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Heteromodal brain areas common to production, listening and reading tasks at the word Level: an fMRI study of 144 right-handers from the BIL&GIN

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Introduction

Neuroimaging studies of the neural bases involved in language have shown a much greater overlap of cerebral regions than the modular implication predicted by classical neuropsychological cases. The conjunction between oral word production and story auditory comprehension revealed the common implication of frontal and temporal regions (Papathanassiou et al., 2000) and it is now admitted that (1) speech perception not only relies on auditory areas but also on motor regions and that (2) speech production not only relies on auditory areas but also on motor regions (Binder et al, 2000; Hickock and Poeppel, 2000; Scott et al, 2000). Some studies have shown that this overlap is also present between reading and listening (Jobard et al., 2007), **but so far no study has simultaneously investigated the overlap of regions involved in the three language tasks (production, perception and reading).**

A crucial feature of these neural convergences across language tasks or modalities pertains to their strong leftward-asymmetry, attesting to the **left hemisphere specialization for language** (see Vigneau et al, 2006 for a review). However, even if language, and more particularly articulation, is left lateralized, it is well established that the **right hemisphere is involved in the prosodic dimension of speech** (Sammier et al, 2015)

The aim of the present study was twofold. (1) **To identify the leftward-hetero-modal brain regions common to three language tasks**, i.e., speech production, speech perception and reading with a comprehensive investigation of how these conjointly activated and asymmetrical areas variations are coloured by the task to permit an elaboration on their function/role (2) **To question the existence of right brain areas** devoted to word processing independently of the task since right areas are involved in paralinguistic analysis such as prosodic and emotional processing. To do so, we used a new atlas named AICHA, which is a functional regional atlas based on resting state fMRI data, totally suited for investigating brain hemispheric specialization (Joliot et al, 2015).

Materials and Methods

PARTICIPANTS

- 144 self-reported right-handed subjects from the BIL&GIN database (Mazoyer et al., 2014) balanced for sex (72 women).
- Mean age: 27 ± 6 years (19-53).

IMAGE ACQUISITION

Imaging was performed on a Philips Achieva 3 Tesla MRI scanner using slow event fMRI runs design.

IMAGE ANALYSIS:

- In the 179 pairs of homotopic Regions of Interest (hROIs) of AICHA atlas (Joliot et al, 2015), BOLD signal variation and asymmetry values were computed for each task and each participant.
- We used a **conjunction analysis of activations and asymmetries** to uncover the hROIs showing both significant left and right co-activation and co-asymmetry during each of the 3 word tasks.

LANGUAGE TASKS

Subjects completed 3 language tasks: speech production (PRODword, Fig 1), speech listening (LISTword, Fig 2) and reading (READword, Fig 3), using a word task (list of words), which is a high-level task even if it is not a complex one.

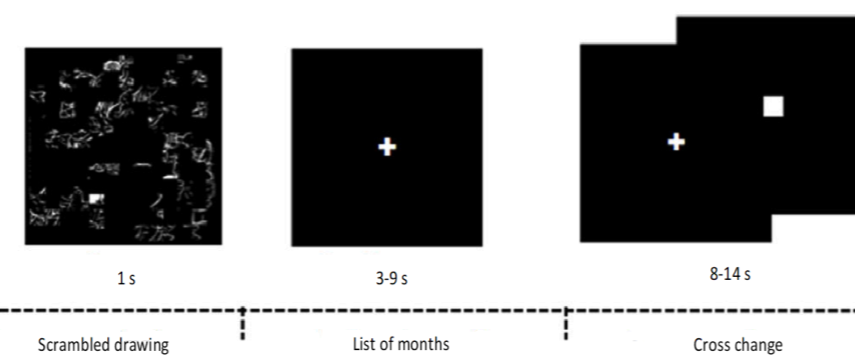


Figure 1: PRODword
When a scrambled drawing was displayed, the subject was asked to covertly generate the list of the months of the years from January to December. The time limit for response was 9 s including the 1-s drawing display. 18 s. There was ten 18-s trial of list production lasting 3 min.

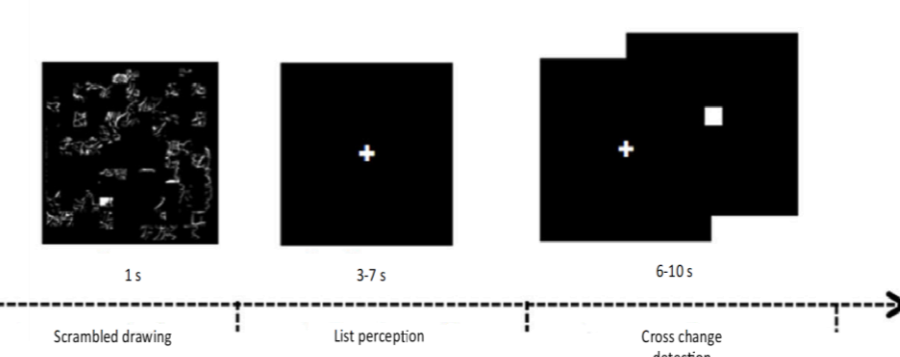


Figure 2: LISTword
When a scrambled drawing was displayed, the subject listened to the list of the months, days of the week and/or seasons. There was thirteen 14-s trial of list listening lasting 3 min 03 s. The mean duration of list trial was $4386 \text{ ms} \pm 484 \text{ ms}$. The time limit for response was 7 s.

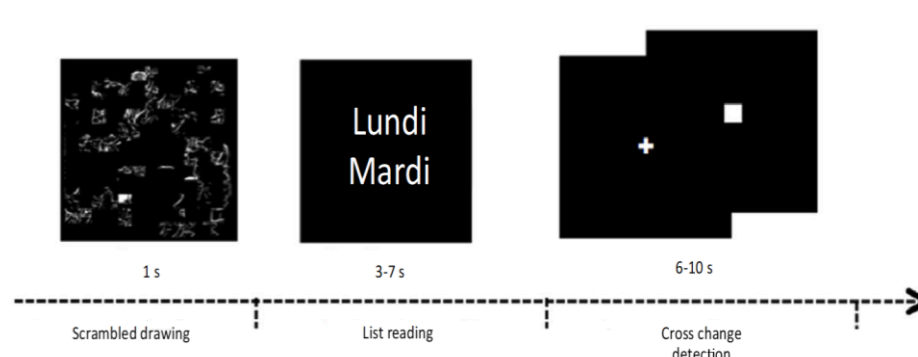


Figure 3: READword
When a scrambled drawing was displayed, the subject read a list of months, days of the week and/or seasons. There was thirteen 14-s trial of list reading, lasting 3 min 03 s.

Results and Discussion

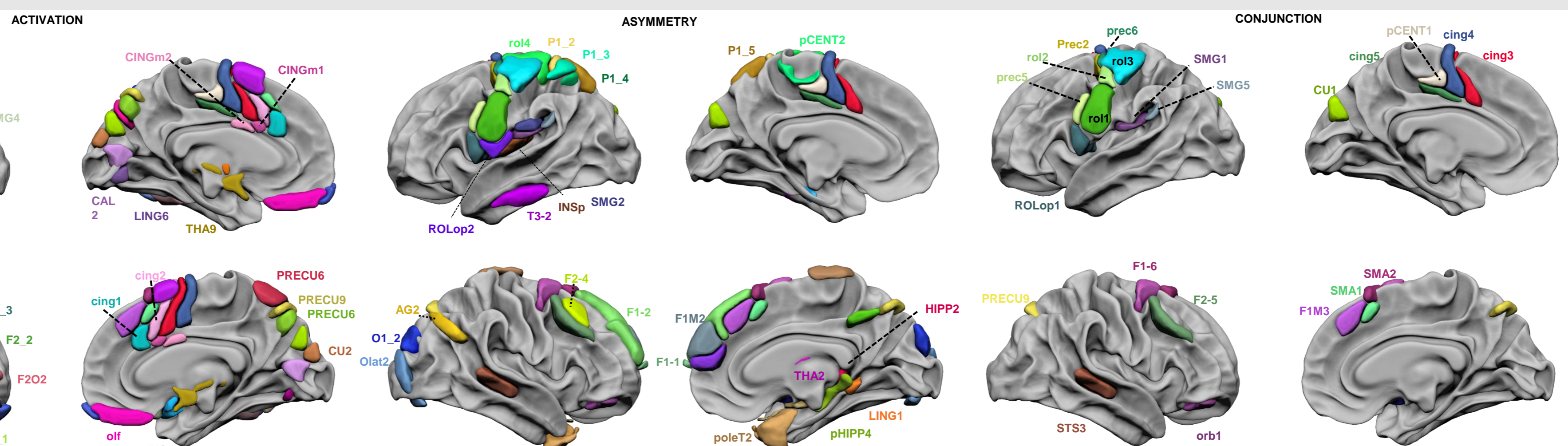


Figure 4: Regions of the AICHA atlas significantly activated in the 3 tasks (first row), significantly asymmetrical in the 3 tasks (second row), and significantly co-activated and co-asymmetrical in the 3 tasks (third row). The hROIs are projected on the white matter surface of the BIL&GIN template with Surf Ice (https://www.nitrc.org/projects/surf_ice/) software. Leftward asymmetrical as well as co-leftward activated and co-asymmetrical hROIs are presented on the left hemisphere and rightward asymmetrical hROIs are presented on the right hemisphere. Selection of hROIs considered as activated or asymmetrical per hemisphere was done according to Bonferroni (p corrected < 0.00027 , 184 hROIs tested), the statistical threshold applied for conjunction of asymmetry and activation for a given task was p corrected $= 0.016$ (Bonferroni correction per region and per task, square root of 0.00027) for each hemisphere and the threshold set for the 3 tasks conjunction was $p = 0.064$ (cubic root of 0.00027, Bonferroni correction)

The present study, based on the fMRI analysis of 3 language tasks performed by 144 healthy adult right-handers reveals, for the first time, **the existence of hetero-modal areas common to production, comprehension and reading at the word level.** While the conjunction between the three tasks revealed a wide functional network (Fig 4), the adjunction of the criterion of asymmetry allowed for determining **the core language areas** involved in word list production, perception and reading (Fig 4).

Left activated and asymmetrical brain areas involved in word-list whatever the task

Interestingly, leftward frontal and precentral areas together with temporo-parietal areas have been revealed to be commonly activated and asymmetrical, leading to the hypothesis of the involvement of phonological action perception circuits such as the phonological working memory loop, in which articulatory gestures are the central motor units on which word perception, production and reading would develop and act according to the motor theory of speech (Liberman & Whalen, 2000).

- The perception-action cycle is involved in reading: The recruitment of SMG1 and SMG2 during PROD together with the recruitment of ROLop1 and rol1 during LIST favours the theory supporting an involvement of action-perception circuits distributed across auditory and motor systems (Pulvermüller & Fidiga, 2016). Interestingly, READ also recruits this perception-action cycle, leading to the hypothesis that subjects subvocalize words they read, which is supported by the gradient of significant activation and asymmetry in rol1 (PROD > READ > LIST). Moreover rol1 has been found to match the location of speech effectors such as the mouth, larynx, lips, tongue and jaws (Brown et al, 2009). The asymmetry in this area was stronger during production and reading, which is consistent with the fact that these tasks involve covert articulation.
- Within the large perception-action model, a set of areas considered as the neural support of the phonological working memory loop proposed by Baddeley (Baddeley et al, 1998) can be identified: on the perception side, SMG1 corresponding to Spt (Buchsbaum et al, 2011) plays an important role in the short term storage of phonological representations by serving as a phonological buffer (Yue et al, 2018) while on the action side, Prec5 is part of a subvocal rehearsal system (Chein & Fiez, 2001).

Right activated and asymmetrical brain areas involved in word-list whatever the task

On the right hemisphere, the common activation and asymmetry of the STS3, which is a prosodic integrative area, during the 3 tasks, could reflect the processing of fine spectral details over time.

The right STS3 closely matches the pSTG described by Beaucousin and others (2007). This area would be a prosodic integrative area, which would process prosodic cues extracted in the aSTG (Ross, 1981). It could be hypothesized that the metrics of lists of the words, resembling a reciting, are processed in this area, which is supported by the greater activation during the listening task.

Future research based on the analysis of intrinsic resting-state connectivity would make it possible to assess the existence of brain networks during reading, listening and production tasks.