SCIENTIFIC REPORT

Spatiotemporal Dynamics underlying the intention to speak

SECTION A. Spatiotemporal dynamics of the intention to speak

This part of the project has been concluded and published.

Introduction

The aim of the project was to determine the neurocognitive events associated to the preparatory motor mechanisms that take place during the planning of self-produced speech.

When we speak we can assert, request or refuse something, that is, we perform intentional communicative actions. The problem of intention in action has attracted great attention in neuroscience, but no study has investigated how intentional speech is generated in the brain. The question we raised here was: how and when does the decision to speak become a conscious intention, i.e. a "wanting to talk", and what brain areas monitor the early emergence of such an intention?

Studies in normal volunteers focusing on upper limb movement have shown that movement intention awareness is anticipated with respect to movement execution. Subjects reliably report the experience of wanting to move ~300ms before movement onset (Libet et al., 1983). Interestingly, this conscious experience is preceded by a neural signal, the Readiness Potential (RP), generated in the motor areas and classically found during preparation of hand gestures and/or oro-facial movements (Libet et al., 1983, Haggard et al., 2002, Sirigu et al., 2003, Wolhert et al., 1993). Neuropsychological results have demonstrated that damage to specific region of the brain, the parietal cortex, disturbs these early stages of motor awareness during self-initiated actions. Patients with parietal lesions can report the exact moment when they started to move their hand, but not the moment when they first became aware of their intention to move. Furthermore, contrary to normal subjects they show an altered pattern of the associated readiness potential. These results indicate that damage to the parietal lobe leads to an inability to monitor the experience of intention and action awareness. These findings suggest that the parietal cortex holds neural mechanisms important for "attention to intention" during movement planning (Sirigu et al., 2003).

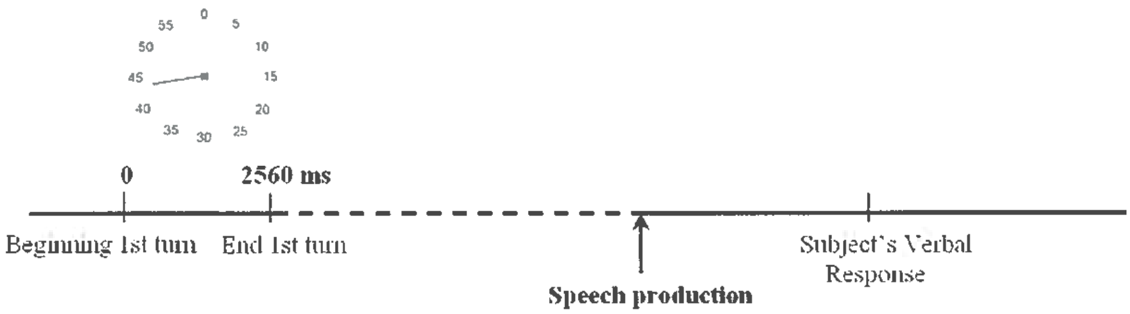
A central question is whether the involvement of parietal cortex in intentional processes generalizes to other motor behaviours and in particular to speech. Similarly to arm and hand movements, speaking is also accomplished trough motor acts. It is now well established that a close interaction exists between the action and the language system (Gentilucci et al., 2000, Fadiga et al., 2002). Neuropsychological results have shown that parietal lobe damage impairs jointly production of gestures related to tools and speech planning (Haland et al. 2000, Cubelli et al., 2000, Damasio and Damasio, 1993). Recent diffusion tensor magnetic resonance imaging studies in humans have shown an indirect pathway, in the lateral sector of the superior longitudinal fasciculus. Two segments within this pathway originating in the parietal lobe project toward regions important for language processing: the posterior segment ends in the inferior temporal region while the anterior segment in the inferior frontal gyrus (Broca's area and its homologous) (Catani et al., 2005).

In the light of these findings it is possible to speculate that these cortico-cortical connexions may enable the parietal cortex to monitor inflow and outflow signals related to the intention to talk and the planning of speech acts.

To investigate this hypothesis we use a paradigm first proposed by Libet (Libet et al., 1983) and adapted from Sirigu et al. (2003). Twelve right-handed healthy volunteers (mean age 24.5) were asked to pronounce the word "*demain*" ("*tomorrow*") at a time of their own choosing, following a trial start cue. While performing this simple task, subjects were instructed, in separate blocks of trials, to focus their attention on either the actual onset of the word pronunciation or the internal decision to pronounce it.

Judgments about the time of each event were performed in the following way: participants looked at the single hand of a clock that started to move at the beginning of each trial and stopped at a random time following speech onset (Fig. 1).

Figure 1. Example of one trial. The discontinuous line indicates the variable time period from the end of the first clock turn and the actual beginning of speech production.



Subjects reported the position of the clock's hand either at the time they started speaking (S-judgment) or at the time they first became aware of their intention to speak (I-judgment). In the intention condition, the experimenter instructed the subjects as follows: "*Note the position of the clock's hand at the time when you feel the desire to speak but you have not start speaking yet.*" At each trial, subjects were told to feel free to speak whenever they wanted, but not before the clock's hand had completed its first turn.

We use magnetoencephalography (MEG) in order to track the spatio-temporal neural dynamics related to speech and to the intention of speaking.

Methods

Participants. 16 healthy participants were included into the protocole. All subjects were French native speakers, right-handed according to the Edinburgh handedness test[35], and reported no history of neurological or psychiatric disorders. A written informed consent was obtained from each participant. Subjects' recordings were screened to eliminate those with frequent blinking or signal artefacts (e.g., due to dental work). Four subjects have been rejected because of artefacts. The remaining twelve subjects have been included for analysis.

Experimental procedure. Subjects sat in front of a screen inside the magnetically shielded room (40 cm from the screen). A calibrated clock-face (radius 2.2 cm; marked in steps of 5 units from 0 to 60 like a usual clock) was visually projected on the centre of the screen (Fig. 1).

At the beginning of each trial, a red clock-hand started to turn clockwise (start-spin) from a random location at the speed of 2560 ms per cycle. Subjects were instructed to pronounce the one-word-like utterance *demain* ("tomorrow") at a time of their own choice after having waited a first complete cycle. They were required to execute the task as spontaneously as they could, avoiding to adopt any strategy (e.g., choosing the position of the hand-clock before speaking and use it to trigger their speech act).

In one block of trials, subjects were instructed to attend to their intention to speak and to report the location of the clock-hand at the moment of their internal decision to speak ("Intention" condition). In a separate block of trials, they were asked to attend to the actual speech onset and report the location of the clock-hand when they started to speak ("Speech" condition).

For each condition, blocks of 100 trials were run, each presented in a random order. In a pre-test session, subjects were trained in the MEG with 100 repetitions of both "Intention" and "Speech" conditions.

Stimuli were presented using the Presentation software (Neurobehavioral System, http://www.neurobs.com/).

Data acquisition

MEG recordings. The continuous raw MEG signals (sampled at 1200Hz) were recorded using a high-density whole-head system (OMEGA; CTF Systems, VSM Medtech, Vancouver, British Columbia, Canada), provided with 275 axial gradiometer channels and 29 dedicated reference channels for environmental noise cancellation. At the beginning of each block, subject's head position relative to the MEG sensors was measured using coils placed at three fiducial points (nasion, left and right pre-auricular points). Head movements did not exceed 1,25 cm between blocks.

Audio data. Subject's verbal responses were recorded through a MEG-compatible microphone and recording software (Cool Edit Pro).

Behavioural data. During each MEG session, participants' verbal time reports were constantly monitored and written by the experimenter. Trials showing uncertainty or failure in reporting the required time were excluded from analysis. Subjects were visually monitored on a closed circuit TV system.

Data Analysis

Behavioural data

Participants' temporal judgments were calculated by subtracting the time of the actual speech-onset from the time at which they reported 1) to have first intended to speak (Intention condition) and 2) to have started speaking (Speech condition). Negative values indicated that subjects' estimate preceded the speech onset, while positive values indicated that it followed the observed event. Latencies of subjects' overt speech production were also calculated, by subtracting the time of speech-onset from the time at which the first clock cycle ended up. Speech signals have been amplified and analysed using Praat software[36]. Trials with no speech responses, corrupted speech or artefacts (e.g.: deglutition, cough) were rejected. Speech onset times were identified by visual inspection of the speech signal.

MEG data

MEG signals were digitally filtered off-line with a bandwidth of 0.2 Hz to 60 Hz, and decimated down to 300 Hz. Signals were analyzed at two levels, namely the magnetic field distribution measured at the sensor surface (sensor level), and the estimated cortical current sources that underlie the recorded magnetic fields (source level).

ANALYSIS 1: SENSOR LEVEL. In a ***first analysis***, the electrophysiological effects of Attention to Intention was assessed by comparing the fields in the period preceding the speech-onset in the two conditions ("intention" vs. "speech") using sample-by-sample t-tests for paired data across all subjects. Differences were considered significant at $p<0.05$ for at least 15 consecutive time samples (Blair, R. C. & Karniski, 1993, Thorpe, S., Fize, D., & Marlot, 1996), for at least four neighbouring sensors. This method can determine precisely the time range and the scalp regions of the difference between the two conditions. The topography of the effect was illustrated in MEG field interpolation maps and Student's t-test maps.

ANALYSIS 2: SENSOR LEVEL. In a ***second analysis***, the spatio-temporal dynamics of cortical sources underlying the measured magnetic field distributions were determined for both the Intention and the Speech conditions. We imaged the foci of activations that were time-locked to the speech onset using Minimum $\ell1$-Norm Current Estimates implemented into the Brainstorm software (http://neuroimage.usc.edu/brainstorm/). The method calculates the source currents of smallest amplitude by applying minimum norm (MN) priors on source amplitudes. This approach was adopted because it does not require prior assumptions about source location and number, contrary to multiple dipole fit methods, and provides detailed information about the time course and the spatial location of brain activity.

MN estimates were applied to the averaged signals (0.2-20 Hz) of individual subjects for each condition, in a time window from -2 sec before the speech onset time to +0.1 after speech onset. Standard Tikhonov regularization (10%) was applied for noise reduction. MN current estimates were computed for each participant individually and for consecutive points in time within a source space consisting of about 10774 vertex points of a template cortex mesh.

To determine the neurophysiological effect specific to the Intention Condition, we compared at each vertex the MN estimates of source amplitudes in the two examined conditions using sample-by-sample paired t-tests. P values have been corrected using Bonferroni correction: vertex were considered significantly different at time t if p(vertex) < 0.05/number of vertices.

RESULTS

Behavioural data

Participants reported to have started speaking (S-judgement) 54 ms earlier than the actual speech onset (± 78 ms Standard Deviation) and they estimated their intention to speak (I-judgement) 352 ms before actual speech onset (±124 ms). Statistical comparison revealed that the two temporal judgments differed significantly p=0.0001 (one-tailed paired t-test).

To ascertain that the specific temporal judgement task of the Intention and the Speech conditions did not affect self-generation of speech act, speech onset latencies were examined in each condition. Average speech onset began 3800 ms (±658 ms) and 3605 ms (±366 ms) following the end of the first clock turn in the Intention and the Speech conditions, respectively. These values did not differ significantly, p=0.26 (two-tailed paired t-test). Thus, speech onset occurred at about the same time in both conditions, irrespective of the temporal judgement subjects were performing. Inter-subject variability of speech production times was determined by the standard deviation averages of the speech onset latencies for the Intention (554 ±430 ms) and the Speech conditions (466 ±237 ms). No significant difference emerged from this contrast p=0.2 (two-tailed paired t-test).

In summary, our behavioural results show that conscious intention of wanting to speak is anticipated with respect to speech production *per se*. Interestingly, temporal difference of a similar magnitude between intention and movement were also reported in the context of hand gestures when subjects focused on their intention to move as compared to when they paid attention to movement execution *per se*.

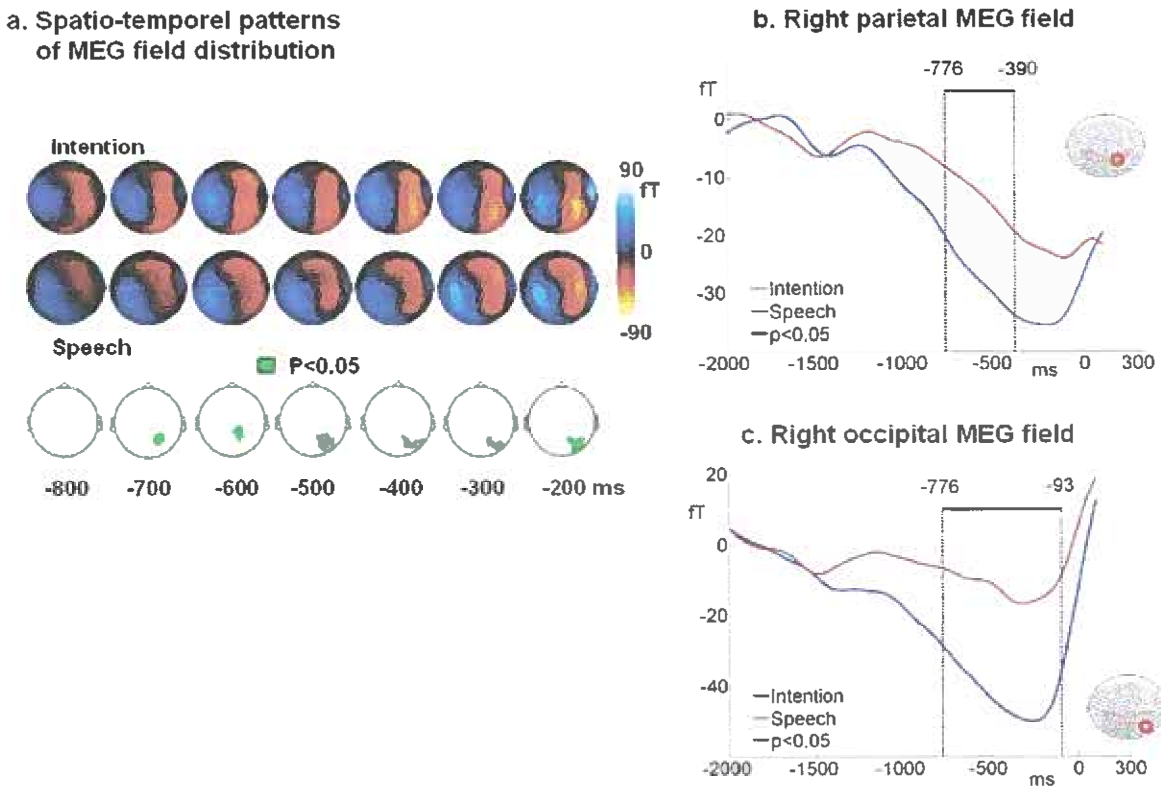
MEG Evoked responses at the sensor level

Mean magnetic field distribution elicited by both Intention and Speech conditions exhibited specific dipolar topographies during the preparatory phase preceding speech production. A large outward flowing field was found over the frontal and temporo-parietal sensor areas on the left side of the scalp, whereas an opposite inward flowing current was spread over the temporo-parietal sensor areas on the right side of the scalp. This spatial field distribution was partially common to the two examined conditions, both involving motor preparation and overt speech (see MEG field maps at the top of Fig. 2-a). However, a difference was observed between the time course of MEG responses in the two conditions. The inward magnetic flow was significantly higher for the Intention judgment ($p<0.05$, two-tailed paired *t*-test) (see contrast at the bottom of Fig. 2 a). Such negativity emerged at the right occipitoparietal sensors during a time window from -776 ms to -94 ms before speech onset ($p<0.05$).

In a further analysis we examined the time-course of negative peaks in separate groups of selected right parietal (Fig. 2 b) and occipital sensors (see Fig. 2 c). In the parietal group of sensors we found that the negativity was significantly stronger in the Intention condition ($p<0.05$; two-tailed paired t-test) during a time window from -776 ms to -390 ms before speech onset. It must be stressed that, this parietal negativity arise 400ms prior subjects' reported time of intention to speak (-352ms before speech onset) and decreases 38ms earlier.

Figure 2. MEG data. **a.** (Top of the left panel) MEG field maps of the grand-average of the signal in Intention and Speech conditions from -800 -200ms before speech onset. A similar pattern of MEG field distribution was found on the left side of the map. Conversely, on the

right side, an early ingoing magnetic field appeared over parietal sensor areas during Intention, whereas it was concentrated over the right frontal areas during Speech. (Bottom of the left panel) Statistical contrast between the grand-average of the signal in Intention vs. Speech shows that the ingoing magnetic field was significantly higher in Intention than in Speech over the right parietal and occipital areas (sample by sample paired t-test, p<0.05, at least 15 consecutive samples). **b.** Averaged signal from a sub-group of selected parietal sensors. Negativity is higher in Intention (blue), than in Speech condition (red). Black lines indicate the time-window in which the signal differed significantly over time, namely, from -776 to -390 ms before actual speech. **c.** Averaged signal from a sub-group of selected occipital sensors. Negativity is higher in Intention (blue), than in Speech condition (red). Black lines indicate the time-window in which the signal differed significantly over time, namely, from -776 to -93 ms before actual speech.


a. Spatio-temporel patterns of MEG field distribution

b. Right parietal MEG field

c. Right occipital MEG field

A similar negativity pattern was found from a sub-group of right occipital sensors. The negative signal amplitudes differed significantly between conditions (intention vs. speech) during a time window from -776 ms to -93 ms ($p<0.05$; two-tailed paired t-test).

These first set of results show that "*attention to intention*" is preceded by an activity in the parietal and the occipital sensors. Although activity in these two regions begins jointly their time course diverged. While the signal generated in parietal cortex is transient, decaying just before the time of the reported intention, the occipital negativity is sustained extending near to speech onset.

MEG Sources of brain activity

Distributed source localisation by Minimum Norm Current Estimates confirmed the MEG evoked field analysis and also revealed a complex spatio-temporal dynamics of neural events distinct for each condition.

Activity related to Intention-condition

When subjects were attending to their intention to speak, we found a local activity in the superior right parietal cortex (BA7) (Intention vs. Speech condition, $p\leq0.05$) occurring from -883 ms to -730 ms before actual speech (Fig. 3 a). This parietal activity was then followed by an increase of the MEG signal for about 70ms (from -740 ms to -670 ms) in the left inferior frontal gyrus or Broca's area (BA 45). Parallel activity was observed in the right ventromedial prefrontal and orbitofrontal cortex (BA 10-11) for about 80ms (from -730ms to -650ms before speech onset). Following, from about -693ms to -530 ms the early parietal activity spread throughout the right superior parietal lobe to include the precuneus (BA5), the right intra-parietal sulcus to extend afterwards in the left superior parietal cortex (BA 7, BA

5). Within the same time window (from -670 ms to -550 ms) a right prefrontal activity (BA10, 11, 46) co-occurred with these parietal activations.

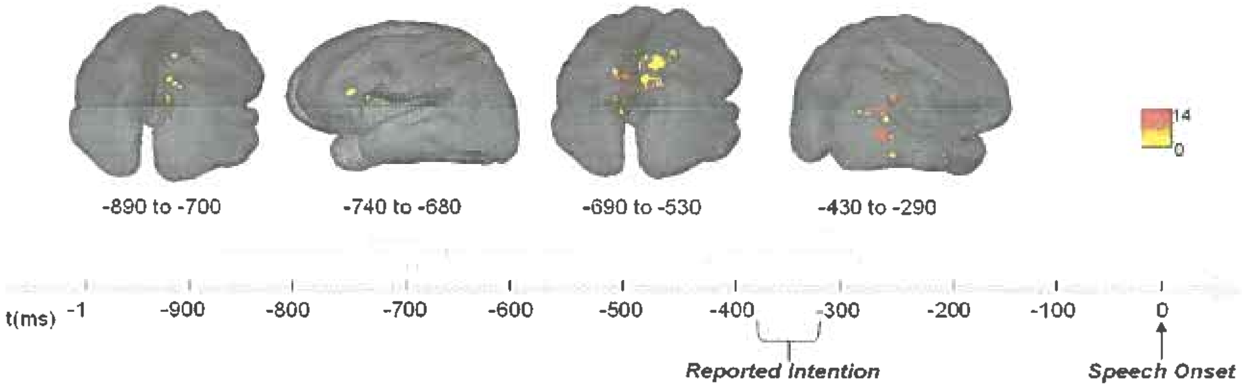
Increased activity was also found within the right primary visual (BA 17) and right secondary visual cortex (BA 18) for about 108 ms during the same time interval (from -698ms to -590ms before speech onset) (see Supplementary Fig. 1 online).

During a subsequent interval (from -430 ms to -293 ms before speech) corresponding to a period when subjective time of intention was completed (as reported by subjects) parietal activity shifted to the right inferior parietal area to include the temporo-parietal junction (BA, 39, 21). Lastly, sources activity in the right occipital region (BA 19) and right superior temporal lobe (BA37) exhibited a transient activity (from -440 to -370 and from -465 -363 ms before speech onset, respectively).

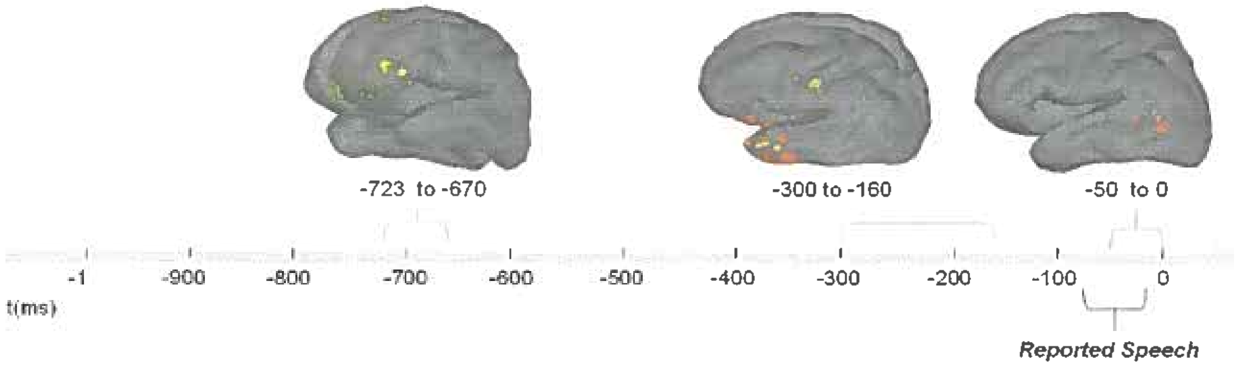
This finding thus confirms that the negativity signal found in the parietal sensors, as revealed by the magnetic field analysis, takes its source very early in the parietal regions and in Broca's area followed by activation in posterior and prefrontal areas (See Supplementary Fig. 2 a online). More importantly source analysis further confirms that the timing of the parietal cortex signal is closely related to that of intention to speak: it arises early and ends just before time of intention.

Figure 3. **a.** Spatiotemporal dynamics of reconstructed sources of brain activity specific to the Intention condition. From left to right, early right parietal activity (BA 7), activity in the left inferior frontal gyrus (BA 45), bilateral parietal activity (BA 7), and right inferior parietal parietal activity (BA 39). **b.** Spatiotemporal dynamics of reconstructed sources of brain activity specific to the Speech condition. From left to right: left prefrontal activity (BA 46), left superior temporal activity (BA 21), and inferior temporal activity.

a. Activity Related to Intention



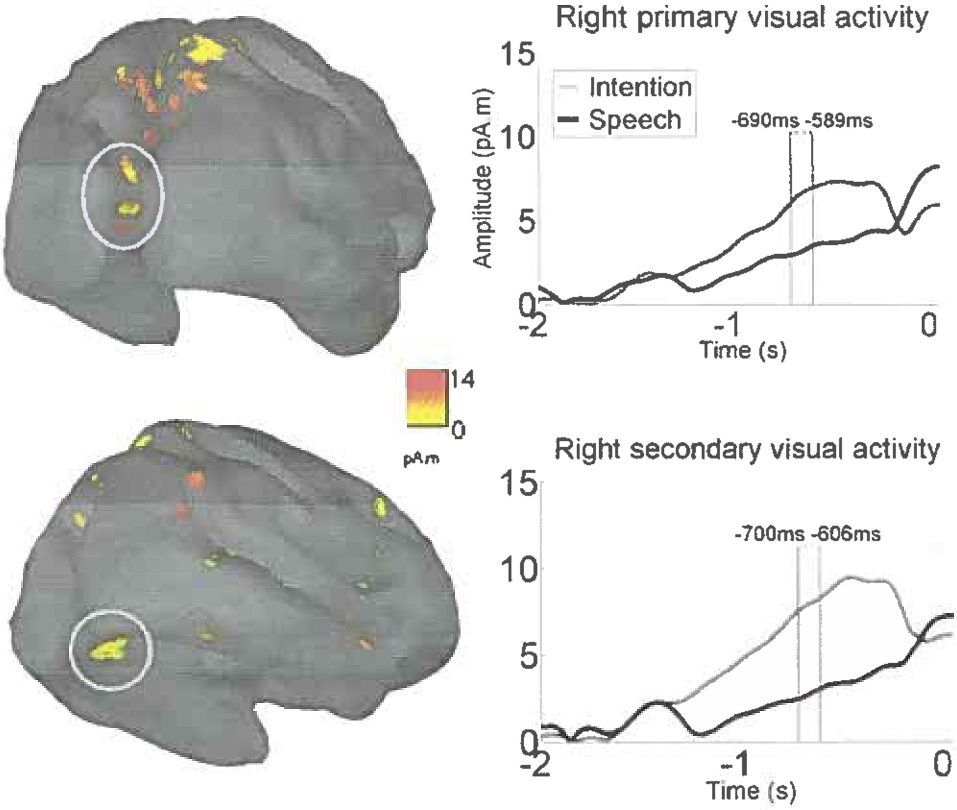
b. Activity Related to Speech



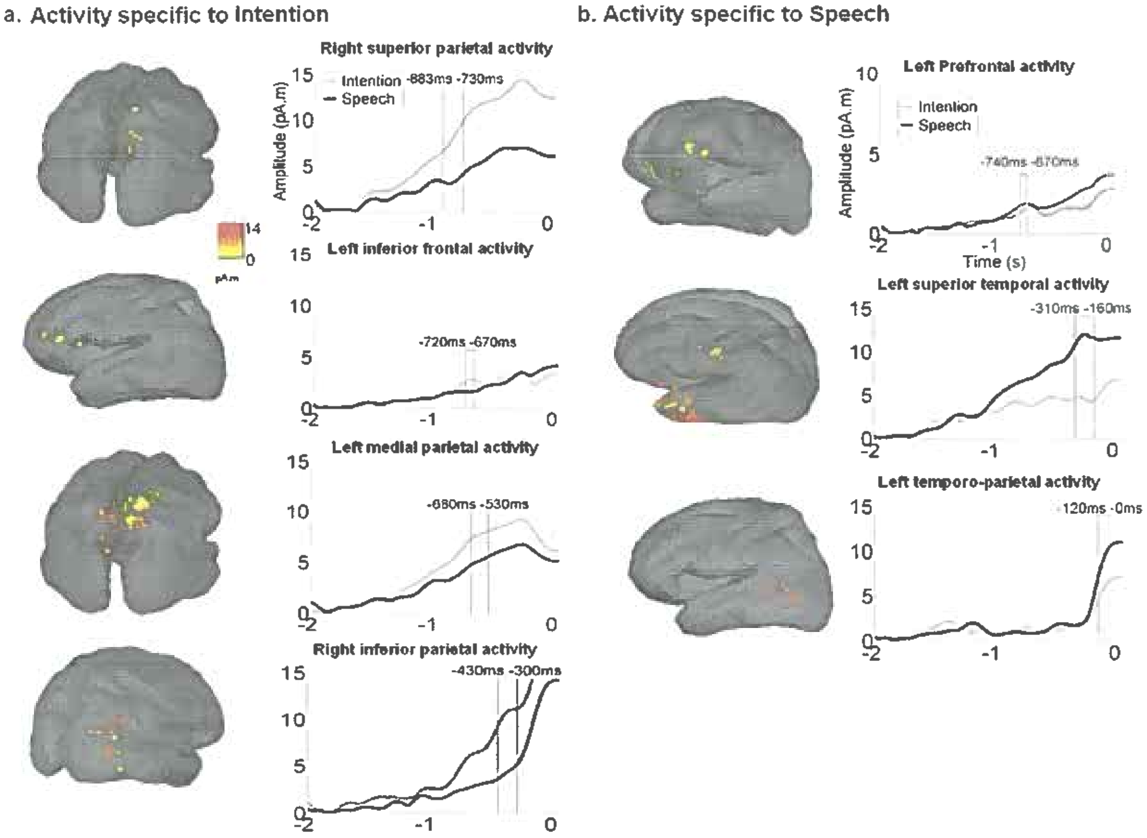
Activity related to speech condition

We also identified cortical sources which were significantly more active in the Speech than in the Intention condition ($p \leq 0.05$). These included a left frontal temporal network of language areas that were activated at distinct time courses (Fig. 3 b). A first earlier speech-specific activity was found in the left frontal cortex (BA 46) lasting for about 50ms (from -740 ms to -670 ms), followed by activity in the left inferior temporal cortex (BA21) (from -670 ms to -530ms). Later (from -320 ms to -160 ms) other foci of activity were found in the left inferior temporal cortex (BA 21-22-38). Interestingly, during the same time window two selective activations were found in the lateral, portion of the motor (M1) and sensory (S1) cortex corresponding to the classical mouth area. Since this activity occurs before but is close to speech onset, it might reflect word movement preparation or word movement rehearsal. (Supplementary Fig. 3 online). Further sources of brain activity emerged in areas know to be involved in language processing such as the right superior temporal cortex (BA37 and 21-22) and the left temporal parietal junction within a time interval from -215 ms and -150ms to speech onset time, respectively. For the specific time course of the reported source activities see Supplementary Fig. 2 b.

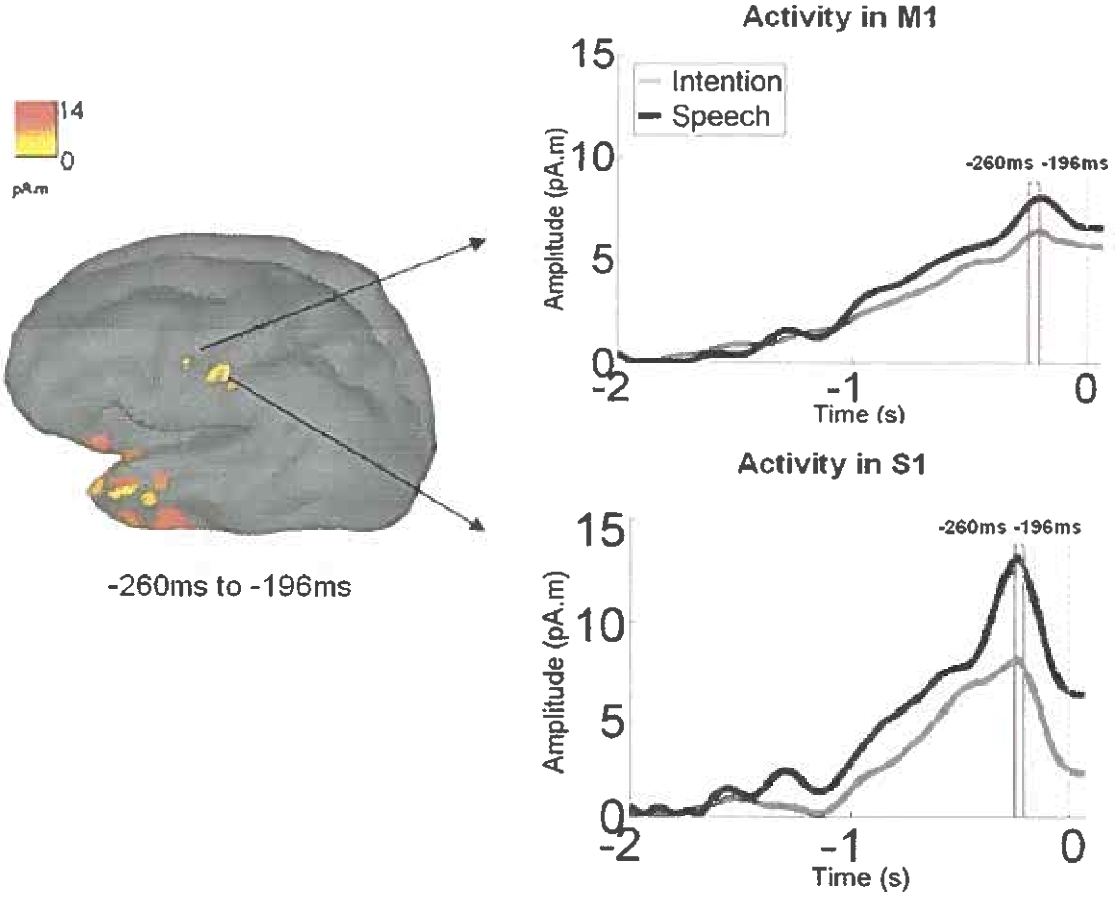
Suppl. Fig. 1. Slopes of the reconstructed signal for the Intention and Speech condition. a. To the left, brain areas activated during the Intention condition and, to the right, slopes of the associated activity. b. To the left, brain areas activated during the Speech condition and, to the right, slopes of the associated activity. The red lines delimits the time window during which the activity is higher significant in each condition.



Suppl. Figure 2. To the left: activity related to Speech in the primary motor (M1) and sensory cortex (S1). To the right, from top to bottom, slopes of the reconstructed signal within M1 and S1 in the Intention and Speech condition. The red line delimits the period during which the two conditions differ significantly.



Suppl. Figure 3. (From top to bottom). To the left: highlighted by the grey circle, right primary and right secondary visual activity related to the Intention condition. To the right: slopes of the reconstructed signal within the visual cortex. The red line delimits the time period during which the two conditions differ significantly.



DISCUSSION

In this study subjects were asked to pronounce a word after a clock's hand had completed its first turn and then to report its position when they first experienced the intention to speak or when they began speaking. We observed that different time courses of the neural events associated to these two examined conditions emerged from the MEG evoked responses measured at sensor level. These different patterns of magnetic field variations at sensor level were reflected also by distinct patterns of neural activity in brain areas specific to the focusing of attention on either the speech intention or the act of speaking, as source localisation analysis showed. The results corroborate our prediction that the parietal cortex plays a key role in monitoring the mechanisms related to motor intention in language, as it does for other motor actions. We further show that parietal activation was followed by increasing signals in additional cortical areas, each being activated within a specific time window throughout the task.

The results from MEG evoked response showed a right parietal readiness signal when subjects focused on their intention to talk. The time-course of such signal is remarkable since it occurs within a time window that immediately precedes reported subjective time of intention (that immediately precedes reported subjective time of intention (from –424 to –38 ms before reported intention). This result is coherent with the hypothesis of an involvement of the parietal cortex in motor intention in speech. Jointly to the parietal activation, monitoring the intention to speak also induced an early activation (from -776 to -93ms before actual speech) in the right occipital area. Note that, contrary to the transient activation found in the parietal cortex however, the occipital negativity encompassed the reported time of intention window going on up to when subjects prepared to speak (-93 ms before speech onset). Because time of intention was anticipated with respect to speech, it is reasonable to assume that in the Intention condition subjects maintained very early in time in a visual buffer a mental image of the clock's hand position. The occipital activation may be thus understood as triggered by a visual imagery process significantly more important in the intention condition compared to speech. Accordingly, the observed occipital activity should be viewed as associated (because of tasks purposes) but not instrumental for intentional processes in speech.

The result obtained from the evoked response analysis at the sensor level, although interesting, does not provide information on which brain areas generate parietal and occipital negativity. Hence, such activity may be driven for instance by cortical sources different from the spatio-temporal distribution of the MEG fields measured at the scalp level. To address this issue we performed a finer-grained analysis to identify the underlying sources of these brain signals. The results showed that different sources of cortical activity contribute to these spatio-temporally distinct effects at the sensor level.

First of all, when we contrasted the activity found in the Intention and Speech condition, the results show a cluster of generators in the right parietal cortex where activity arose very early on (-890 to -700 ms before speech) significantly stronger when subjects were focusing on wanting to speak. These foci of parietal cortex activity spread out fast from right to left inferior parietal areas to decrease within the time window of reported intention. Thus, both the evoked response and source results demonstrated the contribution of parietal regions in monitoring very early motor intention in speech.

Interestingly, source analysis also revealed that when the very first right parietal activity shut down (at -700ms before speech) this is followed 40ms later by a transient left frontal activity in Broca's area, a region known to be important in language and action processing (Nishitani et al., 2004, Rizzolatti et al., 2008, Davis et al., 2008).

It is interesting to note that Broca's region has also been associated to the control of inner speech. Inner speech refers to behaviour where subjects rehearse words silently and according to some authors it involves similar mechanisms as those involved in self-awareness (Levine et al., 1982). We can speculate that when focusing on the intention to speak, self-awareness mechanisms are mandatory. Although the respective role and dynamic interplay between parietal and Broca's region in motor intention processes cannot be established here, we can propose that Broca's area is co-activated with parietal cortex only when intention in action is processed for the purpose of producing speech. This circuit may thus constitute the functional counterpart of the parieto-frontal circuit described at the anatomical level by diffusion tensor studies (Catani et al., 2007).

The task we used in our study (word pronunciation) should have had primarily engaged left hemisphere linguistic functions. Yet, it is the right parietal region that we found activated near the occurrence of time of intention to speak. Although this may be unexpected, the role of right parietal region in motor and body awareness is well known[22]. Awareness of failures in control of action is associated to bilateral activation of parietal regions[23]. Also, increase of activity in the right inferior parietal cortex (angular gyrus) is observed when subjects were require to detect the matching between the expected and the perceived outcome of an intended action (Farrer et al., 1990). Motor intention is assumed to depend on frontal and parietal areas (Haggard, 2005). In the language domain, several studies have stressed its function for pragmatic and communicative aspects (beliefs, reading others' intention) conveyed through speech (Sherrat & Penn, 1990, Surian & Siegel, 2001). Our results further suggest that the right parietal cortex also monitors high level aspects of language such as intention during speech acts.

When subjects focused their attention on speech rather than intention we found early transient activity in dorsolateral and orbitofrontal prefrontal areas (-723 to -670 before speech onset). In this condition motor preparation processes were probably highly activated since subjects were instructed to focus their attention on word pronunciation itself. Prefrontal activations may be thus directly linked to the need to inhibit the motor output from the early stage of our task (Elliott, 2000, Rubia et al., 2000, Lee, et al., 2001).

The idea that in speech condition subjects were focusing on movement preparation and speech rehearsal is also supported by further activity involving the motor and the sensory cortex in the mouth area. Recent research has highlighted the role of these regions in motor imagery (Jeannerod, 1994). Finally, activity was observed in left temporal and temporo-parietal junction when subjects were near to pronounce the word, consistent with the role of this region in speech production (Wise et al., 2001.

In conclusion, our study has shown that a set of specific cortical areas subserves intention in speech. A key contribution is played by parietal regions which seem instrumental in triggering intentional speech mechanisms very early in time. These results extend previous findings (Sirigu et al.˙ 2003, Desmurget et al., 2009), which showed the critical role of parietal area in motor intention. Interestingly, the results suggest that the parietal lobe the plays multimodal role in controlling intention both in action and language. Another contribution arises in Broca's area, where activity occurs right after parietal activity and as proposed earlier, these two regions may represent the cortical circuit specific for controlling intentional processes during speech.

Since we use language for communicative purposes, attending *intention to speak* may also have implicitly triggered a communicative dimension even if this was not encouraged by our task instruction. To further push this reasoning, we can speculate that that the mechanisms involved in intending to speak are also called into play when we use speech to fulfil an explicit communicative purpose (e.g. answering a question). Parietal cortex and Broca's area may be at the source of this behaviour.

The findings reported so far have been published in the paper (see also pdf file in attachment):

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Carota, F, Posada, A., Harquel, S., Delpuech, C., Bertrand, O., Sirigu, A. (2010). Neural Dynamics of the Intention to Speak. Cerebral Cortex 2: 8, pp. 1891-1897.

Scientific divulgation of different this study (at different levels/steps of progression of the analyses) included conference presentations:

Carota, F. "Conscious Intention in speech production: a MEG study" Workshop MEG à Lyon. 1-2 December 2010, Lyon, France.

Carota, F, Posada, A., Harquel, S., Delpuech, C., Bertrand, O., Sirigu, A. (2009). "Cortical dynamics underlying the intentions behind speech-acts: a MEG study". *IPRA* - 11th Conference (2009 Melbourne).

Carota, F. (2009). "Cortical dynamics during the intention to speak". Exciting Biologies Workshop "Biology of Cognition". 16-18 October, Chateau Hotel Mont Royal, Chantilly, France.

Carota, F. (2009). "Dinamiche corticali sottese alla pianificazione del linguaggio. Cortical dynamics underlying language planning". Nuove Frontiere delle Neuroscienze. Faculty of Medicine, University of L'Aquila, Italy, 15-16 May. *Invited talk.*

Carota, F. (2008). "Time course of brain activity during the Intention to speak". Towards a Science of Consciousness 2008, Center for Consciousness Studies, The University of Arizona, Tucson, Arizona. *Plenary lecture.*

A related book chapter is:

Carota, F., Desmurget, M., Sirigu, A. (2010). Forward modelling mediates motor awareness. In Lynn Nadel and Walter.P.Sinnott-Armstrong (eds.), Conscious Will and Responsibility: A Tribute to Benjamin Libet. Oxford University Press.

SECTION B. Cortical Mu rhythm during the production and perception of speech.

This part of the project is still unpublished. Additional results have been obtained with respect to the previous report of April 2011, namely source localisation. A manuscript on these very original findings is about to be submitted: thank you in advance for treating the following original data and results confidentialley.

We performed several analysis of time-frequency in our data, in order to track the signatures of cortical oscillations which may be linked to the intentional and motor mechanisms in speech.

None of the frequency bands we looked at specifically (Alpha, Beta, Theta, Gamma) exhibited a pattern which significantly varied across conditions, and –for seek of completeness- we have also looked at cortical connectivity in the sensor spaces, but the data showed too important individual variations across subjects.

Very importantly for our interests, however, we found important results from oscillations at 8-13 Hz, which correspond to the so called Mu rhythmic activity (see below for a closer description). We then decided to focus on this specific type of oscillatory information, and run specific time-frequency analyses and source localizations on these data. Importantly, we adopted a different methodological approach to the source localisation problem, which was particularly adapted for dealing with time-frequency of cortical oscillations. Below I report and discuss the framework within which this part of the work has been extended.

Introduction

Motor information is pervasive in spoken language. Motor theory of speech perception argues that speech processing relies on the access of motor representations that are also required when speech is produced (Liebermann et al., 1957; Liebermann and Mattingly, 1985).

Ample experimental evidence supports this view, pointing out that brain motor regions are essential for movement planning, initiation and execution (Wise, 1985) also contribute to both production and perception of speech. However, the exact role of the motor areas in the perception of speech is debated.

Previous work has shown that passive listening to phonemes recruits both motor and premotor cortices (Wilson et al., 2004). Evoked activity over the motor cortex that controls tongue muscles increases during the listening of words produced through strong tongue movements (e.g. terra vs. baffo) (Fadiga et al., 2002). Intriguingly, distinct portions of the precentral gyrus are recruited by both articulating and processing speech sounds effected with different outputs (e.g. lips: /p/, or tongue: /t/), This suggest that the motor cortex is somatotopically activated depending on phoneme articulatory features (Pulvermueller et al., 2005). Recent findings further support the view of a causal involvement of the motor system in the processing of speech: lips- and tongue-related sounds are perceived faster when the motor sites controlling respectively lip and tongue muscles are stimulated using TMS (D'Ausilio et al., 2009).

Previous EEG studies have shown that a specific signal, the mu rhythm (8-13Hz), is relevant to track motor area activation during voluntary action (Pfurtsheller, 1981; Hari et al., 1997, Hari, 2002). Mu rhythm originates from the somatosensory cortex at rest (S1) (Pfurtscheller, 1981), especially from the hand area in the somatosensory homunculus (Hari et al., 1997). It includes a higher frequency component around 20Hz generated more anteriorly, in the pre-central motor regions (Hari et al., 1997) and exhibits a somatotopic activation depending on the action effector (Salmelin et al., 1995).

Importantly, Mu rhythm (8-13Hz) is suppressed during and after the execution of voluntary movements (Pfurtscheller & Neuper, 1992). A similar suppression is reported for a number of cognitive tasks, including visual stimulation (Pfurtscheller & Aranibar, 1977; Aranibar & Pfurtscheller, 1978), mental imagery (Pfurtscheller & Neuper, 1997; Salenius at al., 1995), attentional and memory tasks (Klimesch, 1999).

Mu reactivity related to speech is little studied. Mu decrease has been reported during picture naming (Salmelin et al. Salmelin et al., 1995, “Dynamics of brain activation during picture naming”, Nature, 368: 463-465), and auditory tasks (Pfurtscheller & Aranibar, 1977). However, mu modulation during speech perception is debated: some studies show mu increase during *auditory tasks* (Krause et al. 2005), whereas others suggest that particular processes that are ‘embedded’ in auditory perception may rather induce mu decrease (Krause et al., 1997).

Although the functional interpretation of mu is not well established yet, it is widely acknowledged that mu decrease correlates with motor cortex activation, whereas it is controversial whether mu increase underlies motor cortex deactivation (Klimesch, 1996), ‘idling’ (Pfurtscheller, 1992), or inhibition (Jasper and Penfield, 1949; Gastaut, 1952; Jensen, 2005). A further interpretation is that mu increase indicates augmented synchronization of the motor cortex with other cortical regions (Pineda, 1999).

On the light of these findings, here we raise the question whether the motor cortex displays any reactivity to mu rhythm during the production and perception of one’s own speech. Specifically, we asked whether the modulation of mu rhythm reveals a motor link, or rather dissociated cortical mechanisms involved in attending to the production and perception of one’s own speech.

In order to explore this question, we elicited MU responses during voluntary production and perception of subjects' own speech. We used the experimental paradigm firstly introduced by Libet (1982) and adapted from Sirigu et al. (2004). Subjects were instructed to pronounce a word and then to report the time at which they had first started speaking. In a separate block of trials, they were requested to listen to their own pronunciation of the word and then to report the time at which they had first heard their own speech.

MEG was used in order to study the temporal course and the spatial localization of mu reactivity of the motor areas during the task.

Methods

Participants

Sixteen healthy participants were included into the protocol. All subjects were French native speakers, right-handed according to the Edinburgh handedness test (Oldfield 1971), and reported no history of neurological or psychiatric disorders. A written informed consent was obtained from each participant. Subjects' recordings were screened to eliminate those with frequent blinking or signal artifacts (e.g., due to dental work). Four subjects have been rejected because of artifacts. The remaining 10 subjects have been included for analysis.

Experimental procedure

In the magnetically shielded room, subjects sat in front of a screen (40 cm from the screen).

A calibrated clock-face (radius 2.2 cm; marked in steps of 5 units from 0 to 60 like a usual clock) was projected on the centre of the screen (See Fig. 1).

Figure 1

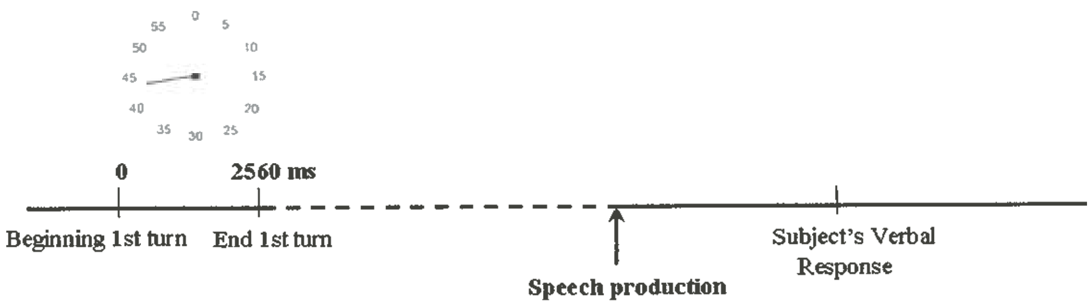

Figure 1. Example of trial. The discontinuous line indicates the variable period from the end of the first clock turn and the actual beginning of speech production.

At the beginning of each trial, a red clock-hand started to turn clockwise (start-spin) from a random location at the speed of 2560 ms per cycle. Subjects were instructed to wait a first complete cycle and then to feel free to pronounce a one-word-like utterance, *demain* ("tomorrow"), at a time of their own choice. They were requested to execute the task as spontaneously as they could, avoiding behavioural strategies (e.g., choosing the position of the hand-clock before speaking and use it to trigger their speech act). In another condition, subjects received an auditory stimulus consisting of their own speech that had been previously recorded while they were producing the word "*demain*".

In one block of trials, subjects were asked to focus their attention on the actual beginning of their speech and then to report the position of the clock-hand at the time when they started speaking (Speech Production condition).

In a separate block of trials, they were instructed to focus their attention on the beginning of auditory stimulus and then to report the time at which they first heard their own speech (Speech Perception condition).

For each condition, blocks of 100 trials were run, each presented in a random order. In a pre-test session, subjects were trained in the MEG with 100 repetitions of both "Speech" and "Sound" conditions.

Stimuli were presented using the Presentation software (Neurobehavioral System, http://www.neurobs.com/).

Data acquisition

MEG recordings. A high-density whole-head system (OMEGA; CTF Systems, VSM Medtech, Vancouver, British Columbia, Canada), provided with 275 axial gradiometer channels and 29 dedicated reference channels for environmental noise cancellation, was used for recording the continuous raw MEG signals (sampled at 1200Hz). Subject's head position relative to the MEG sensors was measured at the beginning of each block, using coils placed at three fiducial points (nasion, left and right pre-auricular points). Head movements did not exceed 1,25 cm between blocks.

Audio data. Subject's verbal responses were recorded through a MEG-compatible microphone and recording software (Cool Edit Pro).

Auditory stimuli. The speech of each subject was recorded during the production of the word "demain" (mean duration 37 ms), by using the Praat software (Boersma and Weenink, 2007). Audio data were digitalised at 44100 Hz with 16 bits using Adobe Audition (Cool Edit Pro). Stimuli were delivered by high impedance nonmagnetic earphones placed over both subjects' ears. They were presented at variable time intervals consistently with the unfixed speech-onset time.

Behavioural data. During each MEG session, participants' verbal time reports were constantly monitored and written down by the experimenter. Trials showing uncertainty or failure in reporting the required time were excluded from analysis. Subjects were visually monitored on a closed circuit TV system.

Data Analysis

Behavioural data

Participants' temporal judgments were calculated by subtracting 1) the time of the actual speech onset from the time at which they reported to have started speaking (Speech Production condition) and 2) the time when the auditory stimulus was actually delivered from the time at which subjects reported to have first heard the auditory stimulus (Sound Perception condition).

Negative values indicated that subjects' estimation of time preceded the event (speech vs. sound) onset, while positive values indicated that it followed the observed event. Latencies of both subjects' overt speech production and perception were also calculated, by subtracting the time of speech and sound onset, respectively, from the time at which the first clock cycle ended up.

Speech signals have been amplified and analysed using Praat software (http://www.praat.org).

Trials with no speech responses, corrupted speech or artefacts (e.g.: deglutition, cough) were rejected. Speech onset times were identified by visual inspection of the speech signal.

MEG data

MEG signals were digitally filtered off-line with a bandwidth of 0.2 Hz to 60 Hz, and decimated down to 300 Hz.

Sensor level. In a first analysis, the Mu rhythm reactivity to the production and the perception of speech was examined at both 8-13Hz and 17-25Hz over the central sensors. Signals from -1s before and +1s after event onset were projected in the time frequency domain, by convolving it with Morlet wavelets. Time frequency maps were normalized (Z score) using a baseline from 0 to 0.5

s after trial beginning. Time frequency of MEG data was compared between the two examined conditions (Speech production vs. perception) in the time period from –1.5 s before to +1.0 s after the event onset, using sample-by-sample paired t-test for data across all subjects using frequency tiles of 10 ms for each following frequency bands: 9/13, 15/25, 25/40, 40/60, 60/100 Hz.

Sample by sample paired t test was applied at 8-12Hz and 17-25Hz frequency bands over the right and left central sensors (figure 3). Differences were considered significant at $p<0.05$ for at least two neighbouring sensors. This method can determine precisely the time range and the scalp regions of the difference between the two conditions.

Source level. In a second analysis, the cortical sources of neural activity registered at sensor level were reconstructed for both Speech production and perception conditions. We examined the spatial distribution of dipole source power at each location as a function of time by comparing the speech production and perception conditions. MEG signals (8Hz to 13Hz) were spatially filtered using Synthetic Aperture Magnetometry (SAM). This minimum-variance beamformer algorithm creates a three-dimensional lattice of optimal spatial filters at a fixed resolution throughout the brain for selected active and passive time windows. A Jacknife t-test was applied to estimate significantly different changes in source power between the two examined conditions during a time window from -200 ms before event onset and +400 ms after event onset time, corresponding to the period of the significant difference common to right and left central sensors. Three dimensional difference images (multisphere model, computed power, subtracted noise) of source power were produced showing mu-reactivity to production vs. perception of speech in localized cortical areas.

SAM virtual channels were applied to sources of activation common to at least 4 subjects in order to virtually reconstruct source signals and determine the time course of source activity. Sample sample-by-sample paired t-test (Bonferroni corrected for all samples and all channels) was used to detect the significant differences of mu modulation in the two examined conditions.

Results

Behavioural results

Participants reported to have started producing their overt speech (Speech-judgement) 54 ms earlier than the actual speech onset. They estimated to have first perceived their recorded speech (Sound-judgement) -1.90 ms in advance of the actual speech onset. Statistical comparison revealed that the two temporal judgments differed significantly (p=0.02).

Time-frequency oscillations at sensor level

In both speech production and perception conditions, lower mu-rhythmic activity (8-13Hz) increased before event onset, i.e. when subjects were preparing either for producing their speech acts (production condition) or for receiving auditory input (perception condition).

After event onset, mu rhythm was suppressed (at both 8-13 Hz and 17-24Hz) when subjects actually uttered their own speech (production condition), whereas it augmented (at 8-13Hz) when they started listening to their own speech (perception condition). Pre-event and post-event modulations of mu in the two examined condition are shown in Fig. 2 a-b. Interestingly, post-event mu diminution and increase elicited by speech pronunciation and perception respectively lasted for about 400 ms, which corresponded to the duration of the one-word like utterance *demain*, as illustrated in Fig. 2 c.

Figure 2

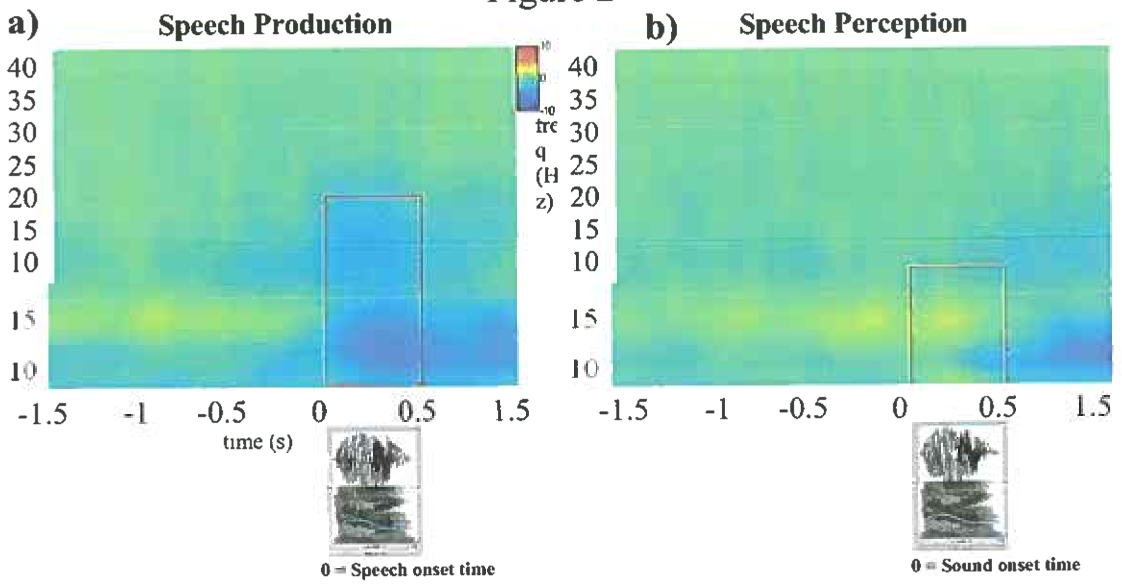

Fig. 2 a-b. Modulation of Mu rhythmic activity resulting from averaged TF maps over the central sensor areas during a) (left panel) Speech Production and b) (right panel) Speech Perception. On the left side of both Z-score graphs, pre-event Mu augmentation (from –1.5 s to 0 before speech and sound onset) is visible in yellow. On the right side of the graphs: a) (left panel) post-event diminution of both 10Hz and 20Hw Mu components specific to the Speech production task (from 0 to about +500 ms after speech onset) is indicated in blue within the red box; b) (right panel) post-event Mu augmentation (from 0 to +400 ms after sound onset) specific to the Speech Perception task is visible in yellow within the red box. The red box margins delimit a time window of about 400 ms, which corresponded to the temporal duration of the target word *demain*: the panels under each box illustrate the speech slope (on the top) with the associated spectrogram and superimposed pitch (on the bottom).

A closer examination of mu latencies during the production condition further revealed that mu started decreasing about -450 ms and -250 ms before speech onset over the left vs. right central sensors, respectively. During speech production, peaks of maximal amplitude were reached about +250 ms after the actual beginning of speech articulation. During speech perception, mu increase reached a maximal peak about -200 ms stimulus onset over both left and right central sensors. Interestingly, over the left central sensors mu started rising later (from actual stimulus onset) than over the right central ones, where it progressively augmented from about -500ms before the actual exposure to auditory stimulus. Such time courses suggest a more prolonged participation of the left central sensors in the production task, and of the right central sensors in the perceptual task.

Statistical contrast between the two examined conditions revealed that mu rhythm decreased bilaterally over the central sensors during speech production as compared to the perception task. However, over the left central sensors, where mu started decreasing progressively from about -400 ms before the actual speech, this effect was more prominent than over the right central sensors, where mu diminution started about -200 ms before speech onset. Please see Fig. 3 below.

Figure 3

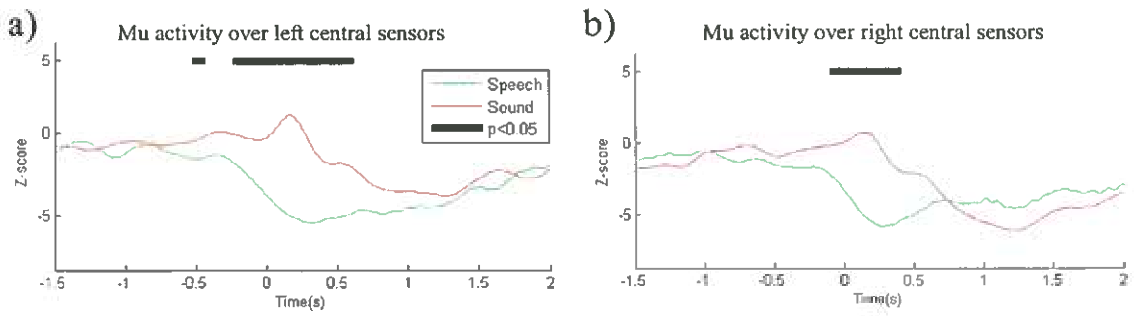

Figure 3 a-b. Time course of Mu frequency power signals at (low Mu component 8-13Hz) during speech production (green) and sound perception (red) -signals averaged over the left sensors (panel a) and over the right sensors (panel b)-. In both graphs, significant differences ($p<0.05$) between the Speech production and perception tasks are marked by the black orizontal line: greater difference between the two examined conditions emerges from the left sensor areas (panel a).

This result suggest a left lateralization of Mu responses to speech-related tasks. Whether the lateralised mu pattern observed at sensor level arose from hemispheric specialization of motor cortex for speech was further assessed by localizing mu rhythm cortical sources.

Cortical Sources of Mu rhythmic activity

Beamforming analysis using Syntetic Aperture Magnetometry revealed a distributional pattern of mu cortical sources which was largely coherent with the result reported at sensor level. Interestingly, the motor regions were significantly more active when subjects uttered the word *demain* (Speech Production) than when they listened to the sound of their own speech (Jacknife t-test, $p<0.05$). Furthermore, although inter-subject variability in individual data showed also bilateral motor activity, a common effect of left hemispheric dominance of the motor cortex was found during the speech production condition in 60% of individual data. A diminution 8-13Hz mu, was observed, more specifically, in the left precentral gyrus (x: -39, y : -15, z: 51), in the left postcentral gyrus (x : -44, y : -21, z : 55) specifically involving the caudal portion of the sensory cortex and the anterior parietal cortex. Please see the a panel of Fig. 4 below.

During speech production, the left motor cortex appeared to be also reactive to the high mu components (17-24Hz). Slopes of mu signals which were reconstructed within the precentral and postcentral gyri using virtual channels indicated that the 8-13Hz and 17-24Hz mu suppression during speech production was significantly stronger compared to the perception condition ($p<0.001$) and begun about 2 seconds earlier than the actual speech onset (Fig. 4 b-c).

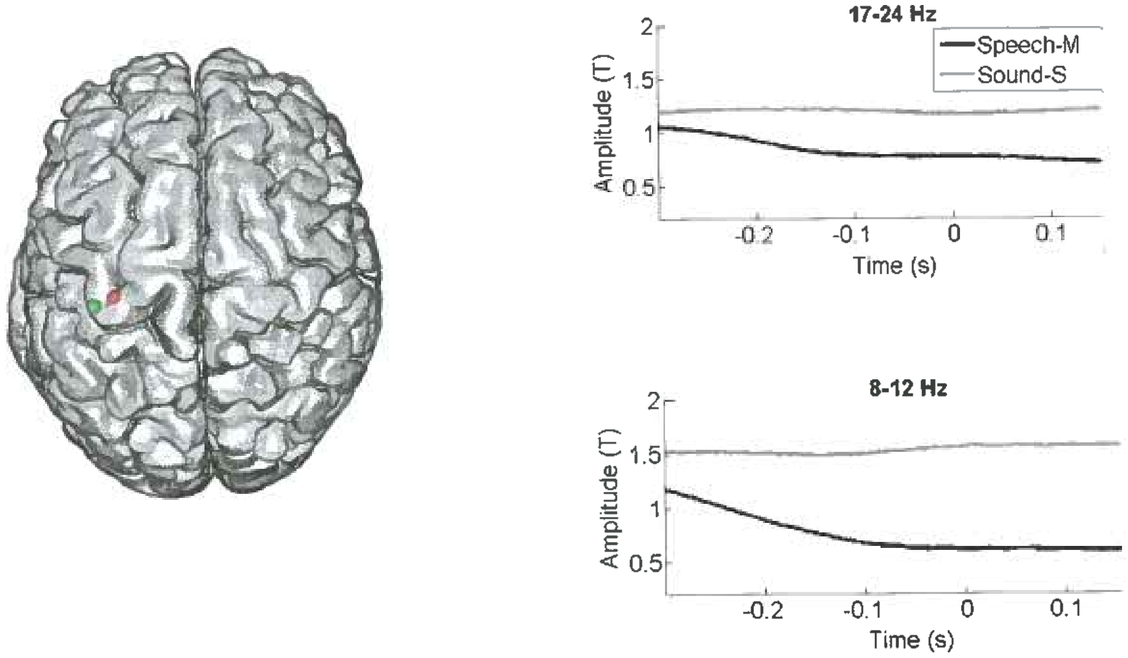

Fig. 4 a. SAM peaks of maximal mu reactivity at 17-25Hz (green peak) and 8-13 Hz (red peak) frequency bands, localized within the motor and sensorimotor cortices during the Speech Production vs. Speech Perception Condition ($p<0.05$). Average of reconstructed signals at the high (17-24Hz) and low (8-13Hz) components of mu are shown in the panels 4b) and 4c) respectively.

Interestingly, the motor regions were responsive to mu about 1 sec before initiation of subjects' own speech.

Discussion

Our experimental paradigm triggered subjects' attention towards two distinct tasks: the self-production of speech and the listening of their own speech. In both conditions, subjects were required to detect and then to report verbally the time at which the relavant event (speech pronunciation or perception) had started occurring.

Time frequency results led us to the first observation that the articulatory and perceptual tasks were accompanied by different modulations of mu rhythmic activity. First of all, mu rhythm was suppressed -as expected- during the production, but not during perception of one's own speech.

Activity related to overt speech production.

Interestingly, during word production, the rhythmic activity at 8-13 Hz started decreasing about -300 ms earlier than speech onset and reached maximal amplitude peaks about 400ms after speech onset.

This suggested that the motor areas were mu reactive during not only the execution but also the preparation of speech.

The results we obtained from source localization further revealed that the mu suppression measured at sensor level during speech production was generated from the left motor areas. Moreover, reactivity to mu appeared in distinct loci of the left motor (M1) and sensory cortex (S1), specifically in the territory which hosts mouth and hand representations (Penfield and Boldrey, 1937). In coherence with our sensor data, the reactivity was earlier than the overt production of subjects' own speech (about 1 sec before speech onset).

Activation of the left mouth area during speech (about -260ms before speaking) has been recently reported in a MEG when subjects attended to the time at which their verbal production begun, but not when they monitored the time of their intention to speak (Carota et al., 2009). Also suppression of 20Hz mu in the mouth area has been reported during preparation of speech (Salmelin et al., 2000), confirming the role of this signal within the motor area in the preparatory motor activity (Kuriki et al., 1999) during speech.

In addition to the mu activity found in the M1 mouth area we also found activation within the hand area during speech production. Previous work has shown overlap between the hand and mouth representations during sensory stimulation in amputees (Flor et al., 1995), and phantom sensations in the amputated limb following stimulation of the mouth area (Ramachandran et al., 1992). Suppression of 20 Hz mu rhythm in the hand area has been observed during finger movements and motor imagery (Schnitzler et al., 1997).

MEG data also indicate that the hand area is specifically recruited by the execution -but not the preparation- of oro-facial movements (Salmelin et al., 2000). Salmelin et al. (2000) reports stronger mu suppression in the mouth than hand area during vocalization tasks, and suggest a somatotopic organization of 20 Hz cortical rhythms (Salenius et al., 1997). Our source results seem to be consistent with this view.

Left lateralization in speech production.

Interestingly, our speech production condition engaged motor events which were left lateralized.

Although the left and right pattern of mu suppression were symmetrical, in fact mu started decreasing about 200ms earlier and lasted about 350ms longer over the left as compared to the right central sensors.

We can note that a similar, lateralized temporal asynchrony of symmetric mu patterns, with earlier mu suppression over the left than the right face area, was also elicited by the preparation of visually guided oro-facial movements (Saarinen et al., 2005), and has been observed between the visual presentation of a word and a 'go' signal for overt speech production in a reading task (Salmelin et al., 2000). However, it has been questioned whether such lateralization effect depends on the visuomotor transformations or motor control involved in the task, rather than being specific to speech (Saarinen et al., 2005).

In this line, we can raise the question whether the left lateralization of mu rhythm observed in our data reflected any hemispheric specialization for spoken language.

In our experiment, subjects were instructed to monitor visually the clock hand position at the time at which they started speaking or listening to their own speech, but no visual cue triggered speech production or perception. Although the visual monitoring of the clock was common to both experimental conditions, the listening to subjects' own speech, which did not involve motor activity as reflected by mu increase, did not induce left lateralized effects.

We cannot exclude on the base of our data that our production task might have involved at different stages, processes that were not specific to spoken language, such as motor control, motor preparation and speech movement rehearsal. However, the left motor activation over the face and hand regions is in keeping with with left hemispheric dominance in speech processing as shown by neuroimaging data (Price et al., 1996; Riecker et al., 2000). Moreover, studies have demonstrated the selective involvement of the left motor cortex during speech articulation (Alexander et al., 1989).

On the light of these findings, we propose that the left hemispheric activation of mouth and hand area within the motor cortex during speech production is specific to self-initiation and self-execution of oro-facial gestures of speech.

Activity related to speech perception.

Differently from speech production, listening to one's own speech did not elicit mu suppression, suggesting that the motor areas were deactivated during speech perception.

Although motor activation during speech perception is weak and can be visible after accurate group analysis within precise regions of interest (cf. Pulvermueller et al., 2005), the patterns of mu increase observed at sensor level lead us to exclude the hypothesis that our perceptual task elicited motor activity which was too subtle to be tracked by MEG recorded mu signals.

The augmentation of mu rhythmic activity during our perception condition reached maximal amplitude peaks about 200ms after stimulus onset, in coherence with the temporal features of the auditory stimulus, which lasted for about 400 ms. This specific time course of mu reactivity to perceptual information seems to be influenced by the perceived, psychological moment of the occurrence of the auditory stimulus, known as perceptual center (P-center) (Morton, 1976).

Mu latencies analysis also showed that the maximal peaks of mu augmentation during word perception temporally preceded for few milliseconds maximal mu diminution peaks observed in the speech production condition.

Although the functional interpretation of increased mu oscillations is still controversial, we can propose here that the listening of one's own speech inhibited neural activity in the motor areas.

During our perceptual task, subjects memorized the time when they first heard their speech and waited until the end of the auditory stimulus before giving their verbal reports. Although this process might have interfered with motor activity during speech perception, deactivation of the motor areas presumably corresponded to increased neural activity in other regions associated to the perception of speech, the auditory cortex *in primis*.

At our knowledge, previous studies of mu rhythm in speech did not investigated specifically whether one's own speech involves different mu modulations as compared to others' speech. Activity in auditory cortex becomes weaker when listening to one's own speech during speaking (Numminen et al., 1999; Heinks-Maldonado et al., 2006), but the processing of one's own voice vs. others' voice as external stimuli does not seem to involve distinct neural substrates (McGuire et al., 1996; Price et al., 1996; Wise et al., 1999).

Interestingly, in our data, the progressive increase of mu activity was more important over the right sensor areas, suggesting that the right motor cortex was deactivated longer than the left ones during our auditory task. Such stronger deactivation of the right motor cortex may indirectly indicate a stronger engagement of a network of regions within the right hemisphere, first of all the right auditory cortex, in speech perception. It is, for instance, established that the right temporal cortex is dominantly involved in the processing of prosodic (Weintraub et al., 1981), affective (Ross and Mesulam, 1979; George et al, 1996; Pell, 1999; Kotz et al., 2003), and pragmatic aspects of speech (Joanette et al., 1991; Chantraine et al, 1998).

Interestingly, the temporo-parietal circuit involved in speech perception also underlies self-recognition and awareness. The STG, for instance, plays a role in self-recognition and supports the ability to distinguish between one's own and others' speech (Fu et al., 2006; Christoffels et al., 2006).

Taken together, both mu signatures at sensor level and mu reactivity at source level suggest that mu rhythmic activity is differentially modulated during the production and perception of one's own speech.

These results bring counterevidence for the assumption that mu rhythm mediates action-perception link and that motor processes are crucial in the perception of speech. Rather, our data are in line with the view that producing and processing speech require distinct cerebral networks.

Final remarks. A substantial advance in our work with respect to the first report that I have sent on the 19th of April 2004 is the successful localisation of the brain sources of Mu rhythmic activity. With this achievement, which is rarely explored in the work on the neurobiology of behaviour in general and, more specifically, of language, we bring a new insight on the functional interpretation of Mu rhythm -which is still under debate in the scientific community-. Taken together, these results contribute to elucidate Mu rhythmic activity in a unique aspect of human behaviour such as speech communication.

The results at sensor level that have been presented in the earlier version of the present report have been complemented with the latter results on source localisation in the paper that we are about to submit to Frontiers in neuroscience.

Carota, F., Harquel, Delpuech, C., Sirigu., A. (under review). Modulation of Mu rhythm during the production and perception of one's own voice.

I will inform BIAL Foundation of the publication of these original results as soon as the paper will be accepted. Like in the previous paper appeared in Cerebral Cortex, we will acknowledge the BIAL Grant 192 for having supported the work.

I wish to take the opportunity of this report to express my heartfelt thanks to the BIAL Foundation for allowing me to undertake and complete the different stages of this challenging and original project.

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