wernicke's area that was repeatedly reported involved in speech or speech-like stimulus processing and is usually considered a region devoted to language (Fiez *et al.,* 1996). However, the results of

the present study challenge this conclusion as did two recent PET (Engelien *et al.,* 1995) and functional MRI (Binder *et al.,* 1994) studies including the passive listening of environmental sounds and noise, respectively, which also showed a posterior extension of the left Heschl's gyrus activation. It seems then that the posterior part of the left superior temporal gyrus, namely Wernicke's area, is already active during simple tones listening, a fact previously noticed with electrical

TABLE 5

NrCBF Lateralization Index during the Selective Attention
Tasks, All Subjects Pooled (17 Subjects, 39 Pairs)

AVOI	Contralateral minus ipsilateral to the attended ear ($N = 39$)		
	ΔNrCBF %	SD	P value
HPT	−1.4	(10.4)	0.42
Sup Temp	1.93	(6.39)	0.06

Note. This index was calculated as the difference between the AVOI contralateral to the attended ear and the homologous ipsilateral region. HPT, Heschl gyrus and *planum temporale;* Sup Temp, superior temporal gyrus minus HTP and the temporal pole; *P* value is for the paired *t* test.

auditory potentials recorded from exposed temporal cortex in man, showing that the auditory cortex includes Heschl gyri but also the posterior two-thirds of the superior temporal gyrus (Celesia, 1976).

Selective Auditory Attention

The major result concerning the activations induced by the selective auditory attention tasks, whatever the attending ear, is the absence of significant temporal cortex activation when comparing the ATT and the LIS tasks. This result questions, for the auditory modality, the amplification effect related to attention described in the visual modality by Posner (1994), since focusing of attention did not result in major increases of activity in the auditory cortices. One should note, however, that NrCBF increases were present in temporal regions, although far from being significant. The absence of significance could be due to a lack of sensitivity of the PET methodology. Indeed, the result obtained in PET is the integration of the activity over 80 s, while ERP analysis is based on averaging triggered by the stimulus. Moreover the N1, Nd, or PN waves are all obtained by contrasting the processing of the attended versus unattended stimuli, a kind of analysis we are not able to perform with PET. Since the N1 effect described for the first time by Hillyard (Hillyard *et al.,* 1973) and further confirmed by Woldorff (Woldorff and Hillyard, 1991; Woldorff *et al.,* 1993) is predominant in the contralateral to the attended ear temporal cortex, we contrasted the ipsilateral and contralateral to attending ear AVOIs of the superior temporal gyrus, trying to overcome this methodological limitation. This analysis provided a very interesting result, namely a functional lateralization favoring the contralateral to attended ear in the superior temporal region. This result is in agreement with neuropsychological studies showing that patients suffering from temporal cortex lesions had reduced amplitude of the N1 and of the early Nd for tones presented in the contralateral to lesion ear

(Woods *et al.,* 1993). Moreover, in a recent PET study on selective auditory attention using both tones and words, the attend condition gave rise to an increase in the contralateral NrCBF temporal cortex together with a decrease in the opposite hemisphere (O'Leary *et al.,* 1996). In the present study the Sup Temp asymmetry is also the result of both ipsilateral small decreases and contralateral small increases. This phenomenon, located in the posterior part of the superior temporal gyrus, very likely corresponds to the larger enhancement of the N1 observed in the contralateral to attend ear side (Hillyard *et al.,* 1973; Woldorff and Hillyard, 1991; Woldorff *et al.,* 1993) and allows us to postulate a temporal cortex localization for the generators of the N1 attentional effect. Indeed, the absence of lateralization effect in the Heschl and the *planum temporale* regions indicates that the generator of the early N1 attentional effect could be in the posterior and lateral part of the contralateral to the attending ear superior temporal gyrus. This idea fits well with the absence of Nd tonotopic changes demonstrated by Alho (Woods *et al.,* 1991) that suggests that the Nd effect could reflect the recruitment of regions additional to primary auditory fields.

Somewhat different findings have been observed in functional imaging studies dealing with attention in other modalities, although the N1 attentional effect has been described in visual and somatosensorial modalities (Näätänen, 1990). For example in Corbetta's work on spatial attention (Corbetta *et al.,* 1991a), visual cortex activity was modulated by the target features to be detected, and the regions known to be involved in form or color processing showed specific NrCBF increases during selective attention to form or color. Interestingly, the auditory cortex functional anatomy is not clearly established in humans, apart from the existence of a tonotopic organization in primary auditory areas (Romani *et al.,* 1982; Lauter *et al.,* 1985) and from the binaural representation of sounds (McGlone and Davidson, 1973). Compared to the visual system hierarchical functional organization, the auditory cortex is very different in that, except for the primary cortex, there is no clear localization for the processing of the sound attributes. The cochlea is bilaterally represented and electrical recordings in humans have shown that, if the contralateral ear is more strongly represented, both ears are represented in each cerebral hemisphere, the larger responses being evoked by binaural stimuli (Celesia, 1976). This binaural representation is coupled with the existence in these regions of an anatomical asymmetry (Galaburda *et al.,* 1988) linked with different functional hemispheric dominance for the processing of language (Damasio, 1992), music (Sergent, 1993), and sounds (Zatorre *et al.,* 1992), the principle of cerebral dominance being the major functional characteristic of this system.
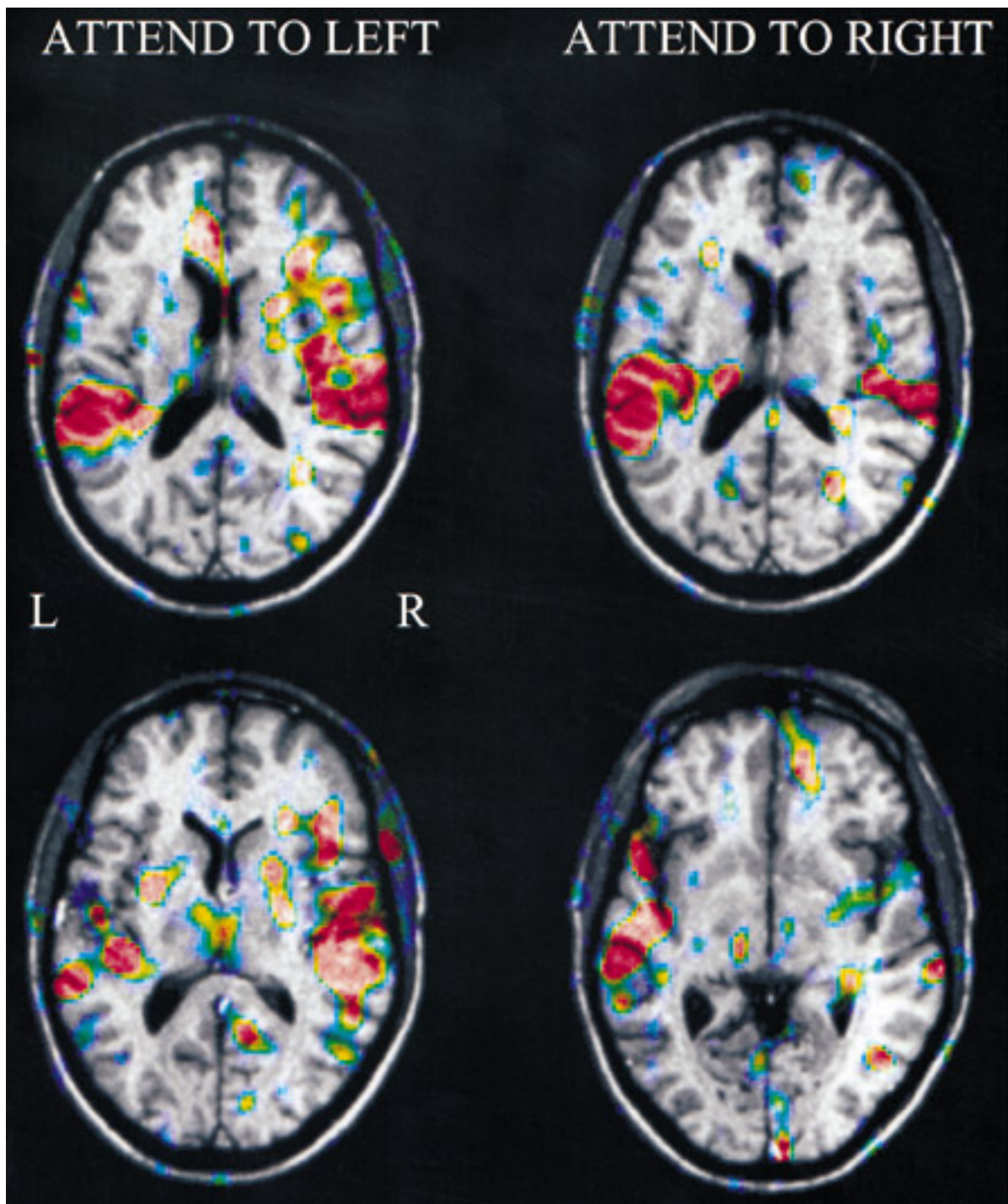
FIG. 3. Example of individual NrCBF PET activation images obtained at the Heschl's gyri level (top) and through the superior temporal gyrus (bottom) in one subject of the third group. Left column, attend to left deviant sounds versus rest; right column, attend to right deviants versus rest. Difference images were obtained by subtracting the mean of the two rest control conditions from the mean of two attentive conditions. After three-dimensional filtering of the difference images and PET–MRI 3D registration, the activation's maps were superimposed onto the subject MRI slices at the corresponding level. Note: in addition to the activations in the Heschl gyrus and the *planum temporale,* there are activations in the posterior part of the superior temporal gyrus. Note also the lateralization effect in the selective attention condition with a greater extent of the right temporal cortex activation in the attend to left condition, together with a greater extent of the left temporal cortex activation in the attend to right condition.

Within this framework, the selective attention can be seen as resulting in a change in the functional lateralization of the temporal regions: decrease of the rightward dominance in HPT, appearance of a lateralization effect dependent on the lateralization of the stimulus to be detected in the Sup Temp region, and NrCBF decrease in the temporal pole contralateral to the pertinent stimulus. This modulation acting through functional lateralization could be specific to the auditory system and constitute the equivalent of the attention local amplification observed in the visual system (Posner and Dehaene, 1994).

The lateralization modulation we observed during auditory selective attention is a phenomenon of the same nature as the functional dominance of the left hemisphere for language, and the temporal poles (TP) seem to play a particular role in auditory processing. We observed, in this study, TP deactivations that were specific to the selective auditory attention task, and lateralized with the pertinent stimulus presentation side. Recall that in a previous work, we have demonstrated that these regions, usually considered as belonging to the limbic system (Mesulam, 1985), were part of the language network: in this previous PET study on the functional anatomy of story listening we found TP bilaterally activated, with a leftward dominance, whether the stories were meaningful or not (Mazoyer *et al.,* 1993). The TP implication during language processing was recently confirmed by Damasio *et al.* who showed their implication during word retrieval (Damasio *et al.,* 1996). It appears then that the temporal poles implicated during the auditory processing of language are deactivated during the auditory processing of tones. Deactivations of the temporal cortices during visual processing have been previously described (Dupont *et al.,* 1993; Mellet, 1996), but it is noteworthy that in the present study TP deactivations were observed during auditory processing. We therefore think that, based on the results we obtained on selective auditory attention and auditory language processing, the specificity for the cognitive activity engaged by the auditory task is supported within the superior temporal gyrus by the modulation of both the regional activations and deactivations patterns and the regional functional lateralization (Mazoyer *et al.,* 1993).

Frontal Network

Anterior and Posterior Cingulate

Based on the results of neuropsychological (Janer and Pardo, 1991) and PET studies (Pardo *et al.,* 1990), the anterior cingulate region, located anteriorly to the genu of the corpus callosum and corresponding to the most anterior part of the anterior cingulate and paracingulate gyri, is considered a region implicated in operations involving target detection (Posner and Pe-

tersen, 1990) as was the case in the present study. The fact that the anterior cingulate activation was larger in ATT than during LIS indicates that this region is not only sensitive to target detection (the number of targets was the same in LIS and ATT), but also participates in the execution of the action as suggested by Posner (1995) or, more precisely, in the selection of action in a way similar to the Stroop paradigm (Pardo *et al.,* 1990). The implication is that this region, part of the anterior attentional network (Posner, 1994), is not restricted to the auditory modality or to the kind of attentional task used in this study. For example it has been reported to be activated during both attend to right and attend to left half visual hemifield in a visual selective attention task compared to passive viewing (Heinze *et al.,* 1994), as well as during a divided visual attention task (Corbetta *et al.,* 1991a).

Considering the results coming from ERP, the anterior cingulate can be considered a candidate for the location of the P3a generator, a late component following the MMN observed in automatic processing tasks and considered as reflecting the attentional switch toward an environmental change (Näätänen and Gaillard, 1983; Renault, 1983). Indeed, using intracerebral recordings, a clear inversion of the P3a was demonstrated during an oddball paradigm in the orbitofrontal and the anterior cingulate cortex (Baudena *et al.,* 1995). In addition, a recent combined SPECT–ERP study found positive correlations between medial frontal regions and the P3a amplitude (Ebmeier *et al.,* 1995). In line with the previous results, the present study confirms the anterior cingulate as a likely location for P3a generators.

This anterior cingulate activation co-occurred with a deactivation of the posterior retrosplenial part of the cingulate gyrus, an observation that had already been made in the above-cited SPECT correlation study, leading the authors to postulate that the posterior cingulate cortex could be related to openness to external stimuli and thus deactivated during focusing attention tasks. Deactivation of the posterior cingulate has been previously described during a passive listening of complex tones and speech sounds (Fiez *et al.,* 1995), and in the present study, the fact that the posterior cingulate presents a larger NrCBF decrease during the selective attention tasks and remains significantly deactivated when comparing ATT to LIS supports the idea that the more focused is the attention the more depressed is its activity.

Precentral Gyri

In the frontal lobe, bilateral precentral activations were observed during both LIS and ATT conditions. Because this region contains primary motor and premotor areas and includes the frontal eye fields (Paus, 1996), one possible explanation could be that these

activations were related to the presence of saccadic eye movements of larger amplitude or frequency than during the REST condition. Indeed during selective listening tasks with focused attention, if the occurrence of eye movements is reduced, long saccades and changes of eye fixation in the direction of the relevant ear have been described (Gopher, 1973), with the direction of the gaze modulating the Nd amplitude (Okita and Wei, 1993). It seems therefore likely that fixation directed toward the attended ear was present in most of the subjects during the ATT condition, and, considering the close relationship between eye movements and attention, a fixation component cannot be excluded during the LIS task (Sheliga et al., 1994).

PET studies performed by our group on saccades have shown the involvement of a network composed of the precentral gyrus, the SMA, and the middle cingulate (Petit et al., 1993, 1996; Lang et al., 1994). Contrary to fixation (Petit et al., 1995), SMA and middle cingulate were not activated during LIS, which leads us to consider the presence of saccades, or gaze fixation, as a partial and secondary explanation for the observed precentral activations. During the ATT task, the right index movement for motor response is very likely to be responsible for the left precentral and SMA activations that were observed but we did not find again any middle cingulate activation and thus were driven to the same conclusion.

Rather, we propose that the bilateral precentral NrCBF increases observed in the present study reflect the activation of the generators of the third component of the N1, a nonspecific negative vertex wave that corresponds to a transient arousal of the organism, the role of which would be to facilitate the motor responses to the elicited stimulus (Näätänen and Picton, 1987). It has been hypothesized that its generators would be in the motor and premotor frontal cortices, both of which are included in the precentral gyri. Regarding the right precentral larger amplitude activation during the LIS condition, it is probably related to the right hemisphere dominance for attention and we suggest that it could be related to the late frontal component of the MMN that shows higher values on the right hemisphere whatever the stimulated ear (Giard et al., 1990). At least two components of the MMN have been identified, an early one the generator of which is supposed to be in the supratemporal plane and a later frontal one. This late component, predominant in the right hemisphere, would correspond to an orienting response and participate in the setting of cerebral arousal state (Giard et al., 1990).

We think therefore that the right precentral gyrus, implicated during both LIS and ATT, can then be considered part of the anterior attentional network. In fact neglect can appear after lesion of the cingulate gyrus, of the prefrontal cortex, but also of the lateral premotor, particularly when the lesion is lying in the

right hemisphere (Mesulam, 1990). Moreover, the persistence of the right precentral and anterior cingulate activations in the selective attention compared to passive listening demonstrates that selective attention enhances the recruitment of the frontal cortices, which is in agreement with the presence of a prolonged prefrontal endogenous negativity observed during such tasks (Woldorff and Hillyard, 1991).

Prefrontal Cortex

The right prefrontal region, made of the superior and middle frontal gyri, demonstrated an activation specific of the ATTL task. Hemispheric differences related to behavioral asymmetries were observed in the late positive peaks in a study on dichotic pitch discrimination, with greater late positive amplitude over the right hemisphere in subjects with strong left ear advantage (LEA), reflecting the right hemisphere dominance for such tasks (Tenke et al., 1993). In the present study the subjects were selected as right-handers, with an important proportion of them probably presenting an LEA, and this differential prefrontal activation could be related to a better performance of the task in the ATTL condition. The right hemisphere dominance for the mediation of intention and the existence of larger activation during processing of warning stimuli delivered to the right hemisphere has already been suggested by Heilman, who demonstrated reduced reaction times of the right hand when warning stimuli were projected to the right hemisphere (Heilman and Van den Abell, 1979). This result is also consistent with electrophysiological studies that demonstrated severe reductions in left ear attention ERP in patients suffering from right dorsolateral prefrontal regions (Knight et al., 1981; Knight, 1984). This selective activation of the right prefrontal for stimuli coming from the left side is not specific to the auditory system and reflects the dominance of the right hemisphere for attention. It has already been described during attention tasks involving sensory discrimination and visual attention. Indeed, in the PET study of sustained attention conducted by Pardo the right prefrontal region was activated with greater extent and amplitude when right-handed subject attention was directed to his left great toe (10 foci) than when directed to his right toe (3 foci) or central dim (2 foci) (Pardo et al., 1991). In the same vein, a previous PET study on visual selective attention has reported an activation of the left superior frontal gyrus in the attend left minus passive viewing contrast, which was not present in attend to right minus passive contrast (Heinze et al., 1994).

CONCLUSION

In conclusion two major networks seem to be involved during auditory attention: (1) A local temporal

network, specific to the auditory system on which selective attention to tones produces a modulation of the functional lateralization with the pertinent stimulus presentation side favoring the contralateral to the attending ear superior temporal cortex; this phenomenon can be considered an equivalent for the auditory modality of the local amplification observed in the visual system. (2) A frontal network, activated during sustained and/or selective attention independently of the modality engaged, made of the anterior cingulum, the right precentral gyrus, and the right prefrontal cortex, is at the origin of the modulation of the electrical activity of the auditory regions by selective attention as suggested by Posner (Posner and Dehaene, 1994). A particular status has to be given to the prefrontal cortex, specifically recruited by the incoming stimuli to the hemifield dominant for attention in visual, somatosensory, as well as auditory modalities that could support the right hemisphere dominance for attention.

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