

Speech processing activates visual cortex in congenitally blind humans

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Abstract

Neurophysiological recordings and neuroimaging data in blind and deaf animals and humans suggest that perceptual functions may be organized differently after sensory deprivation. It has been argued that neural plasticity contributes to compensatory performance in blind humans, such as faster speech processing. The present study employed functional magnetic resonance imaging (fMRI) to map language-related brain activity in congenitally blind adults. Participants listened to sentences, with either an easy or a more difficult syntactic structure, which were either semantically meaningful or meaningless. Results show that blind adults not only activate classical left-hemispheric perisylvian language areas during speech comprehension, as did a group of sighted adults, but that they additionally display an activation in the homologous right-hemispheric structures and in extrastriate and striate cortex. Both the perisylvian and occipital activity varied as a function of syntactic difficulty and semantic content. The results demonstrate that the cerebral organization of complex cognitive systems such as the language system is significantly shaped by the input available.

Introduction

Using brain imaging techniques it has been shown that the acquisition of a sign language leads to an altered cerebral organization of language functions in the deaf, thus demonstrating the close interaction between biological constraints and input conditions in the development of functional neuro-cognitive systems (Neville *et al.*, 1998; Petitto *et al.*, 2000). Similarly, electrophysiological measurements which index lexical processing provided evidence for a bilateral rather than a left-lateralized cerebral organization of language in congenitally blind adults and, moreover, indicated a stronger activation of posterior cortex areas which are usually associated with visual processing in sighted individuals (Röder *et al.*, 2000). During Braille reading activations similar to those observed during reading print were reported in the blind but an additional 'visual' cortex activation was observed (Sadato *et al.*, 1996; Büchel *et al.*, 1998b). However, a comparison of the cerebral organization of language between sighted and blind people employing Braille is limited by two facts: first, in sighted adults visual cortical areas are active during some tactile tasks (Zangaladze *et al.*, 1999); and second, sighted people are not able to read Braille with the same proficiency as blind people.

The present study used natural, auditory language presentation and employed functional magnetic resonance imaging (fMRI) to gain more precise information about the functional neuroanatomy of speech comprehension in congenitally blind adults. A paradigm was used that reliably activates both anterior and posterior left-hemispheric perisylvian regions in healthy, right-handed, sighted adults

(Röder *et al.*, 2002b), and whose task variables, including syntactic processing difficulty and meaningfulness of the message, were found to systematically modulate the amplitude of the haemodynamic response in these brain areas.

The present study has been presented at the Eighth Annual Meeting of the Cognitive Neuroscience Society, New York, U.S. (March 24–27, 2001).

Materials and methods

Participants

Ten congenitally blind, right-handed adults (four females; mean age 25 years, range 21–33 years; see Table 1) with German as first language participated. They were blind due to peripheral defects (but did not have any other impairments). They were all professional readers of Braille, which they had been using since elementary school. The sighted reference group (Röder *et al.*, 2002b) comprised 11 right-handed native speakers of German (six females; mean age 26 years, range 21–37 years). The latter were blindfolded throughout the experiment. All participants reported normal hearing. Informed consent was obtained and they all received monetary compensation for their participation.

Stimuli and apparatus

Each sentence comprised nine German words or pronounceable pseudo-words, starting with an adverbial phrase plus auxiliary, followed by three noun phrases and terminating with a past participle [example of a semantic sentence: 'Jetzt wird der Astronaut dem Forscher den Mond beschreiben.' (English word-by-word translation: Now will the astronaut to the scientist the moon describe); example of

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TABLE 1. Characteristics of the 10 blind participants

Participant number	Age (years)	Gender	Handedness	Profession	Vision status	Braille reading finger(s)	Diagnosis
1	30	Female	Right	MA student	Totally blind	Right index	Retinal degeneration
2	25	Female	Right	MA student	Totally blind	Both index/middle	Retrolental fibroplasia
3	30	Male	Right	Teacher	Totally blind	Left index	Inherited peripheral eye defect
4	21	Male	Right	MA student	Diffuse light	Left index	Retinal detachment
5	23	Female	Right	MA student	Diffuse light	Both index	Retrolental fibroplasia
6	21	Male	Right	MA student	Diffuse light	Both index	Retinal detachment
7	24	Male	Right	MA student	Diffuse light	Left index	Unknown
8	24	Female	Right	Apprentice	Totally blind	Right index	Retrolental fibroplasia
9	21	Male	Right	Apprentice	Totally blind	Both index	Retrolental fibroplasia
10	33	Male	Right	Computer assistant	Totally blind	Both index fingers	Optical nerve atrophy
Overall	25.2	6 Male/ 4 Female	10 Right		4 Diffuse light / 6 Totally blind	2 Right/3 Left/ 5 Both	

TABLE 2. Number of significantly activated voxels ($R > 0.5$) in each ROI in the single-participant analyses

ROI	Hemisphere	Participant number										Accumulated	
		1	2	3	4	5	6	7	8	9	10	L/R	L and/or R
1. Gyrus frontalis inferior	Left	293	1331	206	6235	1718	3490	3976	1105	6831	–	9	9
	Right	484	275	240	5009	683	295	3231	623	2986	–	9	9
2. Gyrus temporalis superior	Left	1753	3759	1371	9392	597	1241	9646	939	3906	933	10	10
	Right	1160	2791	2666	9086	605	318	1710	1536	3701	926	10	10
3. Gyrus frontalis medius	Left	–	–	589	7444	4796	2698	4785	4445	4647	–	7	9
	Right	207	182	2606	4902	146	1539	1968	303	2980	–	9	9
4. Lobus parietalis inferior	Left	104	–	125	6280	915	2757	1474	743	2273	–	8	9
	Right	–	825	477	824	398	–	1158	337	2592	–	7	7
5. Insula	Left	–	483	–	1606	3213	1897	1763	1119	3309	–	7	7
	Right	–	–	–	621	–	536	720	130	–	–	4	4
6. Gyrus cinguli	Left	–	–	–	2517	–	364	1219	–	952	–	4	4
	Right	–	–	–	2660	–	–	–	–	413	–	2	2
7. Gyrus occipitalis medius	Left	1482	5647	3646	7744	4729	1373	2007	6430	4775	879	10	10
	Right	4339	958	3270	3588	1044	–	2485	1692	3501	953	9	9
8. Gyrus occipitalis inferior	Left	–	–	–	1616	542	215	875	1942	–	–	5	8
	Right	1806	–	624	659	–	–	1995	104	836	–	6	6
9. Gyrus occipitalis superior	Left	–	–	–	860	349	–	–	192	–	–	3	6
	Right	135	–	411	713	–	–	2045	–	180	–	5	5
10. Gyrus lingualis	Left	–	–	–	–	2685	–	2834	358	1844	–	4	5
	Right	–	–	333	–	391	–	1180	–	1572	–	4	4
11. Gyrus fusiformis	Left	–	1374	182	1824	752	1259	2051	–	1854	323	8	10
	Right	808	–	2113	352	319	–	3595	172	629	336	8	8
12. Cuneus	Left	–	157	–	645	418	539	706	–	2000	–	6	6
	Right	–	–	–	180	–	928	926	–	1242	–	4	4
13. Sulcus calcarinus	Left	–	–	–	937	2303	125	628	144	1094	–	6	7
	Right	300	–	–	322	–	346	2320	–	259	–	5	5

Column 'L/R' gives the number of participants (n out of 10) who showed significant activity (threshold $R > 0.5$) in each of the left and right hemispheres of a particular ROI; column 'L and/or R' displays the number of participants who had significant active voxels in at least one hemisphere within that ROI.

a nonsemantic sentence: 'Jetzt wird der Tronasaut dem Schorfer den Rond bebreuschen.']. Due to the case markers (der, dem and den) German allows a permutation of the order of the noun phrases: subject, indirect and direct object (S, IO and DO) without changing the literal meaning of a sentence. However, any deviation from the canonical word order (S–IO–DO) increases comprehension time and thus different noun phrase permutations can be used to systematically vary syntactic processing difficulty both for semantic and nonsemantic speech (for more details see Röder *et al.*, 2000; Röder *et al.*, 2002b). Here, we contrasted the syntactically most easy sequences (S–IO–DO, S–DO–IO) with the most difficult sequences (IO–DO–S, DO–IO–S). All sentences were spoken by a professional female speaker and were presented via a home-made tubing system connected to noise-protecting headphones [sound level 75–85 dB(A)].

Procedure

After a familiarization with the different stimulus conditions outside the scanner, all participants received three runs of 10 min 50 s each: each run comprised five conditions: (1) easy semantic speech (ES) (2) difficult semantic speech (DS) (3) easy nonsemantic speech (EN) and (4) difficult nonsemantic speech (DN) and (5) backward speech (B). Conditions were presented in blocks (duration 30 s) of seven sentences each. The sequence of conditions within a block was systematically varied across runs and participants. In each run, conditions (1–4) were repeated three or four times, dependent on the protocol, backward speech (B) occurred eight times with the last backward speech block shortened to 20 s (i.e. a total of 152 sentences were presented per run). While most of the sentences occurred (in different runs) in an easy and difficult word order, none of the

TABLE 3. Activations predicted by the overall language effect in the analysis across congenitally blind participants

ROI	Anatomical structure	Brodmann's area	Left hemisphere				Right hemisphere			
			x	y	z	Voxels (n)	x	y	z	Voxels (n)
1.	Gyrus frontalis inferior	44, 45, upper 47	-46	15	20	7482	46	19	20	5302
2.	Gyrus temporalis superior Sulcus temporalis superior Gyrus temporalis medius	22, 21, 37	-52	43	9	6855	49	40	10	3133
3.	Gyrus frontalis medius	6, 9	-43	4	39	1522	47	6	35	974
4.	Lobus parietalis inferior	40	-36	-40	44	637	36	-40	42	718
5.	Insula	-	-39	23	0	2413	33	22	-1	706
6.	Gyrus cinguli	24, 32								
7.	Gyrus temporalis medius Gyrus angularis Gyrus occipitalis medius)	37, 39, 19, 18	-48	-63	10	8188	41	-70	2	5055
8.	Gyrus temporalis inferior Gyrus occipitalis inferior Gyrus occipitalis medius	37, 19, 18								
9.	Gyrus occipitalis superior	19					16	-83	28	348
10.	Gyrus lingualis	18, 19	-13	-70	-5	425				
11.	Gyrus fusiformis	18, 19	-38	-56	-6	1954	31	-69	-10	3567
12.	Cuneus	18								
13.	Sulcus calcarinus	17					13	-84	15	883

ROI with anatomical structures according to Talairach & Tournoux (1988) and Brodmann's area definitions. Four-predictor across-participant GLM (ES, DS, EN, DN vs. B): $R > 0.40$.

sentences were repeated in the same form. Each run contained up to three semantic or nonsemantic sentences with a clearly incorrect syntactic structure, which had to be silently counted (for more details see (Röder *et al.*, 2002b)).

Image acquisition and analysis

A total of 130 echo planar imaging (EPI) volumes (TR 5000 ms, TE 60 ms, flip angle 90°) were acquired in each of the three runs using a 1.5-Tesla clinical MRI scanner (Signa Horizon, General Electric). Each EPI volume comprised 22 axial slices (thickness 5 mm, gap 0), with an inplane resolution of 3.75 × 3.75 mm (field of view 240 × 240 mm; matrix 64 × 64). For each participant a whole-head 3-D volume (124 continuous axial slices, thickness 1.4 mm, TR 11.1 ms, TE 4.2 ms, number of excitations = 3) was recorded in the same session using a fast spin gradient echo sequence (FSPgr; field of view 240 × 180 mm, matrix 256 × 192, resulting in an inplane resolution of 0.9375 × 0.9375 mm). Data analysis was performed with the software package BRAINVOYAGER (Version 3.9/4.1, BrainInnovation: <http://www.brainvoyager.de>). Data analysis included image preprocessing (elimination of low-frequency signal drifts and possible head movement artifacts), 2-D-3-D alignment and the converting of the data sets into Talairach space (Talairach & Tournoux, 1988). The first two functional volumes of each run were discarded. In the single-participant analyses a four-predictor (ES, DS, EN, DN) General Linear Model (GLM) was calculated for each participant taking all three runs into account (threshold of multiple regression value, $R > 0.5$, cluster size > 100 voxels of 1 × 1 × 1 mm). In order to compensate for the delay of the haemodynamic response the (sinusoidal) predictor functions were shifted in all analyses by one volume (5 s). Across-participant analyses were run using three different GLM designs: first, a four-predictor model was defined as in the single-participant analyses. Second, syntax effects were estimated by comparing the two syntactically easy conditions (ES, EN) with the two difficult conditions (DS, DN). Third, semantic effects were estimated by contrasting the two semantic conditions

(ES, DS) with the two nonsemantic conditions (EN, DN). Significantly activated voxels were assigned to brain areas using the Talairach and Tournoux brain atlas (Talairach & Tournoux, 1988) [called in the following 'regions of interest' (ROIs); see Table 3]. Because the amplitude and variance of voxel time courses may differ between participants, a Z-normalization of each signal time-course was performed. In order to compensate for interindividual differences, the functional 3-D maps were spatially smoothed using a Gaussian kernel of 6 mm FWHM (full width of half maximum) before the across-participant analyses were run. Thresholds were lowered to the same values used for the sighted reference group (Röder *et al.*, 2002b): $R > 0.4$ ($F_{4,3835} = 182.62$, $P < 0.0001$; corrected) was used for the four-predictor model and $R > 0.2$ for the syntax and semantic effects ($F_{4,3835} = 79.9$, $P < 0.0001$, corrected). In addition, the mean percentage signal change was calculated for each significantly activated voxel cluster (threshold $R > 0.5$, cluster size > 100 voxels) within each ROI separately for each participant and condition. A voxel-based group comparison was calculated to reveal those brain areas more active in the blind than in the sighted (threshold $t_{8040} = 8$, $P < 0.0001$, Bonferroni-corrected).

Results

Behavioural results

The count of a blind participant was on average 1.03 (range 0–2) higher or lower than the actual number of sentences with an ungrammatical word order in a run. This is similar to what was reported for the sighted reference group [mean (sighted), 1.29; range 0–3] (Röder *et al.*, 2002b).

Single-participant fMRI analyses

A reliable activation was found in the posterior perisylvian language areas (ROI 2) in all blind participants and in the inferior frontal cortex (ROI 1) in nine out of 10 participants (Table 2). These

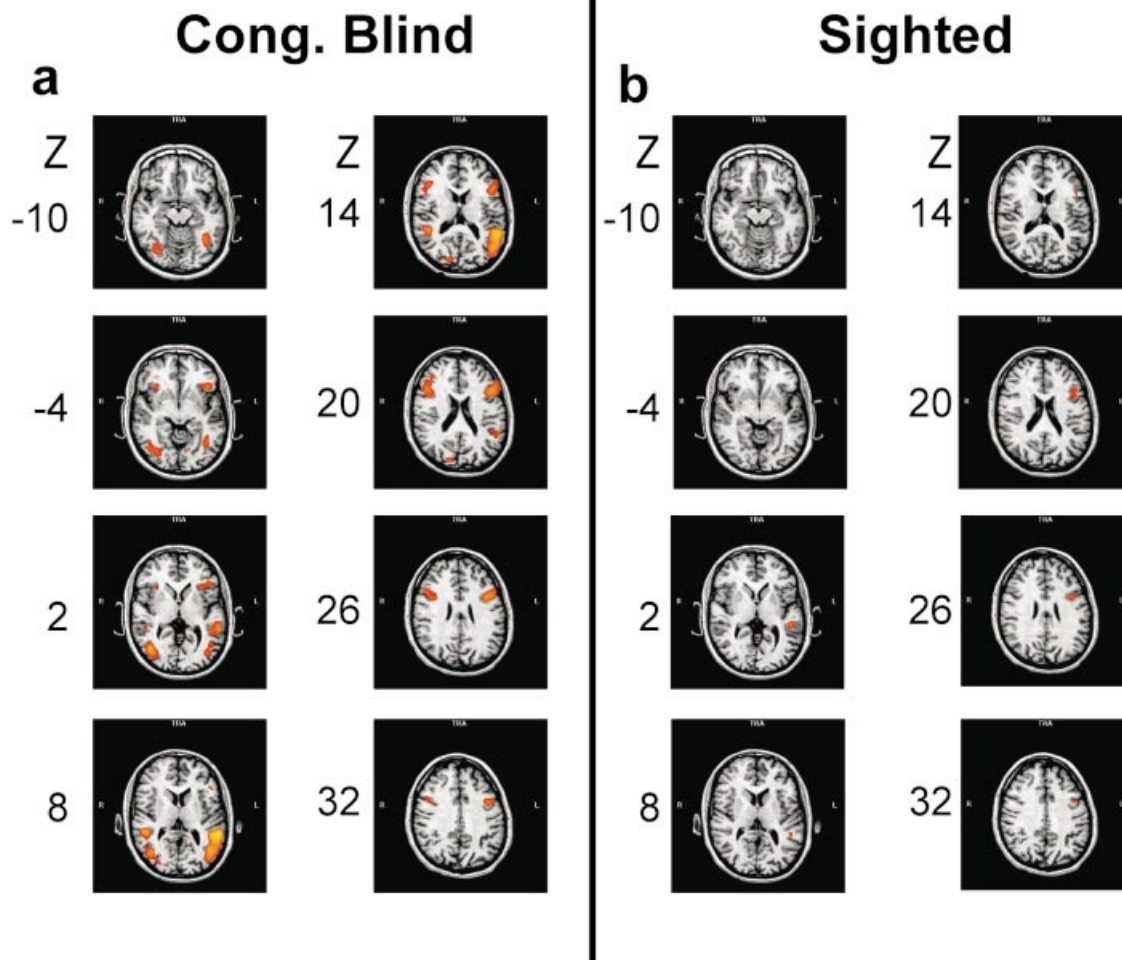


FIG. 1. Significantly activated voxels ($R > 0.40$) as revealed by the across-participant analysis with four predictors (language easy/semantic, difficult/semantic, easy/nonsemantic or difficult/nonsemantic), (a) for the group of the congenitally blind and (b) for the sighted reference group (from Röder *et al.*, 2002b). The colour coding represents significance levels as defined by R -values; the more yellow a pixel is, the higher the R -value is. The activations are projected onto a series of horizontal slices of the brain of one participant (not all significantly activated voxels are visible in the figure).

activations as well as activity in the middle frontal gyrus, cingulate gyrus and inferior parietal region overlap with the active brain areas observed for sighted, right-handed adults (Röder *et al.*, 2002b). However, while only three sighted participants had shown activity in the right frontal cortex and only two in the right temporal region, the blind participants typically displayed significant activations in ROIs within both the left and right hemispheres (see Table 2). Furthermore, in the blind, speech comprehension activated several additional brain regions not active in the sighted group (using the same $R > 0.5$ threshold). All blind participants had significantly activated voxels in extrastriate brain areas (ROIs 7–12) and seven had reliable blood-flow changes in the calcarine sulcus (ROI 13), i.e. in a region known to be primary visual cortex in sighted individuals. The latter activation was observed in all of the participants with some rudimentary sensitivity for light but also in three of the six totally blind participants, including one woman with enucleated eyes (participant no. 8).

Across-participant analyses

The across-participant analyses substantiated the single-participant observations by showing, in the first overall GLM analysis, predominantly bilateral activity in the anterior (ROI 1) and

posterior (ROI 2) perisylvian region, and in occipital brain areas (ROI 7, right ROI 9, left ROI 10, left and right ROI 11) including the right calcarine sulcus (ROI 13). Additional bilateral activity was found in the middle frontal gyrus, inferior parietal lobe and insula (Fig. 1 and Table 3). Higher syntactic processing load (second GLM, Syntax effect) resulted in larger blood flow changes in almost all ROIs of both hemispheres except ROI 8, ROI 12 and right ROI 9. The contrast of semantic vs. non-semantic language (third GLM, Semantics effect) revealed higher blood-flow changes in all ROIs of both hemispheres except the left cuneus (ROI 12). This variation of the haemodynamic response as a function of the processing demands is summarized in Fig. 2a and b, which shows the percentage signal change as a function of syntactic difficulty and semantics, respectively, for two perisylvian (ROI 1, ROI 2) and two occipital (ROI 11, ROI 13) brain areas of the left and right hemisphere.

Group comparison

A direct voxel-based group comparison revealed significantly higher blood flow changes in the congenitally blind for all ROIs except the cingulate gyrus and left medial frontal gyrus (see Table 4).

TABLE 4. Activations predicted by the overall language effect in the analysis of congenitally blind vs. sighted subjects

ROI	Anatomical structure	Brodmann's area	Left hemisphere				Right hemisphere			
			x	y	z	Voxels (n)	x	y	z	Voxels (n)
1.	Gyrus frontalis inferior	44, 45, 47	-43	24	8	1015	48	16	20	2209
2.	Gyrus temporalis superior Sulcus temporalis superior Gyrus temporalis medius	22, 21, 37	-56	43	12	3449	53	-38	17	8634
3.	Gyrus frontalis medius	6, 9					48	9	38	1375
4.	Lobus parietalis inferior	40	-48	-34	27	2279	55	-29	26	2527
5.	Insula	-	-26	16	-10	194	39	23	-10	1011
6.	Gyrus cinguli	24, 32								
7.	Gyrus temporalis medius Gyrus angularis Gyrus occipitalis medius	37, 39, 19, 18	-46	-69	8	11650	46	-65	8	16669
8.	Gyrus temporalis inferior Gyrus occipitalis inferior Gyrus occipitalis medius	37, 19, 18	-30	-77	-4	800	34	-70	-8	1580
9.	Gyrus occipitalis superior	19	-13	-79	36	1513	18	-80	32	2715
10.	Gyrus lingualis	18, 19	-11	-69	-3	2436	19	-72	-2	3770
11.	Gyrus fusiformis	18, 19	-32	-64	-5	4410	32	-75	-3	6818
12.	Cuneus	18	-12	-86	20	3116	10	-79	29	3381
13.	Sulcus calcarinus	17	-6	-72	8	1397	7	-76	14	1906

ROI with anatomical structures according to Talairach & Tournoux (1988) and Brodmann's area definitions. Four-predictor across-participant GLM (ES, DS, EN, DN vs. B), $R > 0.40$.

Discussion

The present fMRI study systematically manipulated syntactic difficulty and semantic content of auditorily presented sentences to investigate possible changes in the cerebral organization of these functions due to altered early visual input. In the congenitally blind these language-relevant operations were accompanied by haemodynamic responses not only in the classical perisylvian language areas of the left hemispheres, as in the sighted (Röder *et al.*, 2002b), but elicited in addition activity in homologous right hemispheric structures and in extrastriate and striate brain regions.

Because the amplitude of the haemodynamic response in right hemispheric and occipital areas varied as a function of syntactic (i.e. for sentences with the same words but in different legal permutations) and semantic processing demands, it is very unlikely that these group differences were due either to an overall difference in arousal, anxiety and nonspecific shifts of attention, with higher resting activation of blind subjects' occipital areas (Arno *et al.*, 2001), or to basic auditory operations. Because the blind and sighted (Röder *et al.*, 2002b) showed similar behaviour performance as well, motivational differences are unlikely too. Thus, the present study documents in each single blind participant a bilateral and posteriorly extended language-related brain activity.

Positron emission tomography (PET) studies in the blind have reported generally higher activation of 'visual' cortex areas in several other tasks including Braille reading and tactile discrimination (Sadato *et al.*, 1996; Büchel *et al.*, 1998a), auditory localization (Weeks *et al.*, 2000), auditory object recognition (Arno *et al.*, 2001) and auditory imagery (De Volder *et al.*, 2001). A direct comparison with the present study, however, is difficult: (i) earlier PET studies reported group average data only; (ii) most previous studies (except Büchel *et al.*, 1998a; Weeks *et al.*, 2000) investigated so-called early-blind adults, i.e. people who became blind within their first 5–10 years of life, while in the present sample only congenitally blind adults were included. When studies with congenitally blind partici-

pants only are considered, the main overlap with the activations observed in the present study is found (despite the different paradigms) within extrastriate and parietal brain areas (BA 18, 19 and 40) (Büchel *et al.*, 1998a; Weeks *et al.*, 2000). The fusiform gyrus showed significant activity changes only when verbal stimuli were employed (Büchel *et al.*, 1998a). In contrast to our results, Büchel *et al.* (1998a) and Weeks *et al.* (2000) did not report primary visual cortex activations.

Finally, a similar gradually modulated activation of occipital brain regions was recorded with scalp electrodes in the blind during an imagery task which required them to mentally rotate tactile patterns across different angles (Röder *et al.*, 1997).

The great variety of tasks eliciting activity in extrastriate and/or striate cortex in blind humans raises the question of their functional role for the blind. One speculation could be that the increasing specialization of brain tissue for perceptual–cognitive functions, which is observed during normal development in sighted children (Holcomb *et al.*, 1992), may not eventuate to the same extent in blind individuals because visual deprivation results in less competition for synaptic space. Therefore, the occipital cortex deprived of visual stimulation may be capable of participating in nonvisual perceptual–cognitive functions including language. In fact, neural transplantation (Schlaggar & O'Leary, 1991) or rewiring studies (Sur & Leamey, 2001) suggest that sensory cortex tissue can process input of a foreign modality. Moreover, single-cell recordings uncovered nonvisual responses in extrastriate cortex of visually deprived animals (Hyvärinen *et al.*, 1981) although findings for the primary visual areas are not as clear (Kennedy *et al.*, 1997; Yaka *et al.*, 1999). On the other hand, speech arrest was not observed during occipital cortex deactivation in blind humans (Cohen *et al.*, 1997) and a blind patient with bilateral occipital lobe damage showed alexia for Braille but preserved speech comprehension (Hamilton *et al.*, 2000). Therefore, it is not possible to exclude the possibility that the higher blood flow changes in and electrophysiological activity of 'visual' brain areas in the blind reflect a coactivation, possibly due to less efficient

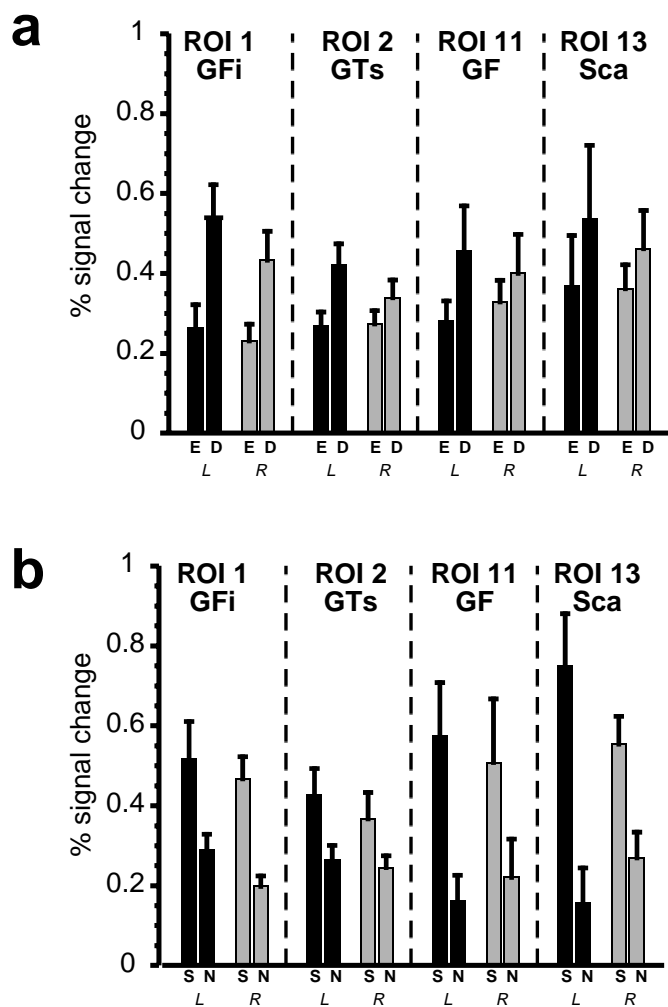


FIG. 2. Congenitally blind: percentage signal changes (with SEM bars) for the left (black) and right (grey) hemisphere within the inferior frontal gyrus (GFi, ROI 1), superior and medial temporal gyrus including the superior temporal sulcus (GTs, ROI 2), fusiform gyrus (GF, ROI 11) and calcarine sulcus (Sca, ROI 13). (a) Syntax effect: semantic/easy, nonsemantic/easy (E) vs. semantic/difficult, nonsemantic/difficult (D); (b) Semantics effect: semantic/easy, semantic/difficult (S) vs. nonsemantic/easy, nonsemantic/difficult (N). The amplitude of the haemodynamic response was significantly higher both for (a) the syntactically more difficult sentences and (b) semantic as compared to nonsemantic sentences.

inhibitory circuits (Rozas *et al.*, 2001) rather than functional specific or necessary activity. In this line, occipital cortex activity of the blind varied in the present study as a function of both semantic and syntactic requirements rather than being specific for one of the two language functions. Indeed, imaging studies have provided evidence for a deactivation of visual brain areas during the processing of auditory stimuli (and *vice versa*) (Laurienti *et al.*, 2002). It could be speculated that this down-regulation of occipital cortex activity does not take place.

The bilateral rather than left-lateralized activation of the classical language areas in the blind supplements earlier electrophysiological findings (Röder *et al.*, 2000). It could be hypothesized that the use of Braille, similar to the use of sign language in the deaf (Neville *et al.*, 1998), results in a stronger engagement of the right hemisphere for language processing, because Braille also relies more upon spatial

components than printed or spoken language (Hermelin & O'Connor, 1971; Karavatos *et al.*, 1984). It is interesting to note that despite the right-handedness of all blind participants their reading hand preferences for Braille were not lateralized to the same extent. The bilateral activation pattern, however, did not covary as a function of the hand used for Braille reading. In a dichotic listening task a decreasing right-ear/left-hemisphere advantage was reported with increasing proficiency in Braille reading (Karavatos *et al.*, 1984) while illiterate blind adults showed the normal left-right asymmetry (Karavatos *et al.*, 1984). Moreover, it may also be that the lack of visual-spatial input in the blind results in less interhemispheric competition and, finally, a bilateral representation of language. Nevertheless, auditory-spatial functions are represented in the blind subject's parietal-occipital cortex as well (Weeks *et al.*, 2000), and left hemispheric lesions result in aphasia in the blind as in the sighted (Birchmeier, 1985; Signoret *et al.*, 1987). It might be speculated that the right hemisphere may exert a supportive influence without being sufficient for speech comprehension. It is interesting to note that several studies with blind children reported delays and deviations from normal language acquisition (Mills, 1988; Pèrez-Pereira & Conti-Ramsden, 1999). However, these initial disadvantages of the blind seem to vanish with age (Pèrez-Pereira & Conti-Ramsden, 1999) and even seem to turn into enhanced speech perception skills in blind adults (Muchnik *et al.*, 1991; Röder *et al.*, 2000; Röder *et al.*, 2002a), eventually turning language into a major compensatory tool of the blind in everyday life (Pèrez-Pereira & Conti-Ramsden, 1999). Intense practice can lead to an enlargement of sensory representations (Elbert *et al.*, 1995) and it has been shown that these effects can be used to oppose maladaptive reorganizations, after the amputation of a limb, which are related to phantom pain (Flor *et al.*, 2001). To what extent the bilateral and posteriorly extended language-related activations observed in the blind do actually contribute to their behavioural advantages remains to be shown.

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Abbreviations

B, backward speech; DN, difficult nonsemantic speech; DO, direct object; DS, difficult semantic speech; EN, easy nonsemantic speech; ES, easy semantic speech; fMRI, functional magnetic resonance imaging; GLM, General Linear Model; IO, indirect object; *R*, multiple regression value; *S*, subject.

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