

Neuropsychologia

“Neural dynamics supporting longitudinal plasticity of action naming across languages: MEG evidence from bilingual brain tumor patients”

--Manuscript Draft--

Manuscript Number:	NSY-D-22-00404R1
Article Type:	Research Paper
Section/Category:	Language
Keywords:	brain tumors; Bilingualism; Action semantics; Speech production; Oscillations; MEG
Corresponding Author:	Lucia Amoruso Basque Center on Cognition Brain and Language San Sebastian, SPAIN
First Author:	Shuang Geng
Order of Authors:	Shuang Geng Quiñones Ileana Santiago Gil Robles Iñigo Pomposo Garazi Bermudez Polina Timofeeva Nicola Molinaro Manuel Carreiras Lucia Amoruso
Abstract:	<p>Previous evidence suggests that distinct ventral and dorsal streams respectively underpin the semantic processing of object and action knowledge. Recently, we found that brain tumor patients with dorsal gliomas in frontoparietal hubs show a selective longitudinal compensation (post- vs. pre-surgery) during the retrieval of lexico-semantic information about actions (but not objects), indexed by power increases in beta rhythms (13-28 Hz). Here, we move one-step further and ask whether a similar organizational principle also stands across the different languages a bilingual speaks. To test this hypothesis, we combined a picture-naming task with MEG recordings and evaluated highly proficient Spanish-Basque bilinguals undergoing surgery for tumor resection in left frontoparietal regions. We assessed patients before and three months after surgery. At the behavioral level, we observed a similar performance across sessions irrespectively of the language at use, suggesting overall successful function preservation. At the oscillatory level, we found longitudinal selective power increases in beta for action naming in Spanish and Basque. Nevertheless, tumor resection triggered a differential reorganization of the L1 and the L2, with the latter one additionally recruiting the right hemisphere. Overall, our results provide evidence for (i) the specific involvement of frontoparietal regions in the semantic retrieval/representation of action knowledge across languages; (ii) a key role of beta oscillations as a signature of language compensation and (iii) the existence of divergent plasticity trajectories in L1 and L2 after surgery. By doing so, they provide new insights into the spectro-temporal dynamics supporting postoperative recovery in the bilingual brain.</p>

Title: “Neural dynamics supporting longitudinal plasticity of action naming across languages: MEG evidence from bilingual brain tumor patients”

Authors: Shuang Geng ^{1,2}, Ileana, Quiñones ¹, Santiago Gil Robles ^{3,4}, Iñigo Pomposo ⁴, Garazi Bermudez ⁴, Polina Timofeeva ^{1,2}, Nicola Molinaro ^{1,2,5}, Manuel Carreiras ^{1,2,5} & Lucia Amoruso ^{1,5,6} *

¹ Basque Center on Cognition, Brain and Language (BCBL); San Sebastian, Spain

² Universidad del País Vasco (UPV/EHU); San Sebastian, Spain

³ Hospital Quiron, Madrid, Spain;

⁴ BioCruces Research Institute, Bilbao, Spain,

⁵ Ikerbasque, Basque Foundation for Science; Bilbao, Spain

⁶ Cognitive Neuroscience Center (CNC), Universidad de San Andrés, Buenos Aires, Argentina

* Corresponding author:

Lucia Amoruso

l.amoruso@bcbl.eu

Basque Center on Cognition, Brain, and Language

Paseo Mikeletegi 69, 2nd floor

20009 Donostia/San Sebastian - Spain

Highlights

- Object and action knowledge are handled via distinct ventral and dorsal systems
- Bilingual patients with dorsal tumors show selective compensation for action naming
- Longitudinal compensation is indexed by power increases in beta rhythms (13-28 Hz)
- Tumor resection triggers a differential postoperative reorganization of L1 and L2
- L2 additionally recruits the right contra-lesional hemisphere after surgery

Abstract

1
2 Previous evidence suggests that distinct ventral and dorsal streams respectively underpin the
3
4 semantic processing of object and action knowledge. Recently, we found that brain tumor
5
6 patients with dorsal gliomas in frontoparietal hubs show a selective longitudinal compensation
7
8 (post- vs. pre-surgery) during the retrieval of lexico-semantic information about actions (but
9
10 not objects), indexed by power increases in beta rhythms (13-28 Hz). Here, we move one-step
11
12 further and ask whether a similar organizational principle also stands across the different
13
14 languages a bilingual speaks. To test this hypothesis, we combined a picture-naming task with
15
16 MEG recordings and evaluated highly proficient Spanish-Basque bilinguals undergoing
17
18 surgery for tumor resection in left frontoparietal regions. We assessed patients before and three
19
20 months after surgery. At the behavioral level, we observed a similar performance across
21
22 sessions irrespectively of the language at use, suggesting overall successful function
23
24 preservation. At the oscillatory level, we found longitudinal selective power increases in beta
25
26 for action naming in Spanish and Basque. Nevertheless, tumor resection triggered a differential
27
28 reorganization of the L1 and the L2, with the latter one additionally recruiting the right
29
30 hemisphere. Overall, our results provide evidence for (i) the specific involvement of
31
32 frontoparietal regions in the semantic retrieval/representation of action knowledge across
33
34 languages; (ii) a key role of beta oscillations as a signature of language compensation and (iii)
35
36 the existence of divergent plasticity trajectories in L1 and L2 after surgery. By doing so, they
37
38 provide new insights into the spectro-temporal dynamics supporting postoperative recovery in
39
40 the bilingual brain.
41
42
43
44
45
46
47
48
49

50
51
52
53
54
55 **Key words:** Brain tumors, Bilingualism, Action semantics, Speech production, Oscillations,
56
57 MEG

1. Introduction

Semantic processing is central to everyday life as it allows humans to fluently manipulate stored knowledge and build meaning on the fly, thus supporting essential communicative functions such as language production and comprehension.

Mounting evidence from behavioral, neurophysiological and imaging studies in healthy individuals and brain tumor patients (Amoruso et al., 2021; Gleichgerrcht et al., 2016; Shapiro, Moo, & Caramazza, 2006; Vigliocco, Vinson, Druks, Barber, & Cappa, 2011) suggests that the semantic representation/retrieval of object and action knowledge is underpinned via partially distinct ventral and dorsal systems respectively involving inferotemporal and frontoparietal nodes. Interestingly, studies using electrical stimulation for intraoperative language mapping during awake brain surgery support this category-based segregation, showing greater number of errors for objects when stimulating temporal regions; and greater number of errors for actions when disrupting activity in prefrontal and parietal cortices (Corina et al., 2005; Corina et al., 2010; Lubrano, Filleron, Demonet, & Roux, 2014; Ojemann, Ojemann, & Lettich, 2002).

In a recent study (Amoruso et al., 2021), we recorded magnetoencephalographic (MEG) activity in healthy controls and patients with low-grade gliomas (LGGs) compromising either ventral or dorsal brain regions while performing a picture-naming task including object and action stimuli. Patients were evaluated in a longitudinal fashion, namely before and after surgery for tumor resection. Results from controls showed segregated beta (13–28 Hz) power decreases in left ventral and dorsal streams for object and action naming, respectively; in a time-window classically associated to lexico-semantic retrieval (~250–500ms). When longitudinally comparing patients' oscillatory MEG responses we found post-surgery beta (13–28 Hz) modulations mimicking the category-based segregation showed by healthy controls, with ventral and dorsal damage leading to selective compensation for object and action naming.

1 Overall, our previous findings provided evidence for the existence of two separable object vs.
2 action semantics subsystems, and pointed to a key involvement of beta oscillations as a
3 signature of adaptive compensation in brain tumor patients.
4
5
6

7
8 Yet, information about language reorganization and oscillatory compensation in bilingual
9 speakers harboring brain tumors is scarce. Specifically, the question of whether and to what
10 extent semantic knowledge is integrated across languages in the bilingual brain is a topic of
11 debate. For instance, it has been suggested that the degree of overlapping across semantic
12 representations varies depending on variables such as age of acquisition (AoA) and language
13 proficiency. In other words, the earlier and more accurately a second language (L2) develops,
14 the more likely it will recruit the same neural devices responsible for the first language (L1)
15 (Abutalebi, 2008; Abutalebi & Green, 2007; Paradis, 2000; Perani & Abutalebi, 2005). Indeed,
16 it has been shown that as proficiency improves, L2 conceptual representations become
17 semantically processed in the same way as in the L1 (Hut & Leminen, 2017). Furthermore,
18 imaging (Consonni et al., 2013; Hernandez, Dapretto, Mazziotta, & Bookheimer, 2001; Willms
19 et al., 2011) and neurophysiological (Geng et al., 2022) evidence indicates that object-action
20 distinctions are sustained by common neuroanatomical and oscillatory components across the
21 two languages a proficient bilingual speaks, further supporting the existence of shared semantic
22 sub-systems across L1 and L2, at least when both are mastered in a native-like fashion.
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42

43
44 Given this evidence, in the present study we wanted to move one-step further and test the
45 hypothesis that the semantic representation/retrieval of action-based knowledge is mainly
46 supported via the dorsal stream and overlaps across the two languages a highly proficient
47 bilingual speaks. To this end, we focused on brain tumor patients with dorsal lesions in fronto-
48 parietal hubs as an experimental model. More specifically, we combined an object/action
49 picture-naming task (Gisbert-Munoz et al., 2021) with MEG recordings and longitudinally
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

1 evaluated (i.e., before and three months after surgery) four highly proficient Spanish-Basque
2 bilinguals undergoing surgery for tumor resection.
3

4 Overall, given the involvement of the dorsal pathway in action processing, we expected to find
5 a selective post-surgery compensation in beta rhythms (13-28 Hz) for the retrieval of action
6 (but not object) knowledge (Amoruso et al., 2021). More critically to the present study, we
7 expected to extend this evidence to bilingual patients and to find similar patterns of adaptive
8 compensation across L1 and L2, indicating language-invariant semantic processing in the
9 bilingual brain.
10
11
12
13
14
15
16
17
18
19
20
21
22
23

24 **2. Materials and Methods**

25 *2.1. Participants*

26 Four highly proficient Spanish-Basque bilingual patients with low-grade gliomas (LGGs) in
27 left fronto-parietal regions took part in this study (see Figure 1 for lesion profile). Patient's
28 demographics, clinical information and lesion characteristics are summarized in Table 1. All
29 patients were recruited at the Cruces University Hospital (Bilbao, Spain) where they received
30 their diagnosis and performed the awake brain surgery for tumor resection. The initial
31 neurological exploration at the hospital revealed no severe motor, somatosensory, or linguistic
32 deficits thus qualifying for the awake brain surgery procedure. Admission diagnoses were
33 weakness/sensory loss in the contralesional leg in patients 1, 2 and 4; and seizure in the case
34 of patient 3.
35
36
37
38
39
40
41
42
43
44
45
46
47
48

49 Patients were evaluated in two sessions: a first session one week before the surgery, and a
50 second session approximately three/four months after the surgery. In each session, behavioral,
51 MEG and structural MRI data were collected.
52
53
54

55 In addition, healthy-control data from sixteen highly proficient Spanish-Basque bilinguals (4
56 men, Mean age = 25.87; SD = 5.25) performing the same picture-naming task were reutilized
57
58
59
60
61
62
63
64
65

1 from a previous study (Geng et al., 2022). This provided a baseline to compare with patient's
2 data and to assist the interpretation of potential divergent patterns indicating language
3 reshaping/compensation in patients.
4
5

6
7 All participants were right-handed as assessed via the Edinburgh Handedness Inventory
8 (Oldfield, 1971), had normal hearing and normal or corrected to normal vision. The study
9 protocol was conducted in accordance to the Declaration of Helsinki for experiments involving
10 humans, and approved by the Ethics Board of the Euskadi Committee and the Ethics and
11 Scientific Committee of the BCBL (protocol code PI2020022). Informed consents were
12 obtained from all participants involved in the study before the experiment.
13
14
15
16
17
18
19
20
21
22
23

24 *2.2. Cognitive and linguistic assessment*

25
26 A battery of standardized neuropsychological and linguistic tests was used to longitudinally
27 evaluate participants on relevant linguistic and cognitive abilities. This battery included
28 measures of general cognitive status as assessed via means of the 30-point screening Mini-
29 Mental State Examination (MMSE) (Folstein, Folstein, & McHugh, 1975); verbal and non-
30 verbal intelligence measured using the KBIT (Kaufman & Kaufman, 2013), and language
31 production in Spanish and Basque via means of the BEST test (de Bruin, Carreiras, &
32 Dunabeitia, 2017).
33
34
35
36
37
38
39
40
41
42

43 *2.3. Picture-naming task*

44
45 Language production was assessed using MULTIMAP, a multilingual picture-naming task for
46 mapping eloquent areas during awake surgeries (Gisbert-Munoz et al., 2021). Briefly,
47 MULTIMAP consists of an open access database of standardized color pictures representing
48 both objects and actions. These images have been tested for relevant linguistic features in cross-
49 language combinations including Spanish and Basque. Target words were matched on
50 frequency, familiarity, number of orthographic neighbors, length and name agreement (i.e.,
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

1 higher than 80 %). Importantly, this task has been previously used to investigate the brain
2 mechanisms underlying bilingual language production in neurotypical (Geng et al., 2022) and
3 brain tumor populations (Quinones, Amoruso, Pomposo Gastelu, Gil-Robles, & Carreiras,
4 2021).
5
6
7

8
9 In separate blocks, participants were instructed to observe the pictures and name them overtly
10 in Spanish or Basque as quickly and accurately as possible. Trials started with a fixation cross
11 in the center of the screen lasting for 1 sec, followed by the picture displayed for 2 secs. ISI
12 randomly varied between 3 and 4 secs. A total of 88 picture items (i.e., 44 for objects and 44
13 for actions) were used. Each picture was presented twice for a total of 176 trials per condition.
14
15 Each block lasted ~ 15 min, and participants were allowed to take a short break between them.
16
17 Above each object, we added the text “Esto es...” or “Hori da...” (“This is...” in Spanish and
18 Basque, respectively) to force participants to produce a short sentence that agreed in number
19 and gender with the target noun. In the case of the action pictures, we included a pronominal
20 phrase to be used as the subject of the sentence, namely “El/Ella...” or “Hark...” (“He/She...”
21 in Spanish and Basque, respectively). This introductory text cue was used to trigger the
22 production of a sentence that began with the given subject and had a finite verb form in the
23 third person singular. See Figure 2.
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39

40 Participants’ responses were recorded to estimate accuracy and naming latencies. We used
41 MATLAB version 2012b and Cogent Toolbox (<http://www.vislab.ucl.ac.uk/cogent.php>) to
42 present the images. Stimuli, Matlab script, and its compiled version are available at
43 <https://git.bcbl.eu/sgisbert/multimap2>.
44
45
46
47
48
49
50

51 *2.4. MEG and MRI data acquisition*

52 MEG signals were recorded in a magnetically shielded room by means of a 360-channel Elekta
53 -Neuromag system (360-channels, Helsinki, Finland). Signals were acquired continuously at a
54 sampling rate of 1 kHz and online filtered between 0.1–330 Hz. Eye movements (EOG) were
55
56
57
58
59
60
61
62
63
64
65

1 monitored using in a bipolar montage placed on the external canthi of each eye (horizontal
2 EOG) and above and below the right eye (vertical EOG). Cardiac activity (ECG) was
3
4 monitored as well by positioning an electrode below the right clavicle and another under the
5
6 left rib bone.
7

8
9 Participant's head position inside the helmet was tracked during the recording session with five
10
11 head position indicator (HPI) coils. The location of each coil relative to standard anatomical
12
13 fiducials (i.e., nasion, left, and right pre-auricular points) was defined with a 3D digitizer
14
15 (Fastrak Polhemus, Colchester, VA). In addition, ~300 points were digitalized over the scalp
16
17 and eyes/nose contours to subsequently align the MEG sensor coordinates space to the
18
19 participant's T1 MRI.
20
21
22

23
24 All participants underwent an MRI session separated in time from the MEG session by at least
25
26 two days in a 3T Siemens Magnetom Prisma Fit scanner (Siemens AG, Germany). High-
27
28 resolution T1- and T2-weighted images were acquired with a 3D ultrafast gradient echo
29
30 (MPRAGE) pulse sequence using a 64-channel head coil with the following acquisition
31
32 parameters: FOV = 256; 160 contiguous axial slices; voxel resolution 1x1x1mm³; TR =
33
34 2530ms, TE = 2.36ms, flip angle = 7°. For each patient, the origin of the T1/T2 weighted
35
36 images (pre- and post-surgery) was set to the anterior commissure. Functional event-related
37
38 scans consisting of 320 echo-planar images were acquired using a T2*-weighted gradient-echo
39
40 pulse sequence with the following parameters: field of view: 192 mm; matrix = 64 x 64; echo
41
42 time = 30ms; repetition time = 2 s; flip angle = 90 degrees. The volume was comprised of 33
43
44 axial slices with 3 mm isotropic voxels without slice gap. The first six volumes of each
45
46 functional run were discarded to ensure steady-state tissue magnetization.
47
48
49
50
51
52

53 54 55 *2.5. Lesion mapping*

56
57 Lesions were manually drawn using the MRICron software (Rorden, Karnath, & Bonilha, 2007)
58
59 on the native space of participants' T1-weighted MPRAGE image by one of the neurosurgeons
60
61
62
63
64
65

1 in charge of the patients' awake craniotomy (Garazi Bermudez). In addition, information from
2 T2-weighted images was used when lesion boundaries were not clear in the T1. The lesion was
3 then normalized to the MNI template and one of the authors (Ileana Quiñones) checked
4 alignment between the delignated lesion and the lesion in the native space. A volume of interest
5 (VOI) was created for each patient at each time point (i.e., pre- and post-surgery). Extent of
6 resection (EOR; in cm³) was measured on postoperative imaging as: (Volume of (preoperative
7 3D Tumor Reconstruction \cap postoperative Resection)*100/preoperative tumor volume).
8
9

10 11 12 13 14 15 16 17 18 *2.6. Behavioural data analysis*

19 Participant's vocal responses were recorded and monitored online by a research assistant during
20 the task. An open-source in-house software ("SPONGE", available at
21 https://github.com/Polina418/Audio_processing) was used to decode and convert the audio
22 files into .wav format and semi-automatically detect speech onsets. Reaction times were
23 measured as the interval between picture presentation and the onset of participant's verbal
24 response. Erroneous responses or utterances containing disfluencies were excluded from the
25 final analyses. Reaction times (RTs) and naming accuracies from individual patients were
26 analyzed using Crawford-Howell (1998) frequentist *t*-tests for single-case analysis, and
27 compared to the control group. This analysis was implemented on RStudio (Version 1.2.5019)
28 using the psycho Package (Makowski, 2018).
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45

46 *2.7. MEG data preprocessing*

47 Continuous MEG data were pre-processed off-line by means of the spatio-temporal signal
48 space separation (tSSS) method (Taulu & Simola, 2006) implemented in Maxfilter 2.2 (Elekta-
49 Neuromag) to subtract the external magnetic noise and correct for participants' head
50 movements. Subsequent analyses were performed using the MatlabR_2014B (The
51 MathWorks, Inc., Natick, Massachusetts, United States) and FieldTrip Toolbox [version
52
53
54
55
56
57
58
59
60
61
62
63
64
65

20170911] (Oostenveld, Fries, Maris, & Schoffelen, 2011). Recordings were down-sampled to 500 Hz and segmented into trials time-locked to picture onset, ranging from 500 ms before to 1000 ms after image onset. A semi-automatic procedure was used to remove trials containing electromyographic artifacts, SQUID jumps, and flat signals. Then, heartbeat and EOG artifacts were detected via means of a fast independent component analysis (FastICA) (Hyvarinen, 1999; Jung et al., 2000) and were linearly subtracted from the recordings. Across participants, the number of heartbeat and EOG components that were removed varied from 1–3 and 1–2 components, respectively.

2.8. MEG sensor-level analysis

Time-frequency representations (TFRs) were calculated on the clean MEG segments. Specifically, we focused on the beta band (13-28 Hz). This choice was methodologically motivated by previous findings from our group (Amoruso et al., 2021), showing that brain tumor patients show longitudinal language plasticity in this frequency band using a similar speech production task. TFRs were obtained using a Hanning tapers approach and a fixed window length of 500 ms, advancing in 10 ms steps, resulting in a 2 Hz frequency resolution. Power was separately estimated for each orthogonal direction of a gradiometer pair and further combined, for a total of 102 measurement sensors. Power was calculated as the relative change with respect to a ~500 ms pre-stimulus baseline. Statistical differences in spectral power between conditions were evaluated using cluster-based permutation tests (Maris & Oostenveld, 2007).

We averaged over frequency bins of interest (13-28 Hz; central frequency = 20.71 Hz) and tested a time-window from 100 ms to 600 ms after picture onset. This time-window was chosen based on methodological constraints imposed by the overt nature of the task, data inspection and neurophysiological evidence from previous studies using this picture naming task (Amoruso et al., 2021; Geng et al., 2022; Quinones et al., 2021), suggesting that recordings not

1 contaminated with articulatory activity can be safely acquired around these time points. The
2 permutation p -value was obtained with the Monte-Carlo method, using 1,000 random
3 permutations. The alpha threshold for significance testing was a p -value below 5% (two-tailed).
4
5
6

7 *2.9. Source activity estimation*

8 Individual T1-weighted MRI images were segmented into the scalp, skull, and brain
9
10 components using the Freesurfer software (Reuter et al. 2012). Co-registration between the
11 MEG sensor space and participant's MRI coordinates was done by manually aligning the
12 digitized points from the Polhemus to the outer scalp surface using the Neuromag tool MRILab
13 (Elekta Neuromag Oy, version 1.7.25). The lead field matrix was computed using the Boundary
14 Element Method (BEM) model implemented in MNE suite (RRID: SCR_005972) (Gramfort
15 et al., 2014), for three orthogonal tangential current dipoles, placed on a homogeneous 5-mm
16 grid. The forward model was then reduced to the two principal components of the highest
17 singular value for each source, corresponding to sources tangential to the skull. All sensors
18 (i.e., gradiometers and magnetometers) were used for source estimation, normalizing the signal
19 of each sensor by its noise variance considering a baseline period before picture onset. Cortical
20 sources of the MEG signal were estimated using a Linearly Constrained Minimum Variance
21 (LCMV) beamformer approach (Van Veen, van Drongelen, Yuchtman, & Suzuki, 1997). The
22 covariance matrix used to derive beamformer weights was computed from the time-frequency
23 window of the significant sensor-level effects and an equally sized baseline period prior to
24 picture onset. To perform group-level analysis, brain maps were transformed from the
25 individual MRIs to the standard Montreal Neurological Institute (MNI) by applying a nonlinear
26 space transformation algorithm implemented in Statistical Parametric Mapping (SPM8,
27 Wellcome Department of Cognitive Neurology).
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54

55 Finally, statistical comparisons between conditions were performed with the location-
56 comparison method (Bourguignon, Molinaro, & Wens, 2018), which has shown to be robust
57
58
59
60
61
62
63
64
65

1 in dealing with spectral leakage problems. This method generates bootstrap group-averaged
2 maps to build a permutation distribution of location difference between local maxima in the
3 two conditions being compared and tests the null hypothesis that distance between them is zero.
4
5 Local maxima are defined as sets of contiguous voxels displaying higher power than all other
6
7 neighboring voxels. The threshold at $p < 0.05$ was estimated as the 95 percentile of the sample
8
9 distribution. All supra-threshold local MEG peaks were interpreted as indicative of brain
10
11 regions likely contributing to the sensor-level effects.
12
13
14
15
16
17
18
19
20

21 **3. Results**

22 *3.1. Cognitive and linguistic results*

23 Individual longitudinal changes in neurocognitive variables are shown in Figure 3. Results
24 indicated that all patients preserved linguistic function in both languages after surgery as well
25 as their cognitive status. Specifically, in the case of Spanish, all patients exhibited ceiling
26 accuracy before and after surgery. For Basque, P2 and P4 performed better after surgery while
27 patients P1 and P3 showed a marginal post-surgery decrease in accuracy. None of the patient's
28 values significantly differed from the control group (Spanish mean value = 98%; Basque mean
29 value = 89%) either before (all $ps > 0.1$) or after the surgery (all $ps > 0.3$), as indicated by
30 Crawford t -tests. In the case of the MMSE, some patients obtained similar maximal scores
31 across sessions (e.g., P2, P3 and P4), while P1 showed a marginal lower score after surgery.
32
33 Nevertheless, across sessions, all patients scored between 30–27, which is considered the
34
35 normal range when evaluating cognitive impairments.
36
37
38
39
40
41
42
43
44
45
46
47
48
49

50 Finally, for the KBIT, P1 and P2 exhibited identical scores across sessions, while patients P3
51 and P4 showed a considerable improvement after surgery.
52
53
54
55
56
57
58

59 *3.2. Behavioral results*

1 Table 2 shows mean accuracy and reaction time values (RT) for each patient, as well as *p*-
2 values for the Crawford-Howell *t*-tests comparing individual patients against the control group.
3
4 Overall, no significant differences were observed in accuracy and RTs, which speaks in favor
5
6 of successful language compensation. Only P2 showed a significant lower performance in
7
8 naming accuracy for actions in Basque after surgery. Nevertheless, his performance was still
9
10 very good (i.e., ~92%).
11
12
13
14
15
16
17

18 3.2. MEG results

19
20 The longitudinal contrasts (post vs. pre-surgery) performed for each naming condition (objects
21
22 and actions) and language (Spanish and Basque) in the beta frequency band (13-28 Hz) showed
23
24 specific significant effects for actions in both languages (all Monte Carlo *ps* = 0.002, two
25
26 tailed). No significant differences were observed for the object naming condition (all Monte
27
28 Carlo *ps* > 0.45, two tailed). Figure 4A shows time-resolved spectra of the action naming
29
30 longitudinal contrast for each language. In the case of Spanish, beta power modulations across
31
32 sessions were highlighted by a positive cluster between ~310-500 ms in left middle-frontal
33
34 sensors. In the case of Basque, the positive cluster was evident between ~180-600 ms and
35
36 comprised left frontal sensors and right fronto-parietal ones. Source localization results (Fig.
37
38 4B) indicated that the longitudinal action effect for Spanish mainly originated in premotor and
39
40 inferior frontal regions of the left hemisphere. The same effect in Basque, showed a similar
41
42 involvement of left premotor cortex but with the additional recruitment of parietal and premotor
43
44 regions in the right hemisphere.
45
46
47
48
49

50
51 Overall, in line with previous evidence for a similar longitudinal contrast in patients with dorsal
52
53 gliomas (Amoruso et al., 2021), we observed beta power increases after the surgery along with
54
55 preserved cognitive and linguistic abilities. Importantly, the direction of the action post- vs.
56
57
58
59
60
61
62
63
64
65

1 pre-surgery effect was consistent at the individual patient's level, namely all patients showed
2 stronger beta power increases after tumor removal.
3

4
5 Then, we reused MEG data from a previous study (Geng et al., 2022) in which a group of
6 healthy highly proficient bilinguals ($n = 16$) performed the same picture-naming task and
7 estimated beta networks involved in action naming for Spanish and Basque, to better
8 understand patterns of potential reshaping in patients. Healthy controls showed similar negative
9 clusters in the beta band (13-28 Hz) for action naming vs. baseline in Spanish (between ~180-
10 500 ms) and Basque (between ~300-500 ms) over bilateral posterior, left parieto-temporal and
11 frontal sensors (all Monte Carlo $ps = 0.004$, two-tailed). See Figure 5. This effect mainly
12 originated in a left-lateralized network comprising superior parietal, premotor and inferior
13 frontal regions, as well as bilateral visual associative areas. Importantly, the contrast between
14 languages did not yield significance, suggesting that action knowledge is similarly processed
15 in the healthy bilingual brain.
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31

32
33 Contrariwise, a significant language effect (Spanish vs. Basque; Monte Carlo p -value = 0.002,
34 two tailed) was observed for action naming in the group of patients after the surgery. This effect
35 was highlighted by a negative cluster in right parieto-temporal sensors, showing less beta
36 power (13-28 Hz) for Spanish as compared to Basque between ~390-600 ms (see Fig.6A).
37
38 Source localization results indicated that the post-surgery language effect originated in parietal,
39 superior temporal and prefrontal regions of the right hemisphere (see Fig. 6B). No significant
40 language differences were observed for action naming prior to the surgery. In addition, no
41 significant differences were observed for either pre- or post-surgery sessions in the case of
42 objects (all Monte Carlo $ps > 0.12$, two tailed).
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

1 Overall, the finding of a significant language effect over right sensors after surgery is in contrast
2 with the results of the control group, for whom no significant differences across languages were
3 observed. This may suggest that while comparable adaptive compensation for processing
4 action knowledge is present across languages before surgery (i.e., indicating language-
5 invariant semantic processing similar to controls); tumor removal can prompt out different
6 patterns of functional reorganization in the L1 and L2.
7
8
9
10
11
12
13
14
15
16
17

18 **4. Discussion**

19 In the present study, we focused on highly proficient Spanish-Basque bilinguals harboring
20 brain tumors in dorsal frontoparietal nodes to investigate (i) whether compensatory
21 longitudinal changes in beta rhythms (13-28 Hz) specifically target action naming and, more
22 critical to our hypothesis, (ii) whether this compensation similarly stands across the two
23 languages a bilingual patient speaks. In keeping with previous findings, we replicated the
24 existence of longitudinal compensation in the beta band, reflected in power increases along
25 with preserved behavioral performance in picture naming. As expected, this oscillatory effect
26 was specifically observed for the action naming condition and was present in both Spanish and
27 Basque, thus supporting the engagement of the dorsal stream in the semantic
28 retrieval/representation of action knowledge across languages. Another critical finding
29 emerged when contrasting action naming between a group of healthy bilinguals and the group
30 of patients (separately within pre- and post-surgery sessions). Prior to the surgery, healthy
31 controls and patients showed no differences across languages, likely indicating language-
32 invariant semantic processing across L1-L2. However, after the surgery, patients exhibited beta
33 power differences between Spanish and Basque in the right hemisphere, suggesting that tumor
34 removal triggered a differential reorganization of the L1 and the L2.
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

4.1. *Lexico-semantic compensation of action naming in bilingual patients with dorsal gliomas*

Previous evidence indicates that the semantic processing of object and action knowledge can be partially dissociated in ventral and dorsal functional networks, respectively (Gleichgerrcht et al., 2016; Kemmerer, 2014; Shapiro et al., 2006; Shapiro et al., 2005). Furthermore, this category-based segregation has been also reported in bilingual speakers (Consonni et al., 2013; Geng et al., 2022; Willms et al., 2011), suggesting the existence of semantic language-invariant systems across L1-L2 supporting object/action dissociations. In line with this evidence, we show that frontoparietal regions in the dorsal stream are critical for processing action-related meaning across the two languages a bilingual speaks and that the resection of tumors affecting dorsal areas lead to a selective compensation for the lexico-semantic processing of action material. Furthermore, we show that this compensation is successful in preserving action naming in L1 and L2, giving the absence of severe production impairments across languages either before or after the surgery.

These findings raise the question of which neuroplasticity mechanisms may have favored language preservation. It has been shown that gliomas can alter functional connectomics profiles and affect global network communication (Cargnelutti, Ius, Skrap, & Tomasino, 2020; Duffau, 2020). In this context, different compensatory strategies can be called into play, including the recruitment of peritumoral tissue, the engagement of secondary ipsilateral regions functionally connected to areas close to the tumor (or its cavity) as well as contralateral homologues, typically in the right hemisphere (Duffau, 2005, 2020; Duffau et al., 2003). Furthermore, plasticity can be seen as a multistage process, firstly occurring preoperatively due to tumor growth and secondly, postoperatively, with reorganization triggered by the surgical trauma itself. Indeed, preoperative plasticity can be damaged during the surgery, and thus a subsequent development and/or reinforcement of reshaping mechanisms is necessary to explain

1 patient's recovery after the intervention (Duffau et al., 2003; Robles, Gatignol, Lehericy, &
2 Duffau, 2008).

3
4 In the present study, we focused on this latter aspect, namely the functional compensation
5 resulting from tumor removal as compared to its presence before surgery. In keeping with
6 previous findings (Amoruso et al., 2021), longitudinal compensation was indexed by post-
7 surgery power increases in the beta band (13–28 Hz). This effect was true for both Spanish and
8 Basque and consistent at the individual patient's level.

9
10 Beta rhythms are one of the most intriguing oscillations in the brain, supporting a wide range
11 of cognitive functions. So far, several accounts have been advanced to explain their mechanistic
12 role in humans. From a general standpoint, beta synchronization has been associated to network
13 dynamics involved in the (re)activation of cortical representations (Spitzer & Haegens, 2017).
14 Similarly, in the language domain, Weiss and Mueller (2012) have proposed that beta
15 enhancement serves to bind distributed sets of neurons into a meaningful representation of
16 memorized contents. Briefly, according to the authors, this will explain how the brain integrates
17 information processed at different timescales and in separate neural regions in order to
18 produce/understand a coherent speech unit. Interestingly, a critical aspect that both views
19 underscore is the role of beta rhythms in facilitating functional networking in the brain. This
20 aligns well with computational frameworks (Kopell, Ermentrout, Whittington, & Traub, 2000;
21 Sherman et al., 2016), suggesting that beta oscillations can synchronize at long conduction
22 delays, enabling high-level interactions between spatially distant brain areas. This property
23 becomes even more critical when considering that functional reshaping triggered by gliomas
24 can affect network-level communication and potentially involve the compensatory recruitment
25 of remote areas in the contralateral hemisphere. This aspect makes beta a plausible candidate
26 to support reallocation of linguistic functions and is consistent with neurophysiological
27 evidence from stroke and brain tumor patients (Kielar, Deschamps, Jokel, & Meltzer, 2016;
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

1 Piai, Meyer, Dronkers, & Knight, 2017; Traut et al., 2019) showing a shift of language
2 processing to the right hemisphere mediated by low frequency bands, including beta.
3

4 While our study mainly focused on beta rhythms, we acknowledge that other oscillatory
5 changes may have occurred in response to the surgery. For instance, recent evidence indicates
6 that bilingual patients with left LGGs can exhibit a rightward shift of parietal alpha (8-12 Hz)
7 oscillations specifically related to L2 processing (Quinones et al., 2021). This effect could
8 indicate the presence of different cognitive demands when processing L2 representations.
9 Indeed, previous studies have linked right parietal alpha activity to increased load during
10 cognitive control (Obleser, Wostmann, Hellbernd, Wilsch, & Maess, 2012) and, in particular,
11 to language control in bilinguals (Bice, Yamasaki, & Prat, 2020; Tao, Wang, Zhu, & Cai,
12 2021).
13
14
15
16
17
18
19
20
21
22
23
24

25 26 27 28 *4.2. Postoperative differences in L1 and L2 reshaping in bilingual patients*

29 Nevertheless, it is worth noting that even though beta effects were present in both languages,
30 longitudinal patterns for Spanish and Basque differed in terms of timing, scalp and source
31 location. Indeed, while Spanish showed a left lateralized effect in premotor and inferior frontal
32 regions, Basque additionally engaged right-hemisphere sources. To better understand this
33 differential pattern, we contrasted action naming between Spanish and Basque separately
34 before and after surgery. The same analysis was paralleled in a group of healthy Spanish-
35 Basque bilinguals to assist the interpretation of potential divergent patterns in patients.
36
37
38
39
40
41
42
43
44

45 Prior to the surgery, action naming in Spanish and Basque did not differ, indicating comparable
46 adaptive compensation for accessing action-based knowledge across languages. This finding
47 was further supported by data from controls showing overlapping oscillatory beta networks in
48 Spanish and Basque during action naming, likely indicating converging lexico-semantic
49 processing in L1 and L2. However, after the surgery, differences between languages became
50 evident. On the one hand, Basque showed higher activity in right parietal, superior temporal
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

1 and prefrontal regions contralateral to the tumor's cavity. Importantly, this rightward activation
2 was not present in healthy controls during action naming, suggesting that this set of regions
3
4 was secondary engaged to achieve accurate lexico-semantic processing of action knowledge in
5 the L2 once the tumor was resected. This is in keeping with previous findings from our lab
6
7 (Quinones et al., 2021) combining fMRI and MEG techniques to map language lateralization
8
9 in bilingual brain tumor patients and showing a stronger shift of activity toward the right
10 hemisphere for Basque as compared to Spanish after surgery.
11

12
13
14
15
16
17 On the other hand, no recruitment of the right hemisphere was observed for Spanish, which
18 instead showed more local changes in ipsilateral areas similarly recruited by controls during
19
20 action naming. Such an oscillatory pattern likely reflects the re-weighting of functional
21
22 connections between preserved healthy regions, implying that during postoperative recovery,
23
24 some of these areas become more active to support adaptive compensation (York & Steinberg,
25
26 2011).
27

28
29
30
31 It has been proposed that plasticity mechanisms follow a hierarchical organization in which the
32 recruitment of the contralesional hemisphere occurs at later stages, when other neural resources
33
34 (e.g., recruitment of perilesional tissue and/or ipsilesional areas) have been depleted. Yet, the
35
36 postoperative involvement of the right hemisphere occurred quite early in the case of Basque
37
38 (i.e., within the ~3 months following surgery; see also Quiñones et al., 2021 for a similar
39
40 finding). While there is evidence showing that contralateral plasticity can be very quickly
41
42 engaged (Duffau et al., 2003), this still leaves open the question of why this compensatory
43
44 pattern was specifically observed for the L2.
45
46
47
48
49

50
51 Previous evidence (Gatignol, Duffau, Capelle, & Plaza, 2009) indicates that L1 and L2 can
52
53 follow different postoperative trajectories in glioma patients, probably due to experiential
54
55 factors such as AoA, language's proficiency and frequency of use. For example, it has been
56
57 hypothesized that the order of postoperative language recovery mirrors the order of language
58
59
60
61
62
63
64
65

1 acquisition (Emmorey & McCullough, 2009; Galloway, 1978). In our study, all bilinguals but
2 one (patient 3) acquired Basque later than Spanish. It could be that the language acquired earlier
3 is more robustly represented in the brain and thus more easily compensated; while the one
4 acquired later may necessitates from the additional recruitment of contralateral homologues
5 —which can promote language recovery during the acute phase (Saur et al., 2006).
6
7
8
9

10 An alternative, although not mutually exclusive interpretation, is that language proficiency
11 might have also played a role. Even though all patients were balanced highly proficient
12 bilinguals, they all reported Spanish as being their L1. The engagement of control regions in
13 the right prefrontal cortex supports this view, suggesting that action naming in Basque may
14 have deployed more cognitive resources, in terms of language control (Hernandez et al., 2001)
15 and semantic monitoring (Shen, Fiori-Duharcourt, & Isel, 2016), than Spanish. This further
16 indicates that reconfigurations preserving semantic processing after surgery may involve the
17 additional engagement and/or changes in the interactions with other networks (i.e., executive
18 control network).
19
20
21
22
23
24
25
26
27
28
29
30
31
32

33 Additionally, the “frequency hypothesis” posits that, in cases of brain damage, the language
34 that is used more frequently before the illness and is more stimulated afterwards is better
35 preserved and will recover better (Gatignol et al., 2009). However, in this study, most of the
36 patients used both languages to an equal degree before and after surgery, which makes it
37 unlikely for this hypothesis to account for the observed results.
38
39
40
41
42
43
44

45 An important aspect to stress is that even Spanish and Basque differed in terms of their
46 oscillatory patterns after tumor removal, naming performance was well preserved in both
47 languages, indicating successful postoperative reorganization - albeit supported by different
48 compensatory strategies - rather than differential L1 vs. L2 deficits (Quinones et al., 2021).
49
50
51
52
53
54
55

56 We can further speculate, based on evidence from intraoperative cortical mapping in bilinguals
57 (Giussani, Roux, Lubrano, Gaini, & Bello, 2007), that while there is a common pattern of L1-
58
59
60
61
62
63
64
65

1 L2 organization in gross anatomical regions; more subtle, distinct microanatomical systems
2 can be localized within these regions for each language (Paradis, 2004). Therefore, the
3 functional connections among the Spanish and Basque microanatomical systems could have
4 been differently impacted by the surgical trauma, resulting in unique postoperative
5 compensation patterns for each language. Indeed, it has been suggested that variability in
6 network(s) reconfiguration is higher after than before tumor resection (Duffau, 2020).
7

8
9
10
11
12
13
14 As a final note, it is worth mentioning that gliomas typically show recurrence patterns in the
15 long-term follow-up after initial resection (Ferracci, Michaud, & Duffau, 2019). Additionally,
16 in many cases, tumor resection cannot be total due to the existence of residual functionality in
17 the area infiltrated by the tumor, as it was the case for one of the patients participating in the
18 present study. Thus, a multistage approach in which successive reoperations take place is
19 counseled (Robles et al., 2008), given it favors plasticity and further functional reallocation
20 away from the tumoral region. In this context, our findings of distinct L1 and L2 plasticity
21 patterns following an initial brain surgery (e.g., the differential recruitment of the contralateral
22 unaffected hemisphere) can be informative to plan follow-up strategies, as it has been shown
23 that when decreased ipsi-lesional engagement is compensated with increased contra-lesional
24 one, subsequent reoperations can be facilitated (Duffau, 2020).
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43

44 *4.3. Limitations and avenues for further research*

45 Our study is not without limitations. First, while we acknowledge that an obvious limitation of
46 our study is the small sample size ($n = 4$), it is important to note that: (i) it is quite challenging
47 to access this type of population (i.e., highly proficient bilinguals with left dorsal gliomas) and
48 obtain pre- and post-surgery measures within the same individuals; (ii) longitudinal designs,
49 like the one employed here allow each patient to be his/her own control across sessions, thus
50 reducing the confounding effect of inter-individual variability and increasing statistical power
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

1 (Zeger & Liang, 1992); (iii) appropriate Crawford *t*-tests were used to analyze data while
2 preserving the unique patterns of each individual patient; lastly (iv) the longitudinal oscillatory
3 effects found in the present study are remarkably robust at the individual patient's level (e.g.,
4 all patients show the same direction of the effect). While these aspects contribute to the
5 scientific rigor of our findings, future studies are needed to investigate whether they can be
6 replicated in larger samples.
7

8
9
10
11
12
13
14 Another potential drawback of this study is that participants were highly proficient bilinguals,
15 so it is uncertain whether the longitudinal patterns observed here would be similar (or not) in
16 individuals with other types of bilingual experience (e.g., less proficient or immersed
17 bilinguals). This is an important consideration for future research as it can provide a more
18 comprehensive understanding of whether changes in beta power can be generalized to other
19 type of bilingual populations.
20
21
22
23
24
25
26
27

28
29
30
31 Finally, our search of neural plasticity indices was circumscribed to functional compensation,
32 overlooking changes in subcortical structures which are critical in supporting reshaping at the
33 cortical level. For instance, dorsal fronto-parietal hubs are known to be subcortically connected
34 by the superior longitudinal fasciculus (SLF) (Kamali, Flanders, Brody, Hunter, & Hasan,
35 2014; Makris et al., 2005). In a previous study (Amoruso et al., 2021) testing Spanish
36 monolingual patients harboring LGGs in the left dorsal pathway, we found that post-surgery
37 beta power increases in the right hemisphere correlated with volume increases in the right SLF,
38 suggesting that functional and structural plasticity are closely intertwined. Therefore, a
39 potential area of research that could provide a deeper understanding into the mechanisms of
40 brain plasticity in bilinguals would be investigating the microstructural (e.g. FA) and
41 macrostructural properties (e.g. volume changes) of relevant white matter bundles, and how
42 they may be linked to functional changes.
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

1 Overall, we replicate previous findings supporting a key role of beta oscillations as a signature
2 of language compensation in brain tumor patients and, more importantly, we extend it to the
3 bilingual population. Furthermore, we show that bilingual patients with dorsal gliomas exhibit
4 a selective compensation for action naming in their L1 and L2, providing evidence for the
5 specific involvement of frontoparietal regions in the semantic retrieval/representation of action
6 knowledge across languages. Finally, we show that while prior to the surgery, L1 and L2 can
7 follow a similar reorganization profile; postoperative reshaping triggered by tumor removal
8 leads to divergent reconfiguration patterns within each language. Taken together, these findings
9 provide new insights into the spectro-temporal dynamics supporting postoperative recovery in
10 the bilingual brain, and the potential roles that disruption of preoperative plasticity triggered
11 by surgical trauma and/or language proficiency may have on this process. Beyond theoretical
12 implications, our results provide valuable clinical information to plan multistage surgical
13 strategies tailored to patients' differential neuroplasticity for each language. Such a strategy
14 can improve EOR in follow-up surgeries while fully preserving all the languages a patient
15 speaks.
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34

35 **Acknowledgments**

36 This research was supported by the Basque Government through the BERC 2022-2025
37 program and by the Spanish State Research Agency through BCBL Severo Ochoa excellence
38 accreditation CEX2020-001010-S, by the Ikerbasque Foundation, the Fundación Científica
39 AECC (FCAECC) through the project PROYE20005CARR and by the by the Spanish Ministry
40 of Science and Innovation through the Plan Nacional RTI2018-096216-A-I00 (MEGLIOMA)
41 and PID2021-123575OB-I00 (SCANCER) to LA, RTI2018-093547-B-I00 (LangConn) to MC
42 and IQ and RTI2018-096311-B-I00 to NM (TrainSynchro).
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

The authors would like to express their deepest gratitude to the patients who took part in this study and their families.

5. References

- Abutalebi, J. (2008). Neural aspects of second language representation and language control. *Acta Psychol (Amst)*, 128(3), 466-478. doi: 10.1016/j.actpsy.2008.03.014
- Abutalebi, J., & Green, D. (2007). Bilingual language production: The neurocognition of language representation and control. *Journal of Neurolinguistics*, 20, 242–275
- Amoruso, L., Geng, S., Molinaro, N., Timofeeva, P., Gisbert-Munoz, S., Gil-Robles, S., . . . Carreiras, M. (2021). Oscillatory and structural signatures of language plasticity in brain tumor patients: A longitudinal study. *Hum Brain Mapp*, 42(6), 1777-1793. doi: 10.1002/hbm.25328
- Bice, K., Yamasaki, B. L., & Prat, C. S. (2020). Bilingual language experience shapes resting-state brain rhythms. *Neurobiology of Language*, 1(3), 288–318. doi: doi.org/10.1162/nol_a_00014
- Bourguignon, M., Molinaro, N., & Wens, V. (2018). Contrasting functional imaging parametric maps: The mislocation problem and alternative solutions. *Neuroimage*, 169, 200-211. doi: 10.1016/j.neuroimage.2017.12.033
- Cargnelutti, E., Ius, T., Skrap, M., & Tomasino, B. (2020). What do we know about pre- and postoperative plasticity in patients with glioma? A review of neuroimaging and intraoperative mapping studies. *Neuroimage Clin*, 28, 102435. doi: 10.1016/j.nicl.2020.102435
- Consonni, M., Cafiero, R., Marin, D., Tettamanti, M., Iadanza, A., Fabbro, F., & Perani, D. (2013). Neural convergence for language comprehension and grammatical class production in highly proficient bilinguals is independent of age of acquisition. *Cortex*, 49(5), 1252-1258. doi: 10.1016/j.cortex.2012.04.009
- Corina, D. P., Gibson, E. K., Martin, R., Poliakov, A., Brinkley, J., & Ojemann, G. A. (2005). Dissociation of action and object naming: evidence from cortical stimulation mapping. *Hum Brain Mapp*, 24(1), 1-10. doi: 10.1002/hbm.20063
- Corina, D. P., Loudermilk, B. C., Detwiler, L., Martin, R. F., Brinkley, J. F., & Ojemann, G. (2010). Analysis of naming errors during cortical stimulation mapping: implications for models of language representation. *Brain Lang*, 115(2), 101-112. doi: 10.1016/j.bandl.2010.04.001
- de Bruin, A., Carreiras, M., & Dunabeitia, J. A. (2017). The BEST Dataset of Language Proficiency. *Front Psychol*, 8, 522. doi: 10.3389/fpsyg.2017.00522
- Duffau, H. (2005). Lessons from brain mapping in surgery for low-grade glioma: insights into associations between tumour and brain plasticity. *Lancet Neurol*, 4(8), 476-486. doi: 10.1016/S1474-4422(05)70140-X
- Duffau, H. (2020). Functional Mapping before and after Low-Grade Glioma Surgery: A New Way to Decipher Various Spatiotemporal Patterns of Individual Neuroplastic Potential in Brain Tumor Patients. *Cancers (Basel)*, 12(9). doi: 10.3390/cancers12092611
- Duffau, H., Capelle, L., Denvil, D., Sichez, N., Gatignol, P., Lopes, M., . . . Van Effenterre, R. (2003). Functional recovery after surgical resection of low grade gliomas in eloquent brain: hypothesis of brain compensation. *J Neurol Neurosurg Psychiatry*, 74(7), 901-907. doi: 10.1136/jnnp.74.7.901
- Emmorey, K., & McCullough, S. (2009). The bimodal bilingual brain: effects of sign language experience. *Brain Lang*, 109(2-3), 124-132. doi: 10.1016/j.bandl.2008.03.005
- Ferracci, F. X., Michaud, K., & Duffau, H. (2019). The landscape of postsurgical recurrence patterns in diffuse low-grade gliomas. *Crit Rev Oncol Hematol*, 138, 148-155. doi: 10.1016/j.critrevonc.2019.04.009

- 1 Galloway, L. (1978). Language impairment and recovery in polyglot aphasia. In M. Paradis (Ed.),
2 *Aspects of bilingualism*. Colombia, SC: Hornbeam Press.
- 3 Gatignol, P., Duffau, H., Capelle, L., & Plaza, M. (2009). Naming performance in two bilinguals with
4 frontal vs. temporal glioma. *Neurocase*, *15*(6), 466-477. doi: 10.1080/13554790902950434
- 5 Geng, S., Molinaro, N., Timofeeva, P., Quinones, I., Carreiras, M., & Amoruso, L. (2022). Oscillatory
6 dynamics underlying noun and verb production in highly proficient bilinguals. *Sci Rep*, *12*(1),
7 764. doi: 10.1038/s41598-021-04737-z
- 8 Gisbert-Munoz, S., Quinones, I., Amoruso, L., Timofeeva, P., Geng, S., Boudelaa, S., . . . Carreiras, M.
9 (2021). MULTIMAP: Multilingual picture naming test for mapping eloquent areas during
10 awake surgeries. *Behav Res Methods*, *53*(2), 918-927. doi: 10.3758/s13428-020-01467-4
- 11 Giussani, C., Roux, F. E., Lubrano, V., Gaini, S. M., & Bello, L. (2007). Review of language organisation
12 in bilingual patients: what can we learn from direct brain mapping? *Acta Neurochir (Wien)*,
13 *149*(11), 1109-1116; discussion 1116. doi: 10.1007/s00701-007-1266-2
- 14 Gleichgerrcht, E., Fridriksson, J., Rorden, C., Nesland, T., Desai, R., & Bonilha, L. (2016). Separate
15 neural systems support representations for actions and objects during narrative speech in
16 post-stroke aphasia. *Neuroimage Clin*, *10*, 140-145. doi: 10.1016/j.nicl.2015.11.013
- 17 Gramfort, A., Luessi, M., Larson, E., Engemann, D. A., Strohmeier, D., Brodbeck, C., . . . Hamalainen,
18 M. S. (2014). MNE software for processing MEG and EEG data. *Neuroimage*, *86*, 446-460.
19 doi: 10.1016/j.neuroimage.2013.10.027
- 20 Hernandez, A. E., Dapretto, M., Mazziotta, J., & Bookheimer, S. (2001). Language switching and
21 language representation in Spanish-English bilinguals: an fMRI study. *Neuroimage*, *14*(2),
22 510-520. doi: 10.1006/nimg.2001.0810
- 23 Hut, S. C. A., & Leminen, A. (2017). Shaving Bridges and Tuning Kitaraa: The Effect of Language
24 Switching on Semantic Processing. *Front Psychol*, *8*, 1438. doi: 10.3389/fpsyg.2017.01438
- 25 Hyvarinen, A. (1999). Fast and robust fixed-point algorithms for independent component analysis.
26 *IEEE Trans Neural Netw*, *10*(3), 626-634. doi: 10.1109/72.761722
- 27 Jung, T. P., Makeig, S., Humphries, C., Lee, T. W., McKeown, M. J., Iragui, V., & Sejnowski, T. J. (2000).
28 Removing electroencephalographic artifacts by blind source separation. *Psychophysiology*,
29 *37*(2), 163-178.
- 30 Kamali, A., Flanders, A. E., Brody, J., Hunter, J. V., & Hasan, K. M. (2014). Tracing superior
31 longitudinal fasciculus connectivity in the human brain using high resolution diffusion tensor
32 tractography. *Brain Struct Funct*, *219*(1), 269-281. doi: 10.1007/s00429-012-0498-y
- 33 Kemmerer, D. (2014). Word classes in the brain: implications of linguistic typology for cognitive
34 neuroscience. *Cortex*, *58*, 27-51. doi: 10.1016/j.cortex.2014.05.004
- 35 Kielar, A., Deschamps, T., Jokel, R., & Meltzer, J. A. (2016). Functional reorganization of language
36 networks for semantics and syntax in chronic stroke: Evidence from MEG. *Hum Brain Mapp*,
37 *37*(8), 2869-2893. doi: 10.1002/hbm.23212
- 38 Kopell, N., Ermentrout, G. B., Whittington, M. A., & Traub, R. D. (2000). Gamma rhythms and beta
39 rhythms have different synchronization properties. *Proc Natl Acad Sci U S A*, *97*(4), 1867-
40 1872. doi: 10.1073/pnas.97.4.1867
- 41 Lubrano, V., Filleron, T., Demonet, J. F., & Roux, F. E. (2014). Anatomical correlates for category-
42 specific naming of objects and actions: a brain stimulation mapping study. *Hum Brain Mapp*,
43 *35*(2), 429-443. doi: 10.1002/hbm.22189
- 44 Makris, N., Kennedy, D. N., McInerney, S., Sorensen, A. G., Wang, R., Caviness, V. S., Jr., & Pandya, D.
45 N. (2005). Segmentation of subcomponents within the superior longitudinal fascicle in
46 humans: a quantitative, in vivo, DT-MRI study. *Cereb Cortex*, *15*(6), 854-869. doi:
47 10.1093/cercor/bhh186
- 48 Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. *J*
49 *Neurosci Methods*, *164*(1), 177-190. doi: S0165-0270(07)00170-7 [pii]
50 10.1016/j.jneumeth.2007.03.024

- 1 Obleser, J., Wostmann, M., Hellbernd, N., Wilsch, A., & Maess, B. (2012). Adverse listening
2 conditions and memory load drive a common alpha oscillatory network. *J Neurosci*, 32(36),
3 12376-12383. doi: 10.1523/JNEUROSCI.4908-11.2012
- 4 Ojemann, J. G., Ojemann, G. A., & Lettich, E. (2002). Cortical stimulation mapping of language cortex
5 by using a verb generation task: effects of learning and comparison to mapping based on
6 object naming. *J Neurosurg*, 97(1), 33-38. doi: 10.3171/jns.2002.97.1.0033
- 7 Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory.
8 *Neuropsychologia*, 9(1), 97-113.
- 9 Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J. M. (2011). FieldTrip: Open source software for
10 advanced analysis of MEG, EEG, and invasive electrophysiological data. *Comput Intell*
11 *Neurosci*, 2011, 156869. doi: 10.1155/2011/156869
- 12 Paradis, M. (2000). The neurolinguistics of bilingualism in the next decades. *Brain Lang*, 71(1), 178-
13 180. doi: 10.1006/brln.1999.2245
- 14 Paradis, M. (2004). *A Neurolinguistic theory of bilingualism*. Amsterdam: John Benjamins Publishing
15 Company.
- 16 Perani, D., & Abutalebi, J. (2005). The neural basis of first and second language processing. *Curr Opin*
17 *Neurobiol*, 15(2), 202-206. doi: 10.1016/j.conb.2005.03.007
- 18 Piai, V., Meyer, L., Dronkers, N. F., & Knight, R. T. (2017). Neuroplasticity of language in left-
19 hemisphere stroke: Evidence linking subsecond electrophysiology and structural
20 connections. *Hum Brain Mapp*, 38(6), 3151-3162. doi: 10.1002/hbm.23581
- 21 Quinones, I., Amoroso, L., Pomposo Gastelu, I. C., Gil-Robles, S., & Carreiras, M. (2021). What Can
22 Glioma Patients Teach Us about Language (Re)Organization in the Bilingual Brain: Evidence
23 from fMRI and MEG. *Cancers (Basel)*, 13(11). doi: 10.3390/cancers13112593
- 24 Robles, S. G., Gatignol, P., Lehericy, S., & Duffau, H. (2008). Long-term brain plasticity allowing a
25 multistage surgical approach to World Health Organization Grade II gliomas in eloquent
26 areas. *J Neurosurg*, 109(4), 615-624. doi: 10.3171/JNS/2008/109/10/0615
- 27 Saur, D., Lange, R., Baumgaertner, A., Schraknepper, V., Willmes, K., Rijntjes, M., & Weiller, C.
28 (2006). Dynamics of language reorganization after stroke. *Brain*, 129(Pt 6), 1371-1384. doi:
29 10.1093/brain/awl090
- 30 Shapiro, K. A., Moo, L. R., & Caramazza, A. (2006). Cortical signatures of noun and verb production.
31 *Proc Natl Acad Sci U S A*, 103(5), 1644-1649. doi: 10.1073/pnas.0504142103
- 32 Shapiro, K. A., Mottaghy, F. M., Schiller, N. O., Poeppel, T. D., Fluss, M. O., Muller, H. W., . . . Krause,
33 B. J. (2005). Dissociating neural correlates for nouns and verbs. *Neuroimage*, 24(4), 1058-
34 1067. doi: 10.1016/j.neuroimage.2004.10.015
- 35 Shen, W., Fiori-Duharcourt, N., & Isel, F. (2016). Functional significance of the semantic P600:
36 evidence from the event-related brain potential source localization. *Neuroreport*, 27(7), 548-
37 558. doi: 10.1097/WNR.0000000000000583
- 38 Sherman, M. A., Lee, S., Law, R., Haegens, S., Thorn, C. A., Hamalainen, M. S., . . . Jones, S. R. (2016).
39 Neural mechanisms of transient neocortical beta rhythms: Converging evidence from
40 humans, computational modeling, monkeys, and mice. *Proc Natl Acad Sci U S A*, 113(33),
41 E4885-4894. doi: 10.1073/pnas.1604135113
- 42 Spitzer, B., & Haegens, S. (2017). Beyond the Status Quo: A Role for Beta Oscillations in Endogenous
43 Content (Re)Activation. *eNeuro*, 4(4). doi: 10.1523/ENEURO.0170-17.2017
- 44 Tao, L., Wang, G., Zhu, M., & Cai, Q. (2021). Bilingualism and domain-general cognitive functions
45 from a neural perspective: A systematic review. *Neurosci Biobehav Rev*, 125, 264-295. doi:
46 10.1016/j.neubiorev.2021.02.029
- 47 Taulu, S., & Simola, J. (2006). Spatiotemporal signal space separation method for rejecting nearby
48 interference in MEG measurements. *Phys Med Biol*, 51(7), 1759-1768. doi: 10.1088/0031-
49 9155/51/7/008

- 1 Traut, T., Sardesh, N., Bulubas, L., Findlay, A., Honma, S. M., Mizuiri, D., . . . Tarapore, P. E. (2019).
2 MEG imaging of recurrent gliomas reveals functional plasticity of hemispheric language
3 specialization. *Hum Brain Mapp*, 40(4), 1082-1092. doi: 10.1002/hbm.24430
4
5 Van Veen, B. D., van Drongelen, W., Yuchtman, M., & Suzuki, A. (1997). Localization of brain
6 electrical activity via linearly constrained minimum variance spatial filtering. *IEEE Trans*
7 *Biomed Eng*, 44(9), 867-880. doi: 10.1109/10.623056
8
9 Vigliocco, G., Vinson, D. P., Druks, J., Barber, H., & Cappa, S. F. (2011). Nouns and verbs in the brain:
10 a review of behavioural, electrophysiological, neuropsychological and imaging studies.
11 *Neurosci Biobehav Rev*, 35(3), 407-426. doi: 10.1016/j.neubiorev.2010.04.007
12
13 Weiss, S., & Mueller, H. M. (2012). "Too Many betas do not Spoil the Broth": The Role of Beta Brain
14 Oscillations in Language Processing. *Front Psychol*, 3, 201. doi: 10.3389/fpsyg.2012.00201
15
16 Willms, J. L., Shapiro, K. A., Peelen, M. V., Pajtas, P. E., Costa, A., Moo, L. R., & Caramazza, A. (2011).
17 Language-invariant verb processing regions in Spanish-English bilinguals. *Neuroimage*, 57(1),
18 251-261. doi: 10.1016/j.neuroimage.2011.04.021
19
20 York, G. K., 3rd, & Steinberg, D. A. (2011). Hughlings Jackson's neurological ideas. *Brain*, 134(Pt 10),
21 3106-3113. doi: 10.1093/brain/awr219
22
23 Zeger, S. L., & Liang, K. Y. (1992). An overview of methods for the analysis of longitudinal data. *Stat*
24 *Med*, 11(14-15), 1825-1839. doi: 10.1002/sim.4780111406
25
26

27 **Table Legends**

28 **Table 1.** Patient's demographics, linguistic and clinical characteristics

29
30
31 **Table 2. Comparison of individual patient scores to control group performance during**
32 **naming in Spanish and Basque.** Mean (M) and *p*-values from Crawford-Howell *t*-tests
33
34
35 comparing accuracy and reaction times (RT) during object and action naming in both
36
37
38
39 languages before and after surgery for tumor resection.
40
41
42
43

44 **Figure Legends**

45
46 **Figure 1.** Lesion delineation for individual patients.
47
48
49
50
51

52 **Figure 2. Examples of object and action stimuli and experimental task.** In separate blocks,
53 participants were requested to observe the pictures and overtly name them in either Spanish or
54
55 Basque as quickly and accurately as possible. Production of nouns and verbs was requested in
56
57 the context of short sentences, which is a more ecological form of speech than isolated naming.
58
59
60
61
62
63
64
65

1 Each trial began with a fixation cross on the screen for 1 second followed by the picture
2 presented for 2 seconds. ISI randomly varied between 3-4 secs.
3
4
5
6
7

8 **Figure 3. Patient's cognitive and linguistic performance before and after surgery.** Charts
9 showing individual patients' scores for the pre- and post-surgery screening of cognitive status
10 (i.e., Minimental Cognitive State Examination [MMSE], verbal and non-verbal intelligence
11 (KBIT) and language production in Spanish and Basque (BEST).
12
13
14
15
16
17

18
19
20
21 **Figure 4. Longitudinal effect in patients for action naming.** Panel A shows time-resolved
22 spectra of the longitudinal action naming effect (post vs. pre) in Spanish (top left) and Basque
23 (bottom left), together with the positive clusters in the beta frequency band (13-28 Hz),
24 indicating power increases after surgery. Line charts show individual patients' mean beta power
25 at each session (before and after tumor resection), averaged over sensors associated with the
26 clusters. Mean beta values are also shown for healthy bilingual controls as indicated by black
27 dotted lines ($n = 16$; Spanish = -0.538, Basque = -0.456). Panel B shows source localization of
28 the longitudinal action naming effect in each language, circumscribed to the time interval
29 highlighted by the clusters. All plotted regions reached a p -value < 0.01 .
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47

48 **Figure 5. Action naming in healthy bilingual controls.** Panel A shows the negative cluster
49 in the beta frequency band (13-28 Hz), indicating lower beta power for naming as compared to
50 baseline, together with the action naming network resulting from the source level analysis.
51
52
53
54 Panel B shows the negative beta cluster corresponding to the same action naming effect is
55 Basque and the resulting network of areas underscored by the source level analysis. In both
56
57
58
59
60
61
62
63
64
65

1 cases, source localization of the effect is circumscribed to the time intervals highlighted by the
2 clusters. All plotted regions reached a p -value < 0.01 .
3
4
5
6

7 **Figure 6. Language effect in patients after surgery.** Panel A shows time-resolved spectra of
8 the language contrast (Spanish vs. Basque) after tumor resection, together with the negative
9 cluster in the beta frequency band (13-28 Hz), indicating lower beta power for Spanish. Line
10 charts show individual patients' mean beta power for each language, averaged over sensors
11 associated with the cluster. Mean beta values are also shown for healthy bilingual controls as
12 indicated by the blue dotted line ($n = 16$; Spanish = -0.39, Basque = -0.551). Panel B shows
13 source localization of the language effect, circumscribed to the time interval highlighted by the
14 significant cluster. All plotted regions reached a p -value < 0.01 .
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

	Age	Sex	Educ. (years)	Occupation	L1	L1 AoA	L2	L2 AoA	L1/L2 % of use	Tumor Location	Tumor Volume (cm³)	EOR (%)
P1	45	F	14	Businesswoman	Spanish	0	Basque	5	50/50	Motor	23.00	76
P2	47	M	20	Aircraft pilot	Spanish	0	Basque	3	95/5	Parietal	87.83	100
P3	56	M	12	Mechanic	Spanish	0	Basque	0	40/60	Frontal	28.68	100
P4	41	M	20	Administrator	Spanish	0	Basque	3	50/50	Parietal	18.29	100

	Pre-surgery				Post-surgery			
	Object		Action		Object		Action	
	Mean	<i>p</i> -value	Mean	<i>p</i> -value	Mean	<i>p</i> -value	Mean	<i>p</i> -value
Accuracy								
<i>Spanish</i>								
P1	100	0.72	99.43	0.77	99.4	0.9	99.43	0.77
P2	100	0.72	100	0.58	100	0.72	100	0.58
P3	97.4	0.5	98.7	0.97	100	0.72	100	0.58
P4	98	0.66	100	0.58	100	0.72	100	0.58
<i>Basque</i>								
P1	99.43	0.82	97.74	0.73	99.4	0.83	99.43	0.68
P2	100	0.62	100	0.5	98.7	0.9	92.59	0.01*
P3	95.65	0.13	100	0.5	100	0.62	98.14	0.87
P4	96.15	0.2	100	0.5	95.34	0.10	100	0.5
RT								
<i>Spanish</i>								
P1	759.9	0.61	897.49	0.64	718.93	0.55	940.6	0.7
P2	868.91	0.78	890.12	0.63	789.25	0.65	882.57	0.61
P3	1009.54	0.98	1209.73	0.84	776.40	0.63	1159.44	0.92
P4	851.7	0.75	1054.56	0.89	981.98	0.96	1113.32	0.99
<i>Basque</i>								
P1	816.41	0.75	1018.07	0.79	881.95	0.86	1075.67	0.89
P2	954.48	0.98	1056.9	0.86	671.65	0.52	789.11	0.45
P3	965.91	0.99	1044.98	0.84	771.97	0.67	1045.46	0.84
P4	856.81	0.81	890.97	0.59	914.55	0.91	1133.53	0.99

P1



P2

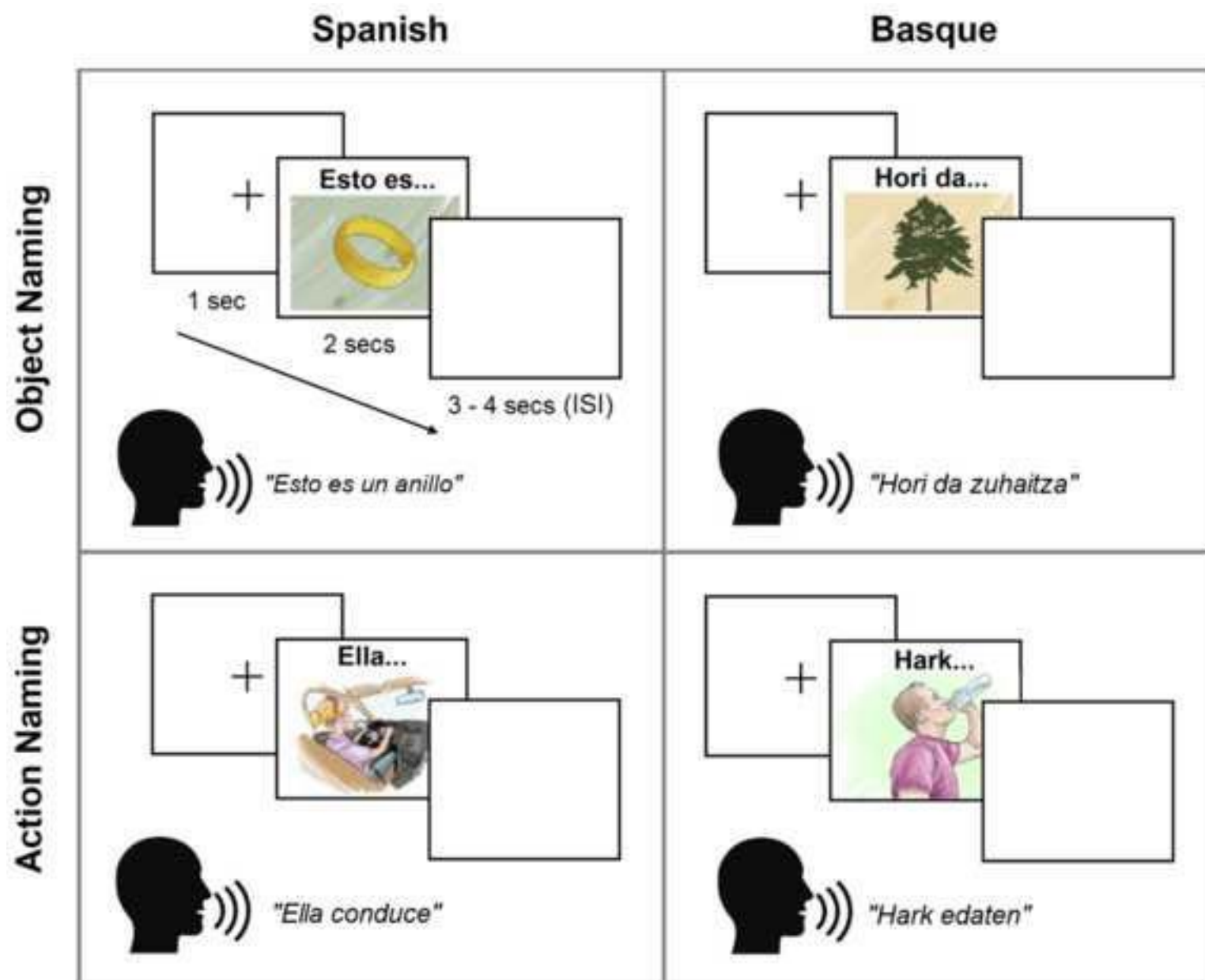


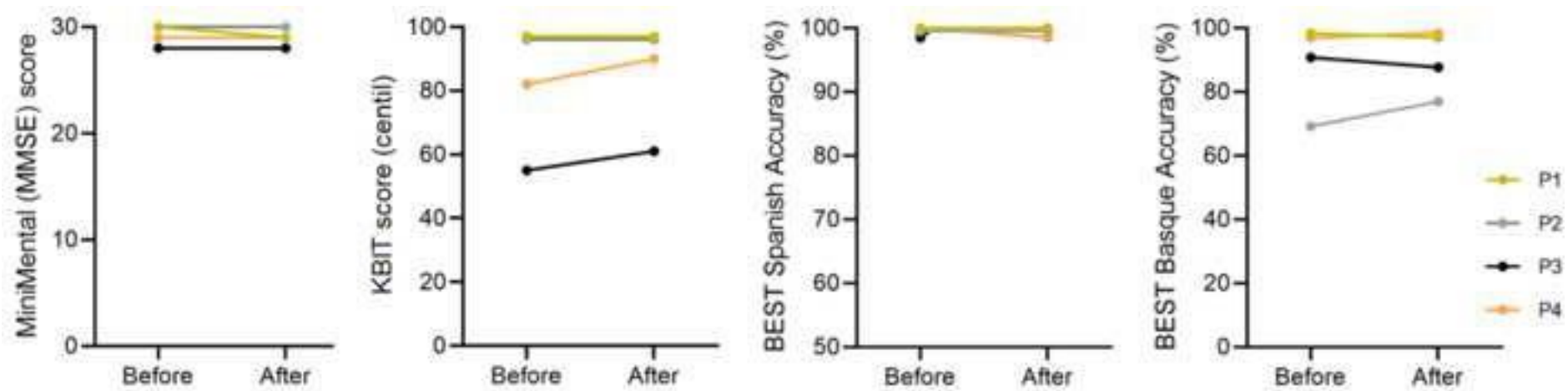
P3

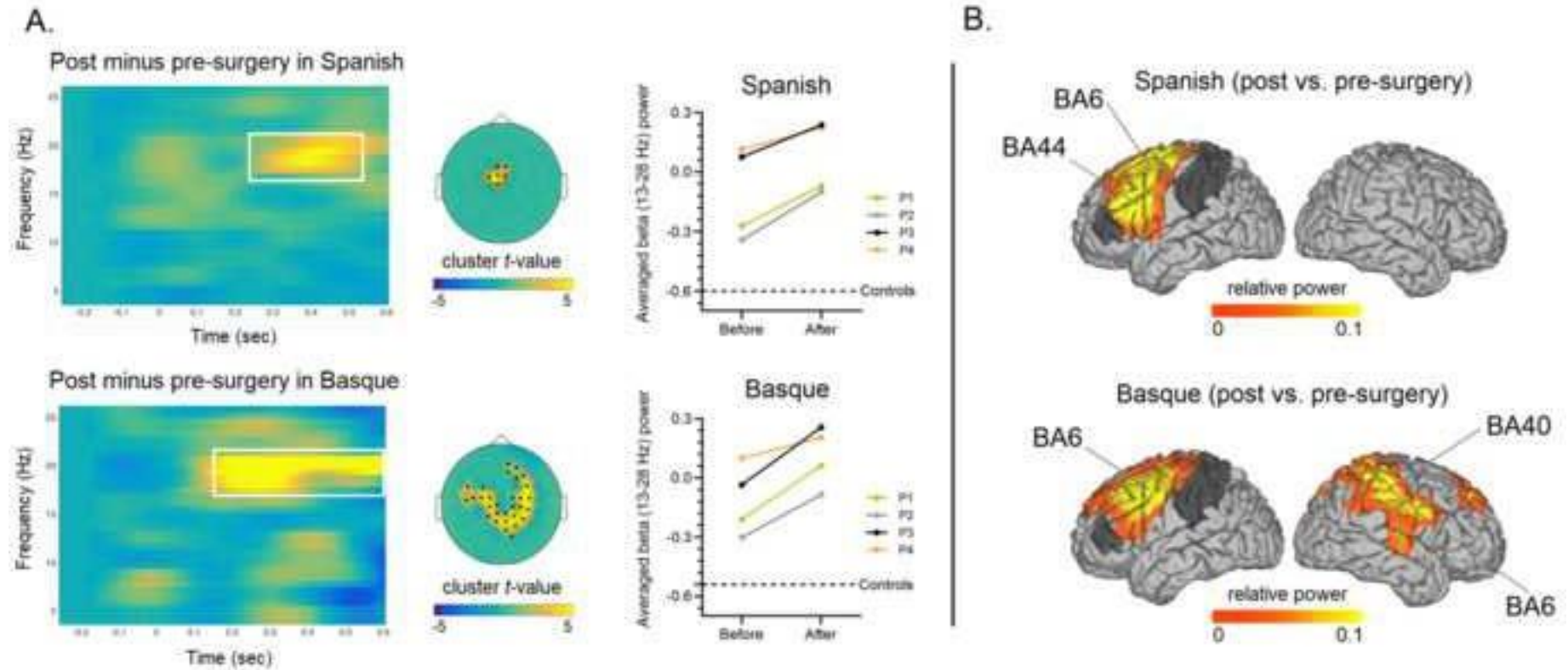


P4

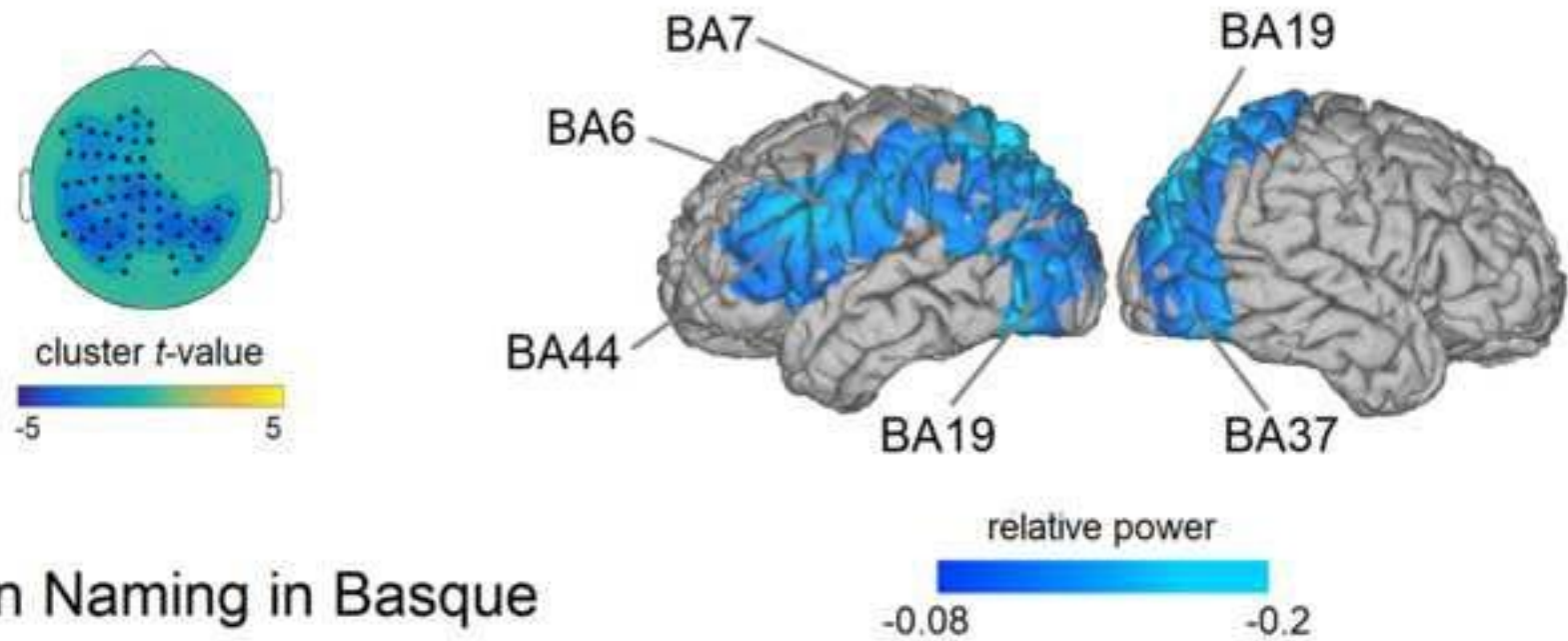








A. Action Naming in Spanish



B. Action Naming in Basque

