Sensory-motor transformations for speech occur bilaterally.

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1 Supplementary Discussion:

1.1 Representation of Sensory-motor transformations: In this study, we present evidence for a bilateral speech sensory-motor system. This system could facilitate access to higher order language processing (e.g. syntax, semantics) via the formation of a unified sensory-motor interface. Here, we draw a distinction between the underlying neural activity of the speech sensory-motor system and the coordination of perception-based and production-based representations that form the sensory-motor interface. Our proposal is that the underlying Sensory-Motor system supports the formation of an interface by performing transformations between a sensory-based coordinate system and a motor-based coordinate system, establishing parity between representations. Parity between perceptual and production representations is a key feature of the interface and enables unified access to centralized language computations (see **Fig S9**).

While the current study presents evidence for sensory-motor transformations via the bilateral speech sensory-motor system, the level of representation within these sensory-motor transforms remains unclear. We can however, rule out some possibilities. For the Listen-Speak Transformation task, we chose to use two non-words, ‘kig’ (/kIg/) and ‘pob’ (/pɔb/). Since we found that S-M electrodes contained activity reflecting sensory-motor transformations when using non-words, we can rule out the necessity of both lexical access[37] (i.e. making contact with word entries in the lexicon), and higher order semantic processing[38] (i.e. meaning). We can also rule out general coupling of auditory and orofacial movements since sensory-motor activations were not present during the Tone-Move task in which a tone was paired with unguided articulator movements. Taken together, we can exclude both higher level processes (lexical / semantic) and low level processes (Pure auditory and motor) as being the locus for sensory-motor transformations for speech.

Upon exclusion of both high and low levels of representation, we are left with the phonological, sublexical representation: Distinctive features[7,38,39], phonemes, and syllables[37,41]. It is tempting to speculate whether the sensory-motor transformation represents the *internal* transformation within a representational category (e.g. a sensory /b/ to a motor /b/ within a phonemic representation) or across representations (e.g. /p/ sensory phoneme to a voiceless + bilabial + plosive motor output - distinctive features). An internal representational shift would suggest that sensory-motor transformations are a distinct phonological representation whereas a representational change would suggest that the sensory motor transform is a representational transform. Furthermore, a better understanding of the specific coordinate system for both speech perception and production would enable a more detailed demonstration of the computation of the transformation. These coordinates could also exist in multiple reference frames that could potentially enable transformations both across and within representations. Future work will be needed to clarify the specific nature of both sensory and motor representations as well as the transformations between them.

1.2 Relation to Visual Sensory-Motor Transformations: Visual sensory-motor transformations have been studied in the domain of looking, reaching and grasping[22,23],[42,43]. A strong emphasis has been placed in the posterior parietal cortex[23,44], the premotor cortex[45], and superior temporal gyrus[46], both bilaterally.

Sensory-motor transformations during visual-motor behavior have often been explored using the anti-saccade/anti-reach paradigms[22,23,47-49]. In these studies, visual targets were presented and then extinguished. After a short delay, the subject had to saccade either to the location of the visual target (pro-saccades) or visually orthogonal to it (anti-saccade). Both visual and motor (saccade) cells were identified. Interestingly, in posterior parietal cortex, a subset of putative visual cells were active both when the visual target was presented in the receptive field and when a target was presented outside the receptive field but a saccade was to be performed into the field. The similarity of saccade and reach task responses under these conditions speaks to the generality of the underlying mechanism. The existence of 'paradoxical' cells in posterior parietal cortex underlies the logic behind the Listen-Speak Transformation analysis in the present study: The sensory signal (visual target/non-word sound) and the motor output (saccade/speaking) are held constant while the sensory-motor transformation is manipulated.

This change in sensory-motor coupling could involve two processes: The first, control, reflects the inhibition of the normal stimulus-response activation between the visual target and the movement goal and second, vector inversion, reflects the specific change in movement goal that replaces the automatic response[50]. Control is believed to be mediated by prefrontal areas including the supplementary eye fields (SEF), frontal eye fields (FEF), and dorsolateral prefrontal cortex[51]. Vector inversion is believed to be carried out in area LIP[22,50]. What remains unclear is the nature and representational level of this vector inversion. While some behavioral evidence exists that saccade reaction time increases linearly with the angle of rotation of the saccade in relation to the cue[52], so far there has been no neural data supporting visual space as the operative space for saccade visual-motor transformations. In this sense, they are similar to speech sensory-motor transformations in that while we can demonstrate a transformation in speech, the space in which this transformation is carried out in remains unknown.

1.3 Relation to Previous Work: There has been very little previous work on the speech sensory-motor system. This is presumably, largely due to limitations with image artifacts due to jaw movements associated with speech production. Using Positron Emission Tomography (PET), Petersen et al.[53] carried out a series of speech contrasts to tease apart various brain regions' contributions to different aspects of speech processing. In one particular contrast, they compared subjects repeating words to subjects passively listening to words. The resulting subtraction analysis revealed bilateral activation in the motor cortex (as well as other areas). While intriguing, it is important to note that while this analysis captures speech production responses, the sensory portion of the task is subtracted. This therefore, does not capture sensory-motor processing of speech. It does, however, give credence to the bilateral nature of aspects of speech production.

Wilson et al.[54] used function magnetic imaging (fMRI) to assess the contribution of putative motor areas to speech perception. Using a block design, they compared passive listening of syllables to the production of syllables and found overlap on the border of Brodmann area 4a and 6 (motor/premotor cortex) bilaterally. Similarly, Hickok et al.[55] found areas (including bilateral motor/premotor and pSTG) that were active during both a listen (jabberwocky sentences) and a covert production block. They also found an area on the posterior Sylvian Fissure (area SPT) that responded both to a series of auditory input and goal directed motor output including both speech and singing[55]. This suggests that the nature of sensory-motor integration could be more general than strictly auditory and motor speech and could encompass the mapping between auditory input and a wider range of goal directed motor output involving the vocal apparatus.

These finding are important for suggesting a bilateral role for sensory-motor processing, but unfortunately, they are limited for several reasons. Firstly, these results do not clearly distinguish between actual motor processing and the sensory consequences of the processing (either overtly produced or simulated consequences of covert production). It is therefore unclear, the degree to which the findings reflect sensory and motor processing or simply sensory processing (input and the sound of one's own voice). All studies also reflect a conjunction analysis that could only reflect the overlap of sensory and motor processes (should this be the case) rather than a transformation between sensory and motor representations.

More recent work using electrophysiology has also explored the relationship between sensory and motor processing for speech[56]. In this study, auditory and visual input was paired with either covert or overt speech production. The time course of the high gamma response was examined and the relative timing of various cortical regions during both the sensory input and either overt or covert output was assessed. While the results are important to differentiate between overt and covert speech production, it is unclear which areas were performing sensory, motor or sensory-motor processing. Furthermore, the right hemisphere's contribution to the task was not assessed.

1.4 Relation to Conduction Aphasia: We have proposed that like speech perception, speech sensory-motor transformations occur bilaterally. This contrasts with higher-order language processing (such as syntax and semantics) that occur in the left hemisphere. This division is in keeping with perceptual proposals for speech and language processing that posit a left/bilateral distinction[11,57,58]. Based on this schism, we proposed that since the diagnosis of conduction aphasia (good verbal perception and production but impaired repetition[9,10]) is traditionally associated with lesions in the left hemisphere, this would therefore suggest that deficits associated with conduction aphasia are due to higher order language deficits. There is a fair amount of evidence for this hypothesis.

One of the largest meta-studies of conduction aphasia examined 20 conduction aphasia patients[59]. Out of the 20 patients examined, the average word repetition percentage was 90.4 %, whereas sentence repetition was only 48%. Foreign word repetition scores were also quite high (82%), suggesting that the deficits could not be due to difficulty in phonetic mapping between sensory and motor representations, but rather due to linguistic complexity. It is worth noting that all patients in the study had left hemisphere lesions.

Verbal repetition deficits however, are not strictly associated with a diagnosis of conduction aphasia. Ardila and Rosselli[60] compared various types of aphasics (transcortical aphasics, Broca's aphasics, conduction aphasics, Wernicke's aphasics, anomic aphasics, alexia without agraphia and global aphasics) and found that all groups had trouble with at least some repetition tasks. They concluded that deficits in repetition could be associated with limitations in auditory short-term memory, phonological production, phoneme recognition, or deficits in semantic and syntactic comprehension. Repetition deficits are therefore present in a number of different aphasic types, which is consistent with a role for higher order linguistic deficits in certain types of repetition tasks (e.g. sentence repetition).

This distinction between left hemisphere (higher order linguistic) and bilateral (sensory-motor speech) is also supported by the anatomy. While there is still much debate as to the degree to which conduction aphasia *as diagnosed*, is due to damage to the arcuate fasciculus[10] or other grey matter lesions[11,28], there is little doubt that white matter pathways play an important role in speech and language processing[61,62]. Could there be an anatomical basis for bilateral sensory-motor transformations that are distinct from left lateralized abstract/linguistics processes? Using diffusion tensor imaging (DTI), Catani et al.[63] found that there were two white matter tracts connecting posterior superior/middle temporal regions with inferior frontal and premotor regions. The first, the direct pathway, connected directly from the posterior STG/MTG to inferior frontal regions and was either only found in the left hemisphere or biased towards the left hemisphere in 82.5% of the subjects examined. Contrastingly, an indirect dual-pathway that first connected the posterior STG/MTG to the inferior parietal lobe and then the inferior parietal lobe to premotor/ inferior frontal regions was found in all subjects *bilaterally*. While it is important to note the uncertainty underlying white matter reconstruction techniques[62], this finding presents a strong anatomical underpinning for our hypothesis: The left lateralized direct pathway is involved in higher order linguistics properties of speech content whereas the bilateral indirect pathways are involved in sensory-motor transformations. It is also worth noting that the path of this pathway largely coincides with the location of our S-M sites (see **Fig 2** and **S4**).

2 **Supplementary Tables**

2.1 Table S1

Subject	Implantation	Age	Gender	WADA	VCI	POI	WMI	PSI	MRI	Epilepsy Characterization
1	Right	42	Female	Left	126	111	99	122	Normal	Localization related epilepsy – Right Temporal
2	Right	32	Female	Left	98	91	83	97	Normal	Localization related epilepsy – Right Frontal
3	Left	44	Female	Left	127	96	120	117	Normal	Complex Partial with secondary
4	Left	24	Male	Left	122	121	124	105	Normal	Localization related epilepsy – Left Temporal
5	Right	51	Female	Left	83	86	108	73	Normal	Complex Partial
6	Right	20	Female	Left	85	88	78	88	Normal	Complex Partial
7	Left	22	Male	Right	85	110	100	92	Normal	Complex Partial with secondary
8	Left	39	Female	Left	82	97	91	83	Left MTS	Localization related epilepsy – Left Temporal
9	Right	17	Female	NA	89	NA	104	112	NA	Complex Partial
10	Bilateral	35	Male	Left	100	105	105	89	Right Frontal lesion	Simple Partial
11	Left	31	Male	Left	107	102	105	108	Normal	Complex Partial with secondary
12	Right	43	Male	Left	114	115	117	120	Normal	Generalized Tonic Clonic
13	Bilateral	40	Female	Left	83	96	83	92	Normal	Complex Partial
14	Right	36	Male	Left	125	105	128	127	Right mesial temporal heterotopia	Complex Partial
15	Bilateral	19	Female	Right	---	---	---	---	Normal	Complex Partial
16	Left	24	Female	Left	108	---	89	84	Normal	Simple Partial

Table S1: Intracranial implant patient demographics. Wada: Language lateralization as determined by Wada procedure (L=Left, R=Right); Wechsler Adult Intelligence Scale III indices: **VCI**: Verbal Comprehension Index; **POI**: Perceptual Organization Index; **WMI**: Working Memory Index; **PSI**: Processing Speed Index; **MRI**: presurgical MRI findings, LH=left hemisphere, MTS=mesial temporal sclerosis; **Epilepsy Characterization:** Classification of epilepsy type/location of seizure onsets; (No neuropsych data available for patient 15).

2.2 Table S2

Subject	Hemisphere	SM/SMA	X	Y	Z	Area	BA
S1	RH	SM	59	8	40	Premotor Cortex	6
S1	RH	SMA	68	-2	13	Premotor Cortex	6
S2	RH	SMA	70	-5	6	Superior Temporal Gyrus	22
S2	RH	SMA	69	-42	24	Supramarginal Gyrus	40
S3	LH	SMA	-67	-50	10	Superior Temporal Gyrus	22
S3	LH	SMA	-68	-58	14	Superior Temporal Gyrus	22
S3	LH	SMA	-69	-61	3	Middle Temporal Gyrus	21
S4	LH	SMA	-58	1	43	Premotor Cortex	6
S4	LH	SMA	-54	-8	48	Premotor Cortex	6
S4	LH	SMA	-52	39	4	Inferior Frontal Gyrus	45
S4	LH	SM	-63	4	18	Premotor Cortex	6
S5	RH	SMA	71	-34	-3	Middle Temporal Gyrus	21
S5	RH	SMA	56	13	-9	Superior Temporal Gyrus	38
S5	RH	SMA	69	-4	17	Premotor Cortex	6
S5	RH	SMA	65	3	25	Premotor Cortex	6
S5	RH	SMA	56	-8	45	Motor Cortex	4
S5	RH	SMA	54	7	47	Premotor Cortex	6
S6	RH	SMA	71	-22	18	Superior Temporal Gyrus	22
S6	RH	SMA	70	-12	16	Motor Cortex	43
S6	RH	SM	68	-9	34	Premotor Cortex	6
S7	LH	SM	-65	-36	21	Supramarginal Gyrus	40
S7	LH	SMA	-66	-45	27	Supramarginal Gyrus	40
S7	LH	SMA	-68	-50	18	Superior Temporal Gyrus	22
S8	LH	SMA	-51	8	48	Premotor Cortex	6
S8	LH	SMA	-57	1	43	Premotor Cortex	6
S8	LH	SMA	-62	3	28	Premotor Cortex	6
S8	LH	SMA	-65	-26	34	Supramarginal Gyrus	40
S8	LH	SMA	-66	-25	17	Superior Temporal Gyrus	42
S8	LH	SMA	-69	-24	1	Superior Temporal Gyrus	42
S9	RH	SMA	68	-2	40	Premotor Cortex	6
S10	RH	SMA	64	-40	27	Supramarginal Gyrus	40
S10	LH	SMA	-66	-40	8	Superior Temporal Gyrus	22
S11	LH	SMA	-64	26	14	Inferior Frontal Gyrus	45
S11	LH	SMA	-63	-11	19	Motor Cortex	43
S11	LH	SMA	-65	-37	13	Superior Temporal Gyrus	22
S12	RH	SMA	69	-7	3	Superior Temporal Gyrus	22
S12	RH	SMA	69	-12	13	Motor Cortex	43
S13	LH	SMA	-68	-51	17	Superior Temporal Gyrus	22
S13	LH	SMA	-67	-33	29	Supramarginal Gyrus	40
S13	RH	SMA	61	-54	8	Superior Temporal Gyrus	22
S14	LH	SMA	-61	8	4	Premotor Cortex	44
S14	LH	SMA	-69	-14	3	Superior Temporal Gyrus	42
S15	RH	SMA	64	-42	29	Supramarginal Gyrus	40
S15	RH	SMA	60	7	28	Inferior Frontal Gyrus	9
S16	LH	SMA	-51	-21	61	Somatosensory Cortex	1
S16	LH	SMA	-57	-33	56	Somatosensory Cortex	40

S16	LH	SMA	-51	18	25	Inferior Frontal Gyrus	9
S16	RH	SMA	51	-35	66	Somatosensory Cortex	1
S16	RH	SMA	55	-30	60	Somatosensory Cortex	2

Table S2: Sensory-motor activations and locations for each of the 47 electrodes in the database. X,Y,Z are given in Talairach coordinates.

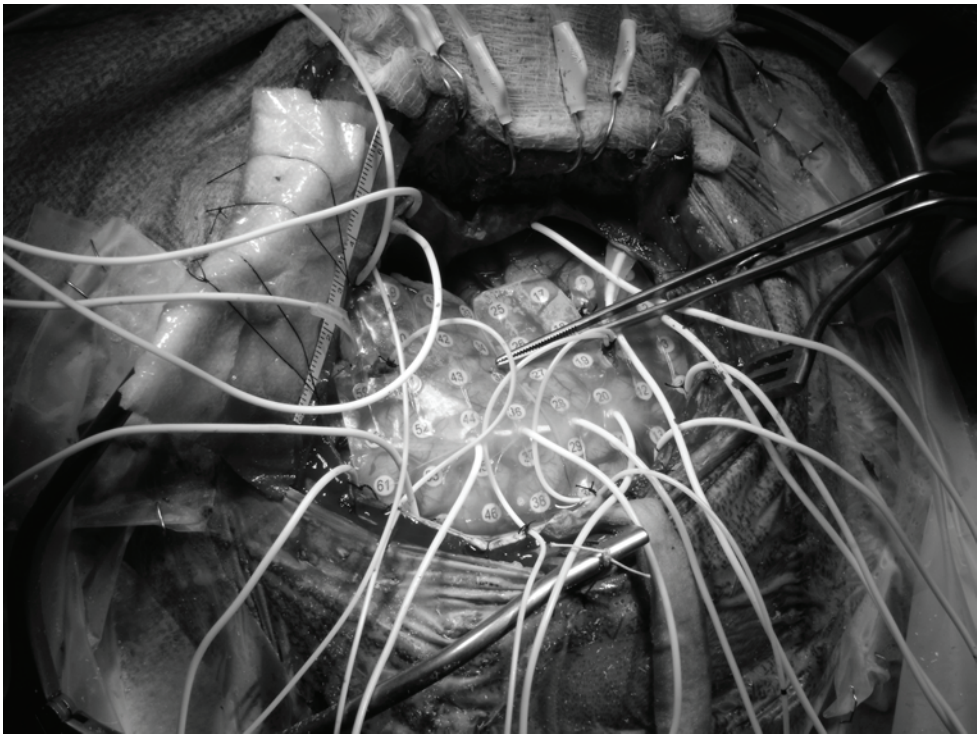

Figure S1: Surgical implantation image showing grid electrodes being placed subdurally.

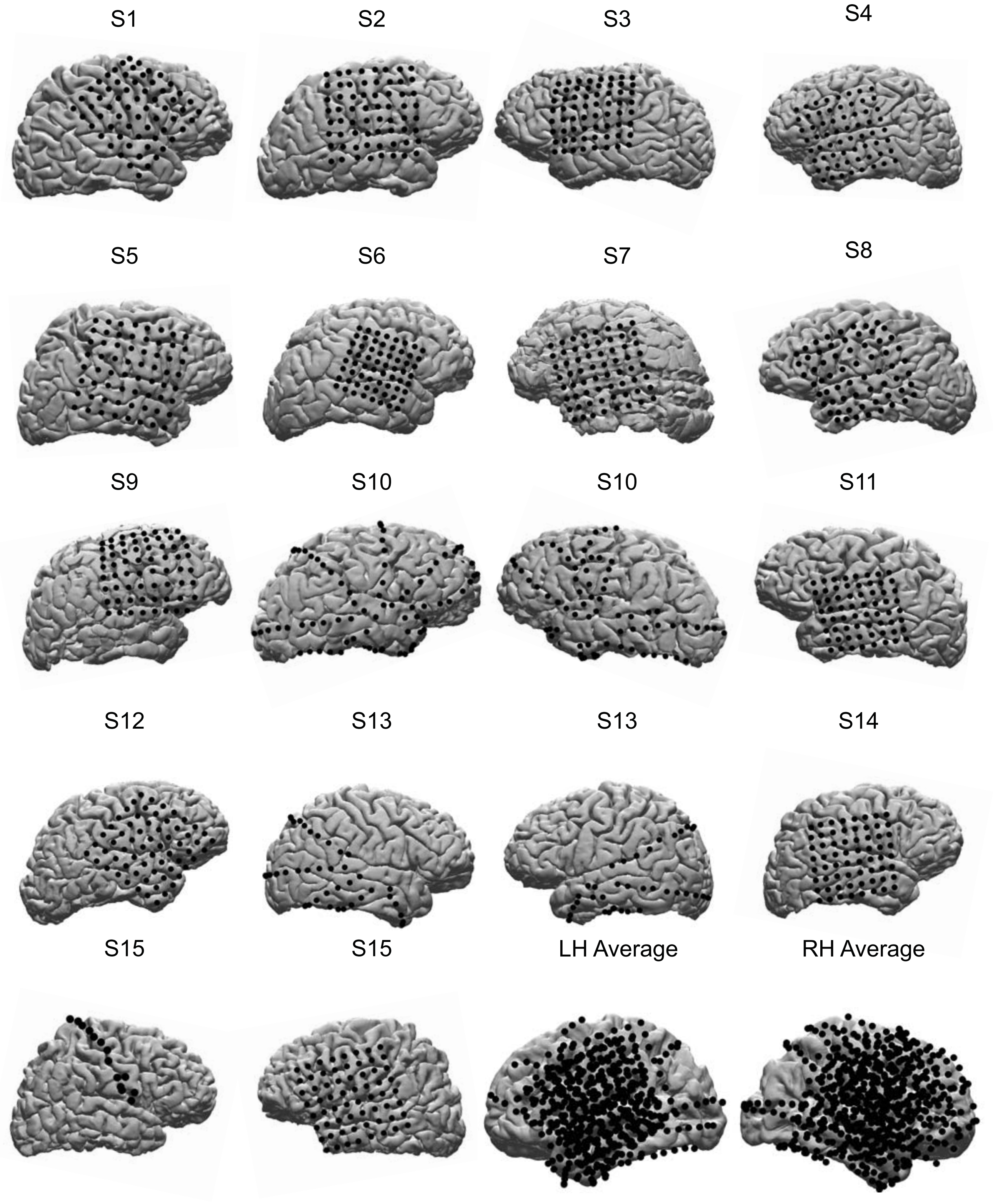

Figure S2: Electrode coverage for each of the sixteen subjects and for left and right hemisphere average brains. Each grid or strip electrode is shown by a black disk on the per-subject brain (S1-S16), and for all electrodes on the average subject brains (LH Average and RH Average).

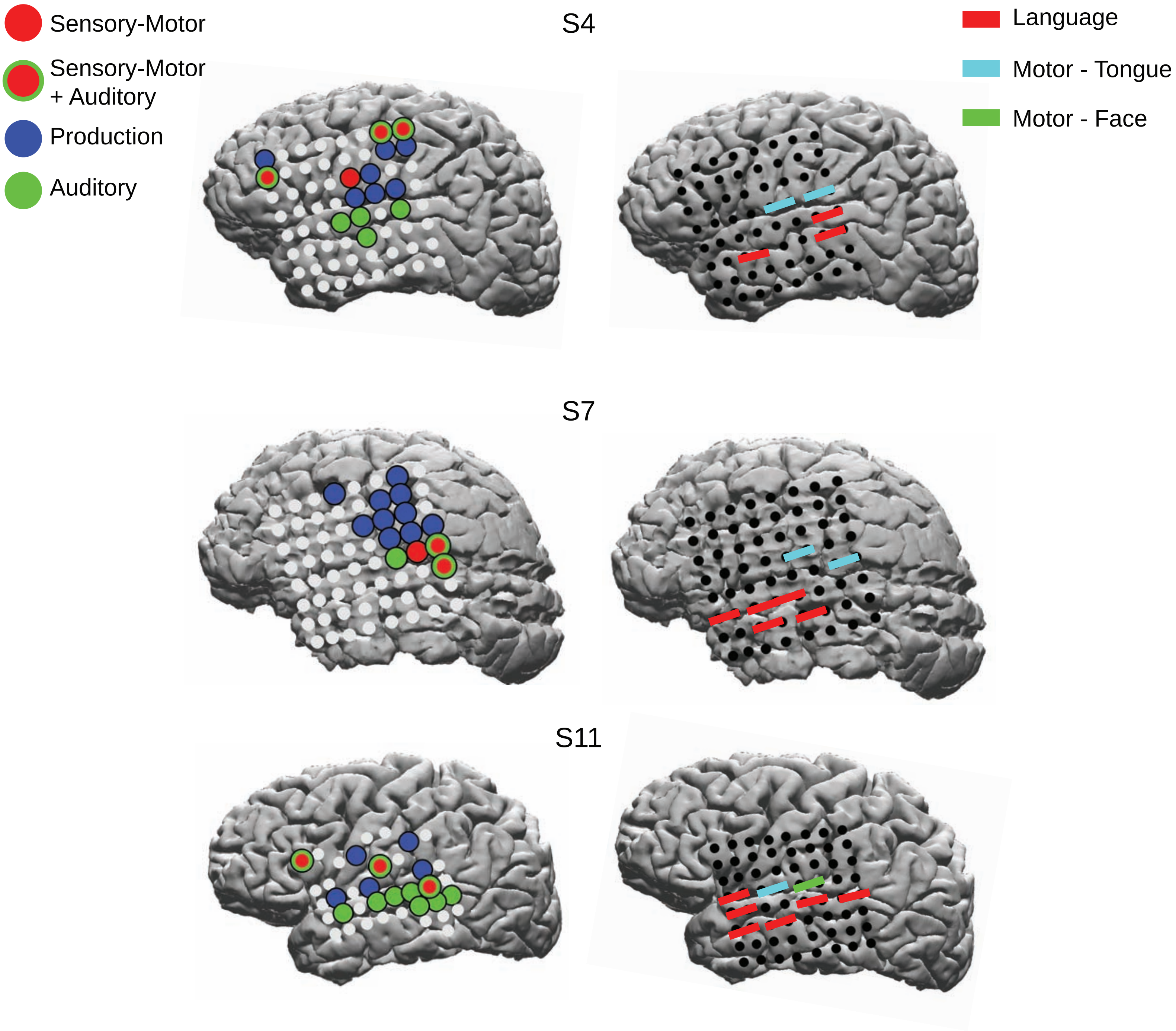

Figure S3: Results of stimulation mapping (right) for a subset of subjects (S4, S7, S11) as compared to neural (high gamma – 70-90 Hz) activations (left). Color codes for neural activity are the same as in **Fig 2**. Specific activations are color coded: Language sites (red), motor/tongue (cyan) and motor/face (green). While in some cases, stimulation mapping matches approximately with neural activation (e.g. language+auditory in S11), in other subjects, mapping is not nearly as similar (language+auditory in S7). Active motor stimulation sites were also not restricted to sites immediately around the central sulcus: Sites are seen in inferior parietal cortex as well (S4, S7).

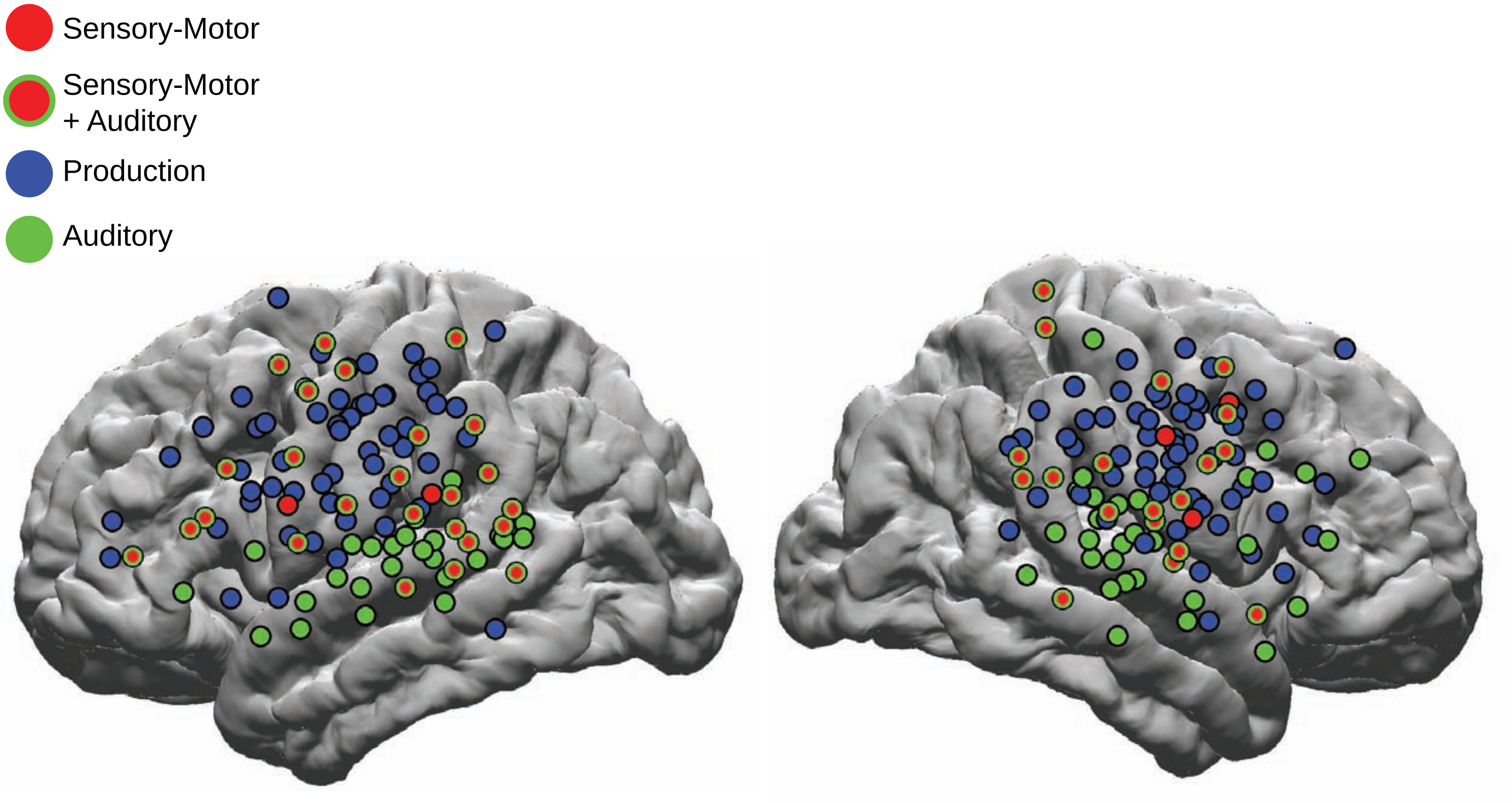

Figure S4: Significant electrodes projected onto a population average brain with actual size electrodes. Electrodes with significant high gamma (70 – 90 Hz) activity are shown on an average brain for each hemisphere. PROD (blue), AUD (green), and S-M with Listen (red with green outlines) and without Listen (red) condition activation are shown as their actual size (4 mm diameter) in reference to the average brains. AUD electrodes mainly localize to the super temporal gyrus and middle temporal gyrus while PROD electrodes localize to the inferior parietal lobule, precentral gyrus, and postcentral gyrus.

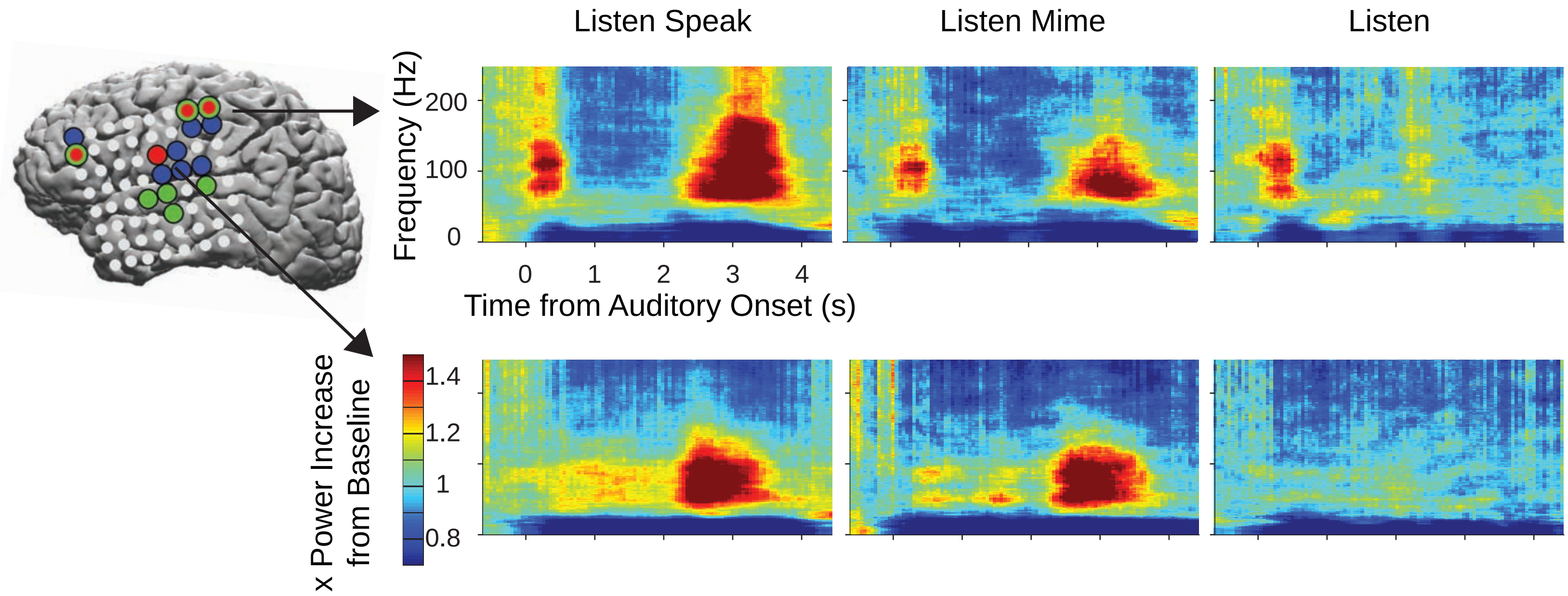

Figure S5: Example S-M electrode with and without significant neural activity in the Listen condition. An example subject (S4) with a S-M electrode that displays significant high gamma (70 – 90 Hz) neural activity in the Listen condition (red with green outline, spectrograms on top) and a S-M electrode without significant activity (red, spectrograms on bottom) for Listen-Mime, and Listen conditions. Spectrograms indicate power change relative to baseline.

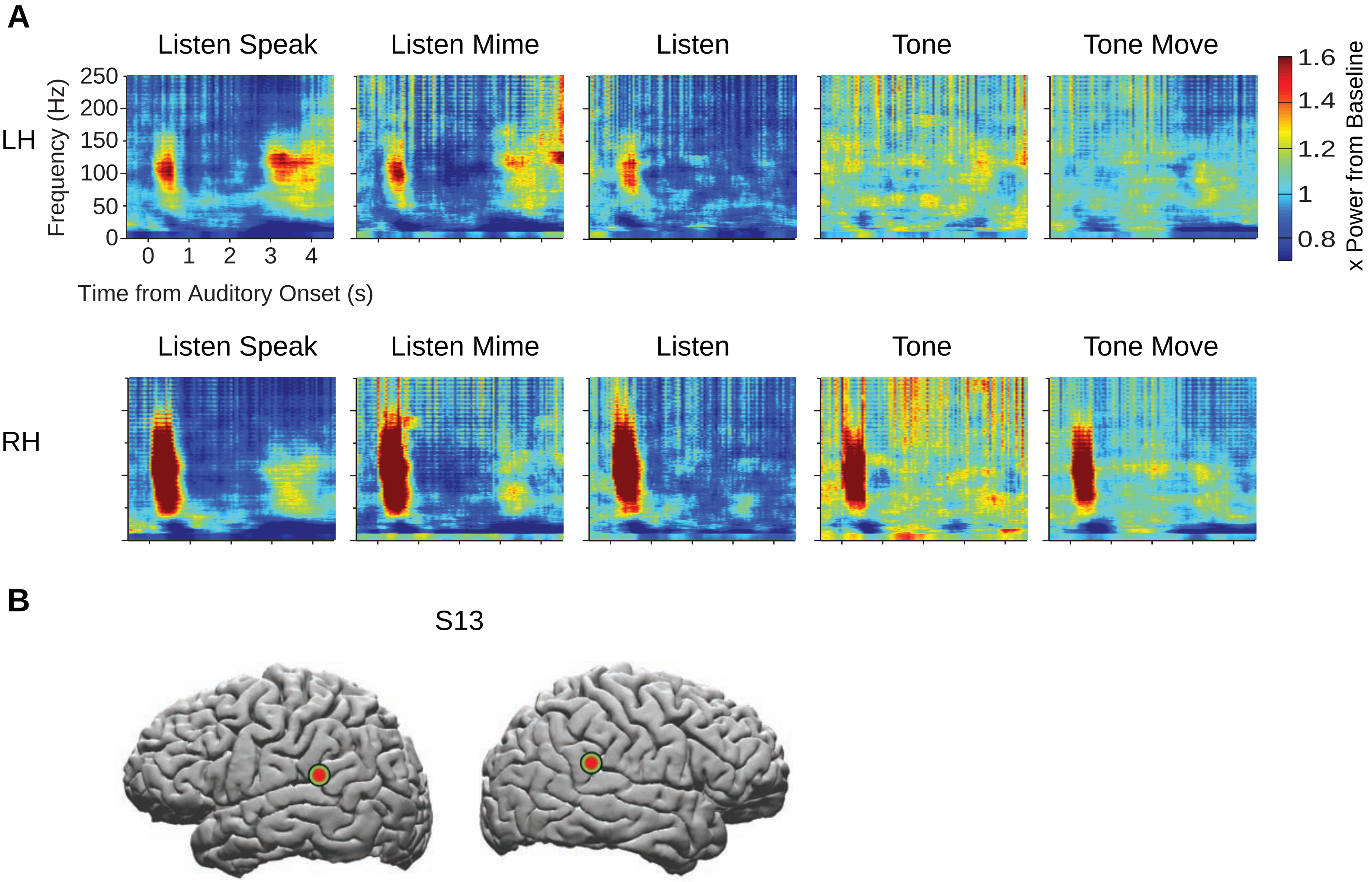

Figure S6: Neural activation for Tone-Move task. Spectrograms are shown for the neural responses for two example electrodes from one subject who performed the Tone-Move task. Each row displays the responses for each condition for a single electrode from the left hemisphere (LH – top row) or the right hemisphere (RH – bottom row). **B)**. Electrode locations from subject S13 for S-M electrodes in each hemisphere. Both electrodes demonstrate sensory-motor neural responses (see main text) for Listen-Speak/Listen-Mime/Listen task conditions. Activations during the Tone-Move condition do not show sensory-motor activations (although note the auditory activation in the RH electrode), demonstrating a specificity for speech sensory-motor transformations.

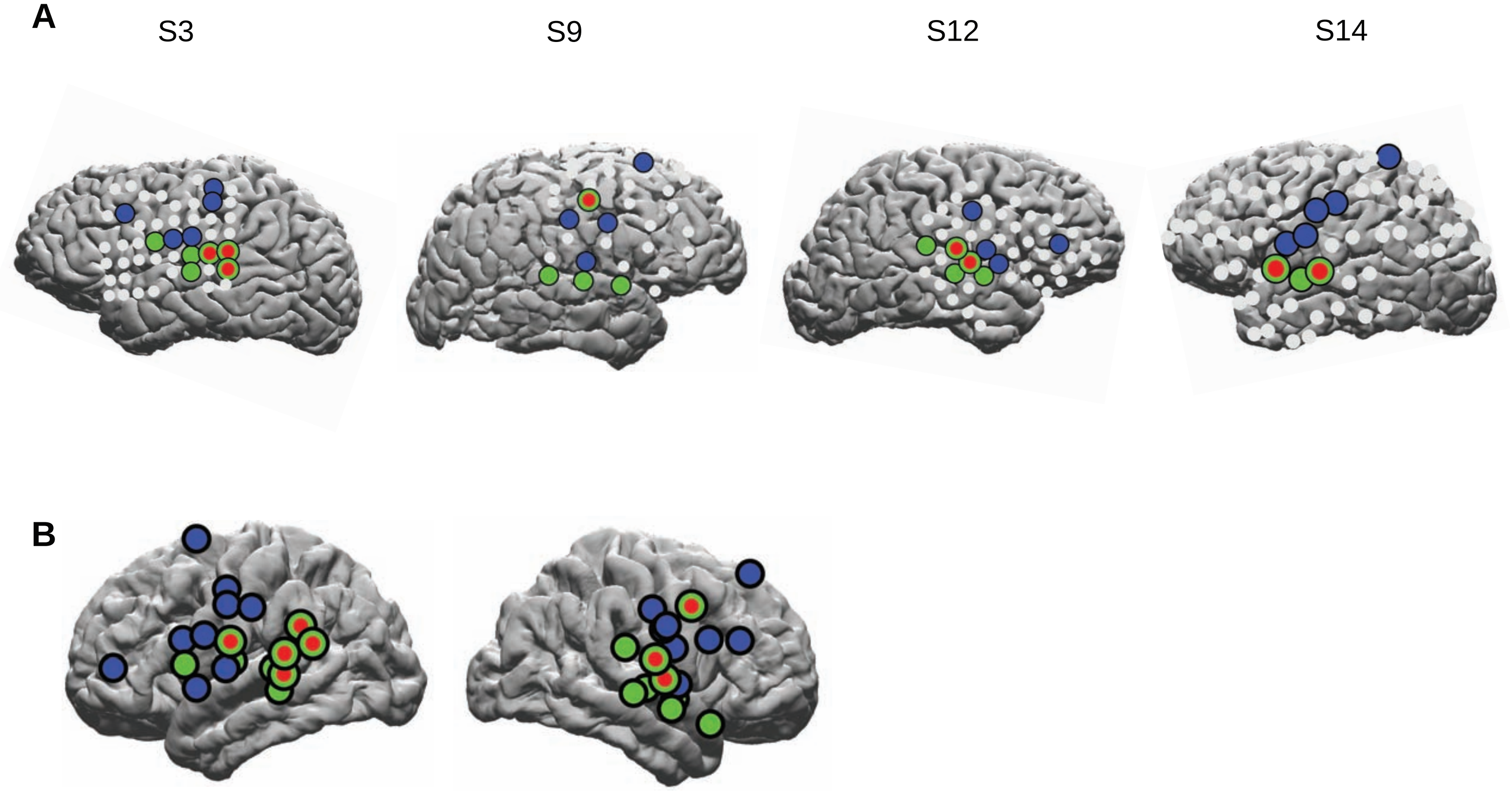

Figure S7: Electrode coverage for Listen-Speak Transformation task. **A)**. Individual Subject coverage for 4 subjects. Color scheme same as **Fig 2**. **B)**. Population coverage.

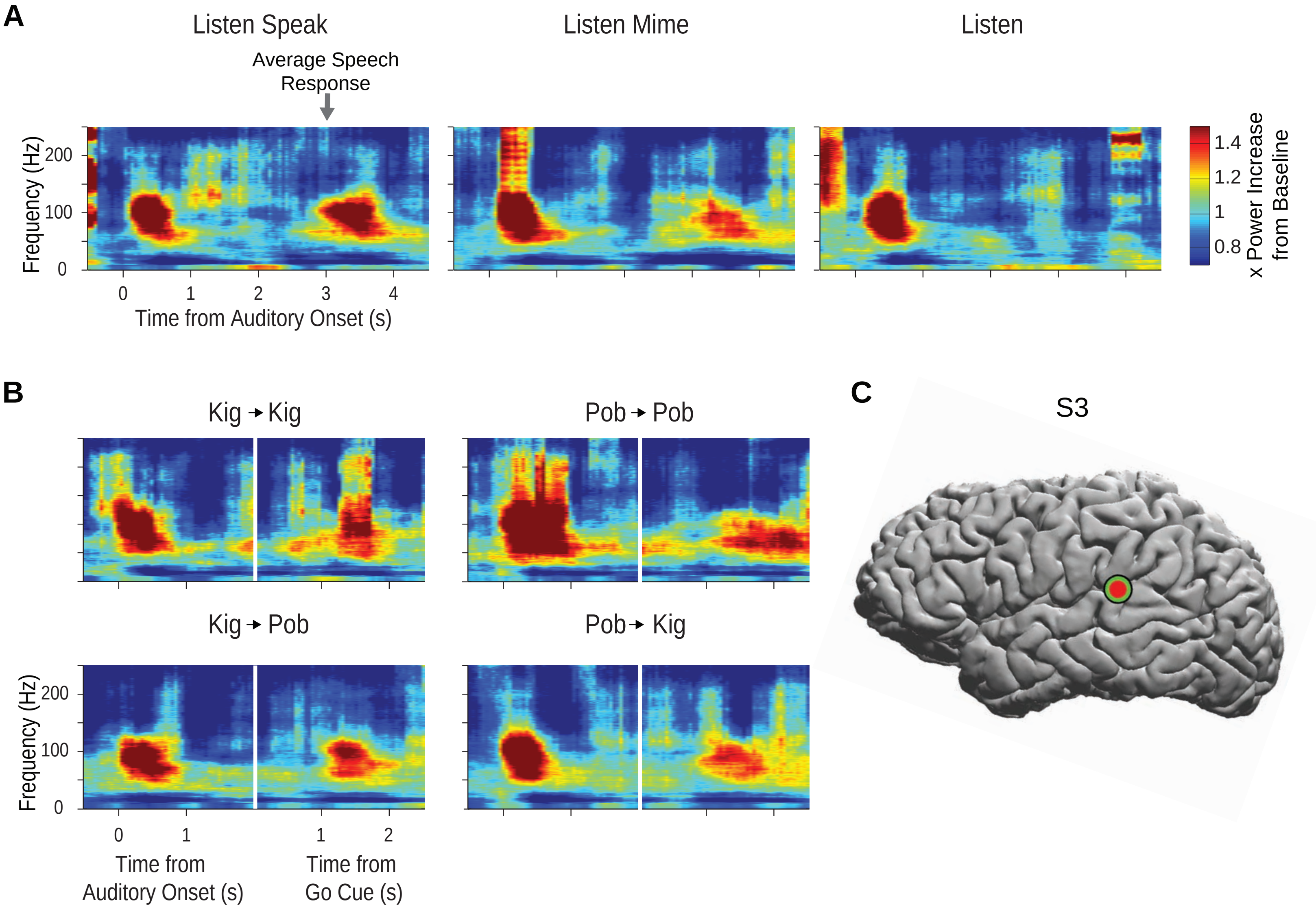

Figure S8: Example response for Listen-Speak Transformation task. **A)**. Spectrograms are shown for the Listen-Speak/Listen-Mime/Listen conditions. **B)**. Spectrograms for all four of the transformation conditions. The white line in the middle of the spectrograms indicates that the timing of the 'Go' cue was randomized. Spectrograms indicate power change relative to baseline. **C)**. Example electrode location from subject S3.

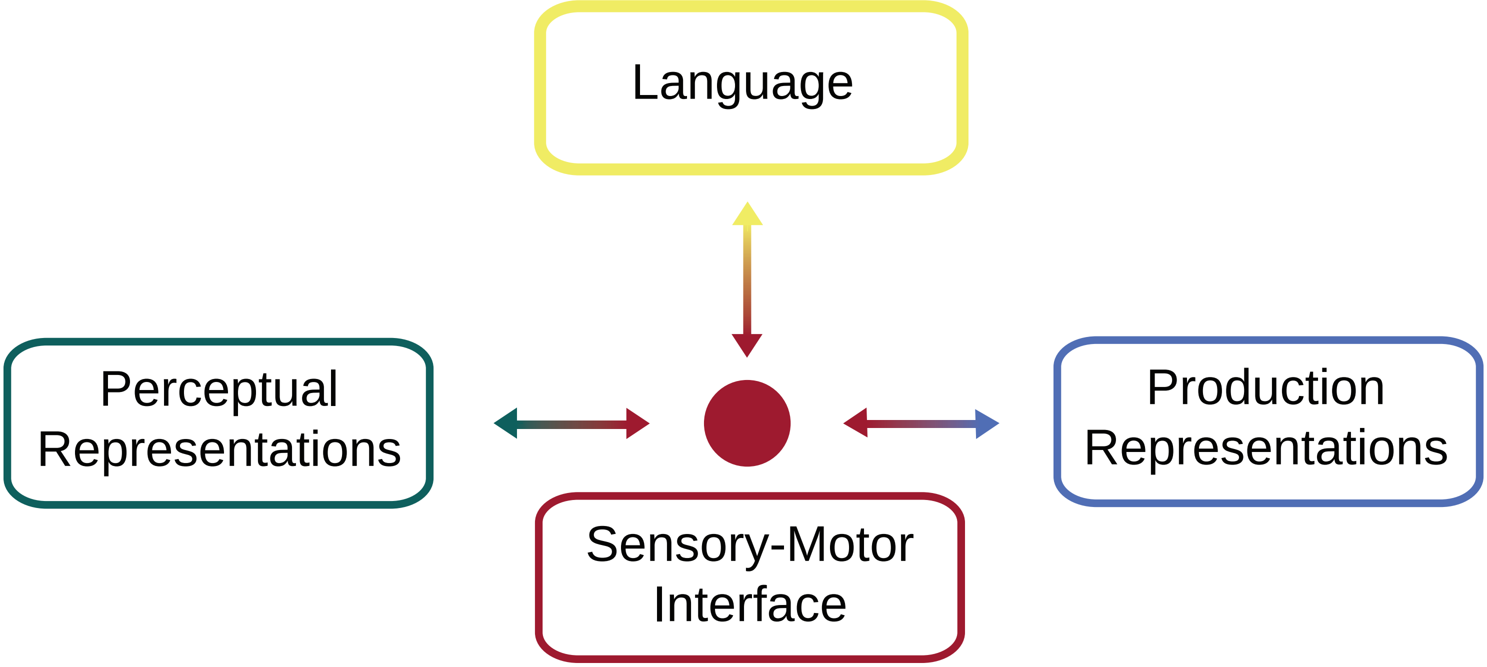

Figure S9: Model of Sensory-Motor Interface. Perceptual representations (green) and production representations (blue) intersect at the sensory-motor interface (red). The underlying Sensory-Motor system supports this representation by performing a transformation from a sensory-based coordinate system to a motor-based coordinate system. This establishes parity between representations. This parity then enables unified access to centralized language computations.

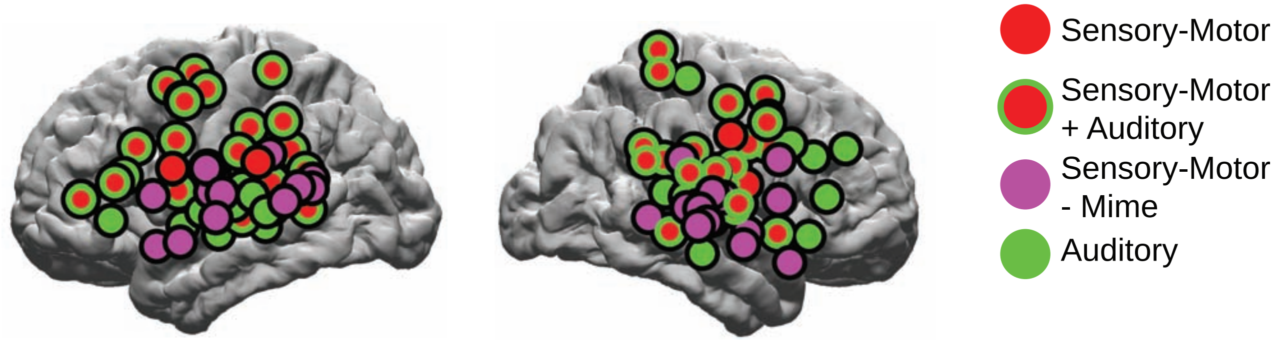

Figure S10: Validation of the Listen-Mime control. Subject average brains are show for left hemisphere (left) and right hemisphere (right) patients. S-M electrodes (red) and S-M electrodes with AUD responses (red with green outline) are shown as in **Fig 2**. S-M minus Mime (magenta) are electrodes that would be classified as S-M without the Listen-Mime control (i.e. significant activation in all three tasks during the auditory epoch and in the production epoch during Listen-Speak only), while AUD electrodes (green) shown here are the subset of AUD electrodes that still would be classified as AUD without the Listen-Mime control (i.e. no significant neural response to 'hearing your own voice'). 12/26 (46%) of AUD electrodes in the left hemisphere and 16/31 AUD electrodes (52%) in the right hemisphere would be incorrectly classified as S-M without the Mime Control (28/57 total - 49 %).

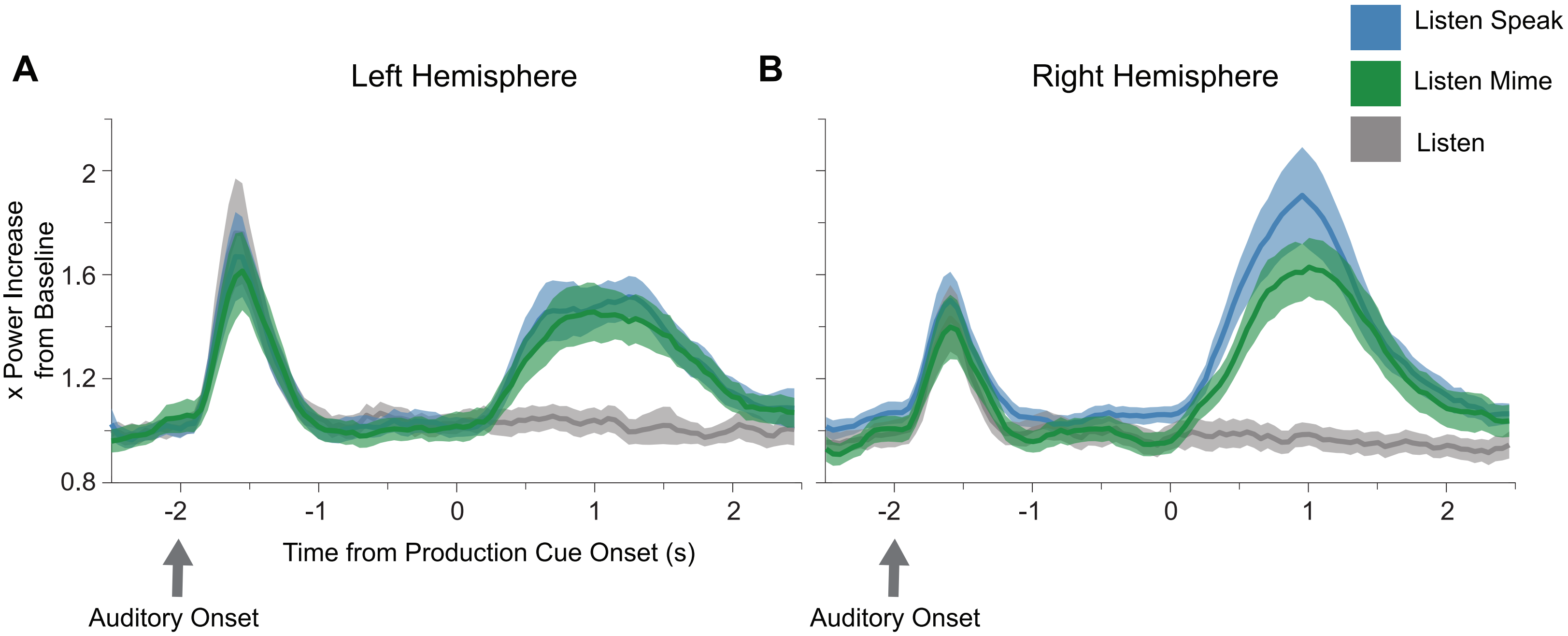

Figure S11: High gamma (70-90 Hz) power for each hemisphere. High gamma band neural activity (mean power 70 – 90 Hz) averaged across all S-M electrodes. **A)** Left hemisphere and **B)** Right Hemisphere. Listen-Speak (light blue), Listen-Mime (green), and Listen (gray). Activation after the auditory stimulus is not significantly different in all three conditions (FDR-corrected permutation test). Power within each task epoch for Listen-Speak task and the Listen-Mime task did not differ either within or between hemispheres. Power for the Listen task was significantly lower in both hemispheres in the production epoch only. The gray arrows denote the onset of the auditory stimulus. The shaded portions are the standard error of the means (SEM).

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