

# Lateralization of Speech Production Starts in Sensory Cortices—A Possible Sensory Origin of Cerebral Left Dominance for Speech

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**Speech production is a left-lateralized brain function, which could arise from a left dominance either in speech executive or sensory processes or both. Using functional magnetic resonance imaging in healthy subjects, we show that sensory cortices already lateralize when speaking is intended, while the frontal cortex only lateralizes when speech is acted out. The sequence of lateralization, first temporal then frontal lateralization, suggests that the functional lateralization of the auditory cortex could drive hemispheric specialization for speech production.**

**Keywords:** articulation, auditory cortex, functional MRI, task set, reading

## Introduction

Speech production is seen as a left-hemispheric process (Damasio and Geschwind 1984; Borovsky et al. 2007; Devlin and Watkins 2007; Davis et al. 2008; Sanai et al. 2008), when in fact little is known about which processing steps specifically require left brain regions. A central question to this problem is whether left dominance in speech production is driven by speech executive or sensory systems. One possible approach to this question consists in examining the sequence of lateralization during speech production using functional imaging. When planning an action, the anterior prefrontal cortex preactivates the neural circuitry that is going to be used in the upcoming task (Dosenbach et al. 2006; Sakai and Passingham 2006). During speech production, it monitors sensory feedback to adjust behavior (Dosenbach et al. 2006). Whether the brain only preactivates those regions that are used for speaking (executive) or also prepares for auditory and somatosensory feedback is unclear, but if the sensory systems were already preactivated during action selection, they would be in the position to play a determinant role in left-hemisphere dominance during speech production. We therefore set out to determine whether the executive or sensory system lateralizes first during the cognitive sequence leading to speech production.

In a functional magnetic resonance imaging (fMRI) experiment, we separated the first processing step of speech production, the intention to speak, from speech execution, using a cue-target paradigm in which participants were prompted to read a sentence either out loud or covertly without knowing in advance its content (Fig. 1). We used reading rather than spontaneous speech to separate the first step of speech preparation, namely the intention to speak from linguistic computation and articulatory preparation. Because specific speech planning was impossible before the target was presented, this speech preparation phase did not involve preparation of specific sensorimotor transformations—a process that strongly lateralizes to the left

temporoparietal junction (sylvian parietotemporal area, SPT) (Wise et al. 2001; Hickok et al. 2003). We assume that if we observed left-lateralization of the speech executive network (including area SPT, Broca's area, anterior insula, premotor cortex, etc.) already during speech preparation, left dominance for speech production may be driven by executive regions. If, conversely, we observed initial left-lateralization of the auditory and somatosensory feedback systems, left-hemispheric dominance in speech production may be driven by sensory asymmetry (Hutsler and Galuske 2003).

## Materials and Methods

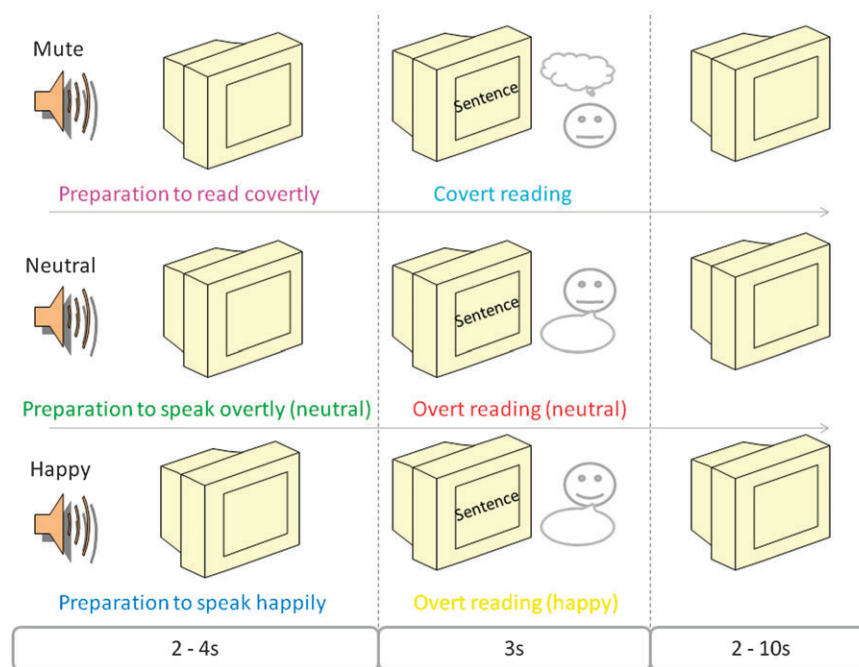
### Experiment 1

Twenty-six healthy subjects participated in a 3 T functional MRI experiment during which they read sentences either covertly without orofacial movement or aloud (factor 1), depending on an auditory instruction that preceded sentences by a variable delay ranging from 2 to 4 s (Fig. 1). We could thus temporally dissociate speech preparation from execution (factor 2) and assessed the influence of overt speaking on each phase. Covert reading was used as cognitive baseline to subtract out speech perception-related neural computation after confirming that it did not yield significant lateralized effects relative to silent baseline (see Supplementary Fig. 1). Lateralization was tested by contrasting voxelwise condition-specific brain activity with contralateral values.

### Data Acquisition

We performed a functional MRI experiment involving reading sentences in the scanner in healthy participants. Subjects gave informed consent to participate in the study, which was approved by the local ethics committee. Prior to scanning, participants were familiarized with the experimental setting.

Twenty-six healthy subjects, half female, were recruited from hospital personnel and students. Mean age was 29 (range: 19–44), 2 female left-handers were included. To ensure that subjects had normal speech production and reading skills, we screened the past medical history and assessed speech rate, naturalness, and errors during 4 speaking conditions: open conversation, reading a standard newspaper text, calling an unknown person by phone, talking to a passerby. Subjects with reading difficulty or speech production anomalies were excluded from the study. Handedness was assessed using the Oldfield hand preference inventory (Oldfield 1971). Subjects wore headphones for noise protection and delivery of acoustic cues; their heads were immobilized by a cushion. Visual stimuli were projected on a screen and viewed through a mirror. The material involved 44 written phonologically balanced, semantically neutral German declarative sentences with identical syntactical structure (“Britische Zeitungen verbreiten gerne Gerüchte,” translated “British newspapers enjoy spreading rumors”). They were presented for 3 s, preceded 2–4 s earlier by an auditory instruction (“mute,” “normal,” or “happy”) indicating whether sentences should be read covertly or overtly with normal intonation or intoned happily (factor 1). We instructed subjects to read covertly with normal intonation. Trials thus consisted of 2–4 s during which



**Figure 1.** Study design. In our  $2 \times 2$  factorial design, factor 1 corresponded to the 3-level effect of task, while factor 2 identified the trial phase (preparation or execution). For analysis of speech preparation and production, preparation and execution of covert reading (first row) served as cognitive baseline (see also Supplementary Fig. 1). For analysis of prosody preparation and production, neutral intonation (second row) was used as baseline.

subjects cognitively prepared for either task followed by 3 s of task execution (Fig. 1). Importantly, during the preparation phase, the linguistic material was not yet known to the subject so that preparation for sensorimotor transformation of a specific sentence was not possible. Our paradigm therefore allowed for a temporal dissociation of task preparation from specific speech motor preparation and execution (factor 2). The intertrial interval varied within a range of 2–10 s (mean 6 s). Subjects' behavior was recorded with an MRI-compatible microphone (mr confon); recordings were analyzed after filtering out the scanner noise (Adobe Audition) for task performance.

Data were collected using a 3 T magnetic resonance scanner (Siemens Trio) by constant acquisition of 902 volumes of a gradient echo planar imaging (EPI) sequence with an echo time of 30 ms, repetition time (TR) of 2 s, and voxel size of  $3 \times 3 \times 3 \text{ mm}^3$  (1 mm gap, 33 slices to cover the entire brain). This sequence was shown to be efficient and safe to study brain activity during overt speech production (Preibisch et al. 2003). Anatomical scans were obtained using a magnetization rapid-acquisition gradient echo sequence (144 slices, 1 slab, TR 2300 ms, voxel size  $1 \times 1 \times 1 \text{ mm}^3$ ) and confirmed the absence of brain lesions.

### Data Analysis

The EPI images were spatially preprocessed (realignment, normalization to an EPI template and smoothing with an 8 mm full-width at half-maximum isotropic Gaussian kernel) using the standard parameters of statistical parametric mapping (SPM5; <http://www.fil.ion.ucl.ac.uk/spm/>). The data were analyzed within the general linear model framework: Auditory instructions were modeled as events and the preparation and execution phases were modeled separately for each task (overt or covert). Only the orthogonal regressor components were taken into account to ensure the temporal specificity of the responses (Poline et al. 2007). Transient activations due to the auditory instructions were regressed out, while the preparation phase regressors captured phasic activity that is typically linked to maintenance of task sets (Dosenbach et al. 2006). The conditions of interest were modeled using a boxcar function with the respective duration convolved with a canonical hemodynamic response function. Data were corrected for serial autocorrelations and globally normalized. Because we used covert reading as cognitive baseline in subsequent analyses, effect sizes reflect local percent signal change in comparison

with covert reading. The effect of the cognitive baseline itself is illustrated in Supplementary Fig. 1 and confirms the absence of lateralization effects ( $P > 0.1$ ) in the baseline except for the frontal eye field (rightward eye movement during reading).

### Simple effects, interactions, and correlations

We calculated the conditions of interest in each individual and added realignment parameters to the model as effects of no interest to correct for movement artifacts. Conditions were entered in a 2-way analysis of variance with conditions of interest and subject as factors. Possible gender and handedness effects were regressed out, even though when specifically tested they did not appear significant. To test for preparation and execution of sensorimotor transformation, the contrast overt versus covert reading was calculated separately for the 2 phases, yielding distinct effects for the intention to speak and for speech production. We additionally tested for preparation and execution of prosody generation using the contrast happy intonation versus neutral intonation, separately for the 2 phases. Interactions between phase and task were tested using the appropriate contrasts. We report results thresholded at  $P < 0.005$ , corrected for multiple comparisons on the voxel level (false discovery rate, FDR; Genovese et al. 2002).

We tested for lateralization of brain activity by contrasting individual contrast images with their flipped counterparts. To account for minor differences in exact localization of corresponding brain regions, we additionally smoothed images with 6 mm full-width at half-maximum isotropic Gaussian kernel. Results are reported at  $P < 0.005$ , corrected for multiple comparisons on the voxel level (FDR) over the entire brain (Table 1) but also corrected within the volume of the corresponding contrast images (Table 2). To further illustrate lateralization effects, we plotted percent signal change in regions of interest, separately for preparation and execution phase and hemisphere, with their respective standard error mean in Figure 2C. Coordinates of activations are given in the Montreal Neurological Institute (MNI) space. Brodmann areas corresponding to the activations were identified using probability maps from the anatomy toolbox for SPM (Eickhoff et al. 2005) or the stereotactic atlas of the human brain (Lancaster et al. 2000).

### Experiment 2

We ascertained the specificity of our findings from the main experiment by performing a control experiment in 16 new right-handed healthy

**Table 1**

Significant changes in brain activation due to overt speech.

Region	BA	Preparation to speak overtly vs. covertly		Interaction	Execution of overt vs. covert reading		Lateralization (L>R)	Preparation to speak happily vs. read covertly		Execution of happy speaking vs. covert reading	
		Coordinates	Z (p) value	Z (p) value	Coordinates	Z (p) value	Z (p) value	Coordinates	Z (p) value	Coordinates	Z (p) value
Mesial frontopolar cortex	10	0 54 0	5.78 (0)	Inf (0)				0 54 2	6.18 (0)		
Cingulate motor area	24	0 28 30	6.68 (0)	7.32 (0)				−2 28 32	6.9 (0)		
Pre-SMA	8	0 16 36	7.64 (0)	6.07 (0)				0 10 44	Inf (0)		
SMA	6	0 0 58	7.33 (0)	6.6 (0)				0 0 58	7.78 (0)		
L lateral frontopolar cortex	10	−28 62 6	5.39 (0)	6.98 (0)				−28 62 6	4.7 (0)		
R lateral frontopolar cortex	10	32 62 0	4.6 (0)	5.13 (0)							
L frontal operculum	47	−58 10 −6	6.1 (0)	5.27 (0)				−58 12 −4	6.45 (0)		
R frontal operculum	47	52 16 −14	Inf (0)	5.12 (0)				56 12 −10	7.78 (0)		
L inferior frontal gyrus	44	−58 10 6	6.11 (0)		−52 14 4	3.98 (0.01)		−54 28 −2	5.22 (0)	−52 18 2	5.02 (0)
R inferior frontal gyrus	44	62 16 4	4.6 (0)					62 16 4	4.79 (0)	52 18 2	3.97 (0.001)
L anterior insula	13	−38 20 0	5.42 (0)		−28 34 0	3.92 (0.012)		−36 22 0	5.01 (0)	−46 12 4	7.03 (0)
R anterior insula	13	42 20 −6	4.67 (0)					38 24 −6	4.78 (0)	46 16 6	4.88 (0)
L M1	4	−52 −8 30	Inf (0)		−58 −10 28	Inf (0)		−54 −8 30	7.06 (0)	−52 −10 30	7.28 (0)
L SI	3	−42 −20 36	4.62 (0)		−42 −20 46	6.23 (0)	5.11 (0)	−42 −16 38	7.13 (0)	−40 −14 30	7.49 (0)
R M1	4	56 −2 26	Inf (0)		58 −4 22	Inf (0)		56 −2 26	Inf (0)	56 −4 20	7.18 (0)
L anterior STG	22	−60 −14 2	6.71 (0)		−62 −14 −2	Inf (0)		−60 −16 4	6.88 (0)	−62 −14 4	7.22 (0)
R anterior STG	22	62 −6 4	Inf (0)		62 0 −6	6.71 (0)		62 −8 4	Inf (0)	62 −10 4	5.01 (0)
L auditory cortex (Planum temporale)	41	−50 −22 6	6.26 (0)	3.72 (0.002)			5.46 (0)	−50 −24 6	6.56 (0)		
R auditory cortex (Heschl gyrus)								54 −14 6	7.82 (0)		
L STS	22			5.99 (0)	−62 −36 4	7.79 (0)				−62 −34 4	7.25 (0)
R STS	22			6.7 (0)	52 −32 0	Inf (0)				52 −32 −2	Inf (0)
L SPT	40			6.91 (0)	−48 −44 24	5.79 (0)	4.76 (0.003)			−48 −44 26	5.84 (0)
L inferior parietal lobule	19	−16 −80 48	4.77 (0)					−16 −76 50	5.9 (0)		
R inferior parietal lobule	19	14 −80 48	5.32 (0)	4.16 (0)				18 −72 56	5 (0)		
L caudate nucleus		−12 14 −2	4.86 (0)	7.01 (0)				−8 14 2	3.57 (0)		
R caudate nucleus		12 16 −2	4.64 (0)	6.16 (0)				12 18 2	3.8 (0)		
L pallidum		−20 12 −6	4.51 (0)								
R pallidum		16 18 −4	4.58 (0)								
L ventral striatum								−20 10 −4	7.84 (0)		
R ventral striatum								20 12 −6	7.13 (0)		
L thalamus					−14 −16 2	Inf (0)				−14 −16 2	Inf (0)
R thalamus					16 −4 4	6.3 (0)				16 −14 2	6.66 (0)
L substantia nigra				7.6 (0)	−10 −20 −18	7.54 (0)					
R substantia nigra				7.54 (0)	12 −18 −16	7.56 (0)					
L cerebellar hemisphere				Inf (0)	−16 −62 −24	Inf (0)				−16 −62 −24	Inf (0)
R cerebellar hemisphere				Inf (0)	16 −62 −22	Inf (0)				16 −62 −22	Inf (0)

For abbreviations please see main text. *P*-values reflect a false-discovery rate-based correction for multiple comparisons over the entire brain. Note that the left IFG and left anterior insula show only sub-threshold activation for execution of overt vs. covert reading.

**Table 2**

Significant brain activations due to happy intonation.

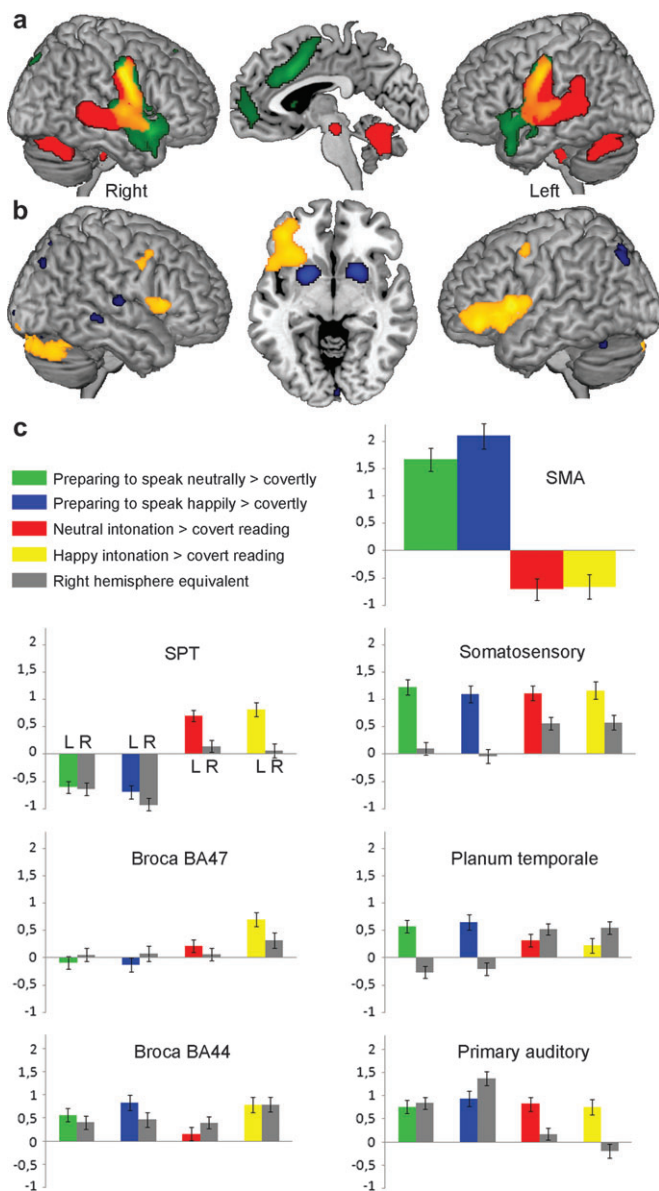
Region	BA	Preparation to speak happily vs. intention to read neutrally		Interaction	Execution of happy vs. neutral intonation		Lateralization (L>R)
		Coordinates	Z (p) value	Z (p) value	Coordinates	Z (p) value	Z (p) value
L frontal operculum	44			4.57 (0.001)	−46 14 6	6.16 (0)	
R frontal operculum	44				44 18 6	4.83 (0.001)	
L anterior insula	13			3.8 (0.004)	−36 28 −2	4.93 (0)	
L inferior frontal gyrus	47			5.07 (0)	−42 42 −10	5.54 (0)	4.45 (0.003)
L premotor	6				−36 4 44	3.94 (0.005)	
R premotor	6				34 8 42	3.76 (0.007)	
R superior temporal sulcus	22	68 −34 −6	3.88 (0.011)		50 −26 −8	3.22 (0.029)	
R auditory cortex (A1)	41	52 −16 10	4.14 (0.005)	4.08 (0.007)			−4.37 (0.001)
L inferior parietal lobule	19	−14 −72 52	4.7 (0.001)	4.34 (0.003)			
R inferior parietal lobule	19	34 −76 38	3.64 (0.023)	5.12 (0)			
L ventral striatum		−22 6 −6	6.83 (0)	6.31 (0)			
R ventral striatum		20 10 −4	6.45 (0)	6.22 (0)			
R cerebellar hemisphere				3.96 (0.003)	34 −60 −30	5.39 (0)	

*P*-values reflect a false-discovery rate-based correction for multiple comparisons over the entire brain. For lateralization effects, *p*-values are corrected for multiple comparisons in the volume defined by the respective contrast images.

subjects (6 male, mean age 27, range: 21–38) in an analog experiment. To test whether the left-lateralized preparatory activity detected in experiment 1 was specific for speech preparation, the prosodic task was substituted by a task in which subjects had to perform orofacial

nonspeech movements. For this purpose, we used imperative clauses that all referred to a specific oral movement of the tongue, lips, and cheeks. To avoid tapping into a Go/NoGo scenario, these sentences were solely associated with the Go instruction “execute.” In analogy to





**Figure 2.** Preparation and execution of speech production. (A) Preparation to speak neutrally (green, vs. preparation to read covertly) and neutral speech production (red, vs. covert reading) at  $P < 0.0001$ , corrected. (B) Preparation to speak happily (blue, vs. preparation to speak neutrally) and happy speech production (yellow, vs. neutral speech production) at  $P < 0.05$ , corrected. Note the mobilization of the bilateral ventral striatum for the intention to speak happily. (C) Interhemispheric comparison of effect sizes in regions of interest. The percent signal change of conditions of interest compared with preparation or execution of covert reading is plotted. Error bars correspond to standard error mean. Note the hemisphere-specific reduction of auditory cortex activity during actual feedback compared with somatosensory cortex.

the covert and overt reading conditions, the subjects did not know during the preparation phase which movement they were about to perform. To avoid contamination of the preparation phase with effort or affect, we trained subjects and used only nonspeech oral movements that subjects judged easy and felt comfortable to perform. Because we could thus only study 11 nonspeech oral movements, we increased the temporal jitter to 3–6 s (mean: 4.5 s) and added one-third null events in which the instruction was not followed by presentation of a sentence to improve statistical power. Behavior was visually monitored.

Data analysis was identical with experiment 1, except that we additionally studied the interaction between task (speech or non-

speech movements) and lateralization (nonflipped vs. flipped images) in a  $2 \times 2$  factorial design. We report results of this interaction at  $P < 0.005$ , corrected for multiple comparisons (FDR) within the volume of the respective contrast images.

### Connectivity Analyses

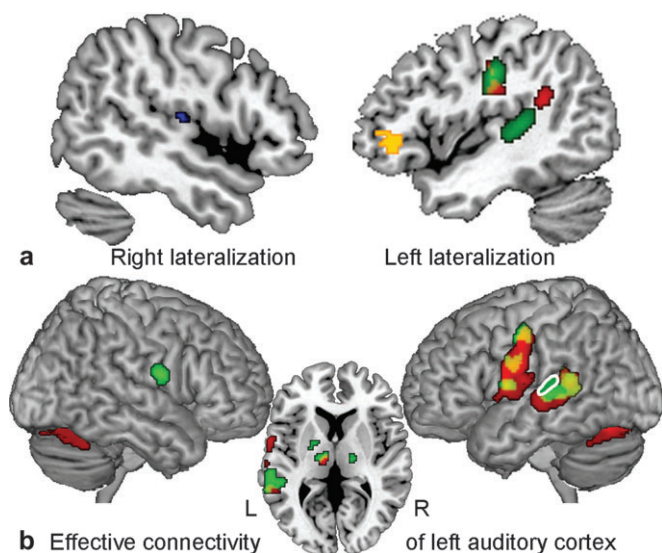
Effective connectivity was assessed using the standard procedure implemented in SPM for the study of psychophysiological interactions (PPIs) (Friston et al. 1997). This technique detects main-effect independent changes in correlations between brain regions dependent on a contextual variable, in our case the instructed sensorimotor transformation. We directly targeted changes in correlations with the left planum temporale induced by overt versus covert reading separately for the preparation and execution phase. We only included those 39 subjects from both experiments that showed individual maxima for the respective contrasts in the studied regions within a radius of 2 cm from the group maxima in the anatomical borders of the seed region. We probed connectivity changes of the left planum temporale resulting from sensorimotor transformation separately for intention to speak and speech production using random effects statistics ( $t$ -contrasts). We considered task-induced changes of functional connectivity to be significant at  $P < 0.005$ , corrected for multiple comparisons over the entire brain (FDR).

### Results and Discussion

Preparing to speak (vs. preparing to covertly read) involved bilateral mesial prefrontal and perisylvian regions (Fig. 2A, green clusters; Table 1). Mesial activation encompassed the frontopolar (BA 10) and anterior cingulate cortices, the pre- and proper supplementary motor areas (SMAs), and the caudate nuclei. Consistent with reduced spontaneous speech production and preserved speech repetition ability after lesions to the mesial prefrontal cortex (Damasio and Geschwind 1984), the SMA was more strongly involved during speech preparation than during execution (Fig. 2A,C). Critically, activity in prefrontal areas was not left-lateralized during speech preparation (Fig. 2A,C). The perisylvian region was also bilaterally activated with the exception of the planum temporale and the articulatory somatosensory cortex, which were the only 2 regions to show a strong left-lateralization (Figs 2C and 3A, green clusters; Table 1). In agreement with its role in linguistic sensorimotor transformation (Hickok et al. 2003), the left SPT did not show preparatory activity (Fig. 2C). Speech production (overt vs. covert reading) involved the preactivated bilateral perisylvian network together with the left-lateralized SPT (executive system) and articulatory somatosensory cortex (red clusters in Figs 2A and 3A, Table 1). In sum, while the sensory system already left-lateralized during speech preparation, the executive system did so only during speech production.

We controlled in 16 additional subjects that the observed effects were specific to speech preparation and not related to preparation for just any kind of orofacial movements (speech or nonspeech). Because only speech produces auditory feedback, preparatory left-lateralization of the planum temporale was only seen when preparing for speaking ( $Z = 3.95$ ,  $P = 0.005$ , corrected). Anticipatory effects in the somatosensory cortex were only slightly more lateralized for speech than for nonverbal orofacial movements ( $Z = 2.89$ ,  $P = 0.016$ , corrected). This speaks to the view that the auditory channel is presumably the primary source of articulatory feedback control during speech production (Guenther et al. 2006).

To further disentangle executive from sensory origin in lateralization of speech production, we also tested a condition



**Figure 3.** Analyses of lateralization and functional connectivity. (A) Voxelwise analysis of lateralized activity displayed at  $P < 0.001$ , uncorrected (for visual purposes only). Preparatory brain activity for overt speaking (green, vs. preparation to read covertly) lateralizes to the left secondary auditory cortex and preparatory brain activity for happy speaking (blue, vs. preparing for neutral intonation) lateralizes additionally to the right primary auditory cortex. Speech production (red, overt vs. covert reading) and prosody generation (yellow, happy intonation vs. neutral intonation) lateralize to the left SPT and BA47, respectively. Note the absence of lateralization in BA44 for happy intonation (see bilateral activation in Fig. 2B). (B) Psychophysiological interactions between left auditory cortex (seed marked in white) and the speech production network displayed at  $P < 0.01$ , corrected. During speech preparation, increased functional connectivity (green, vs. preparation to read covertly) is found between the left planum temporale and the STS ( $-48 -40 14$ ,  $Z = 5.11$ ), the bilateral articulatory motor cortex ( $-58 -2 10$ ,  $Z = 4.8$ , and  $54 -2 18$ ,  $Z = 5.29$ ), and ventrolateral thalamus ( $-10 -12 8$ ,  $Z = 4.59$  and  $14 -16 6$ ,  $Z = 4.28$ ). During speech execution (red, vs. covert reading), effective connectivity is only maintained with the left articulatory motor cortex ( $-58 2 18$ ,  $Z = 5.1$ ) and thalamus ( $-10 -16 8$ ,  $Z = 5.16$ ), together with the left STS ( $-52 -40 12$ ,  $Z = 4.49$ ) and bilateral superior cerebellum ( $-18 -82 -20$ ,  $Z = 4.73$  and  $20 -86 -22$ ,  $Z = 3.7$ ).

where participants were instructed to pronounce sentences with a happy intonation. As prosody perception is a right-dominant process (Wildgruber et al. 2006), we expected this task to modulate frontotemporal interactions during both speech preparation and speech production, but more specifically to right bias the preactivated sensory feedback network. Consistent with this hypothesis, preparing for speaking happily (relative to neutral speech) right-lateralized neural activity in the primary auditory cortex, indicating that while the left planum temporale still prepares for providing speech auditory feedback, the right primary auditory cortex additionally prepares for prosodic control. There was no further preactivation of the speech executive system during speech preparation (blue clusters in Figs 2B and 3A; Fig. 2C and Table 2), but execution of happy intonation further mobilized the left anterior and posterior Broca's area, the latter together with its right homotopic cortex (yellow clusters in Figs 2B and 3A; Fig. 2C and Table 2).

Given the sequence of lateralization, we assume that the additional recruitment of the right prefrontal cortex during prosody production is a consequence of the right-dominant preparation for prosodic control. During the production of happy speech, prosodic feedback is presumably integrated into the speech motor program in posterior Broca's area via commissural fibers, after a relay in the right prefrontal cortex (Wildgruber et al. 2006). Activity in left anterior Broca's area

(BA47) could reflect the increased demand for executive control. By comparing preparation for neutral (left-dominant at the sensory level) with prosodic speech (right dominant at the sensory level), we confirmed that lateralization during speech preparation reflects the anticipation of the sensory consequences of the planned action.

To determine which components of the bilateral preparatory network possibly drive auditory cortex preactivation during speech preparation, we sampled the left planum temporale and probed PPIs. When left auditory cortex was preactivated, its functional connectivity with the left superior temporal sulcus and with bilateral articulatory motor cortex was enhanced (green clusters in Fig. 3B). Importantly, when integrating auditory and somatosensory feedback during speech production, the left articulatory motor cortex decorrelated from its right homolog ( $L > R$ :  $Z = 5.11$ ,  $P = 0.004$ , corrected, red cluster in Fig. 3B). Interestingly, the same pattern was observed subcortically: While the left auditory cortex was functionally coupled to bilateral ventrolateral thalamus during speech preparation, actual feedback integration restricted effective connectivity to left thalamocortical loops ( $L > R$ :  $Z = 5.03$ ,  $P = 0.004$ , corrected). These findings further argue for a role of sensory feedback lateralization in driving left dominance in the frontal lobe. By propagating into more rostral prefrontal cortices, such a functional lateralization could amplify itself to the point of appearing strongest around Broca's area (Broca 1861). Although PPI do not permit to infer directionality, our results are compatible with auditory cortex receiving action plans via bilateral feed-forward signals generated in the motor cortex (Guenther et al. 2006) and relaying information in a lateralized manner to more specialized association cortices that carry out specific feedback analyses. Lateralization of feedback control in anticipation of speech production presumably arises from an intrinsic anatomofunctional asymmetry of auditory cortex fostering the analysis of fast acoustic modulations like those that permit to contrast phonemes in the left and of slow acoustic modulations like those that convey prosodic contours in the right hemisphere (Hutsler and Galuske 2003; Giraud et al. 2007).

Our findings finally show that anticipation of auditory feedback induced a sensitization of neurons that will detect feedback (Fig. 2C, primary auditory cortex and planum temporale) (Eliades and Wang 2008). This sensitization was not observed in the somatosensory cortex (Fig. 2C), which suggests that feedback mechanisms in auditory and somatosensory cortices are fundamentally different. While auditory feedback relies on a sensory system that differentiates between internally and externally generated speech, somatosensory signals from the vocal tract generally reflect proprioception (Guenther et al. 2006). In addition, the auditory feedback signal may undergo strong external perturbations (noise, interferences with other speakers, etc.). Thus, auditory neurons may need to gain in sensitivity to accurately detect feedback (Eliades and Wang 2008).

While the common idea is that speaking is a left-hemispheric cognitive operation (Damasio and Geschwind 1984), we show that before speech is acted out, and even before linguistic computation has taken place and precise articulation is planned, the brain prepares for the sensory consequences of speaking. This preparation selectively involves those sensory regions that will most efficiently process feedback signals, which results in biasing the functional neuroanatomical framework of action

toward that of perception. These findings are compatible with the postulate that left dominance for language arises from intrinsic tuning of left auditory cortex for speech sounds (Hutsler and Galuske 2003; Giraud et al. 2007).

### Supplementary Material

Supplementary material can be found at: <http://www.cercor.oxfordjournals.org/>.

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### Notes

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