bcbl

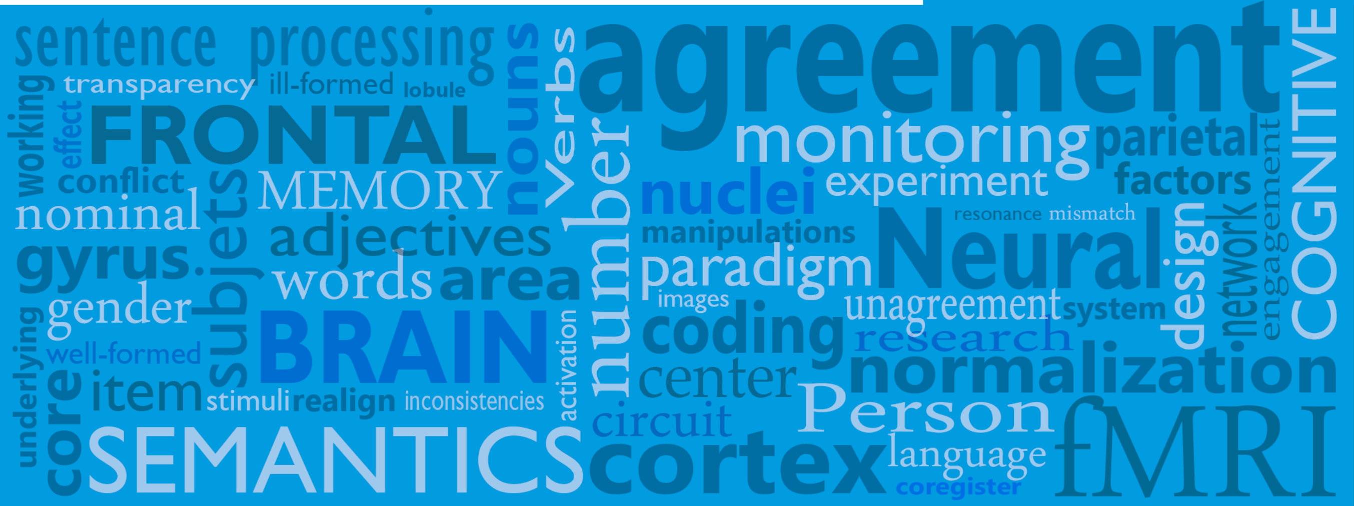
BASQUE CENTER
ON COGNITION, BRAIN
AND LANGUAGE

Abstract: Language comprehension is incremental, involving the integration of formal and conceptual information from different words, together with the need to resolve conflicting cues when unexpected information occurs. However, despite the extensive amount of findings regarding how the brain deals with these information, two essential and still open questions are 1) whether the neural circuit(s) for coding syntactic and semantic information embedded in our linguistic code are the same or different, and 2) whether the possible interaction(s) between these two different types of information leaves a trace in the brain response.

The current thesis seeks to segregate the neuro-anatomical substrates of these processes by taking advantage of the Spanish agreement system. Experimental manipulations concerning different agreement features and the elements involved in an agreement relation, allowed us to characterize the neural network underlying agreement processing. To distinguish between purely syntactic mechanisms and those where semantic and syntactic factors would interact during language comprehension, different types of agreement relations and/or agreement features were manipulated in well- and ill-formed constructions. The interaction effect between the different factors included in each experiment was always the critical comparison.

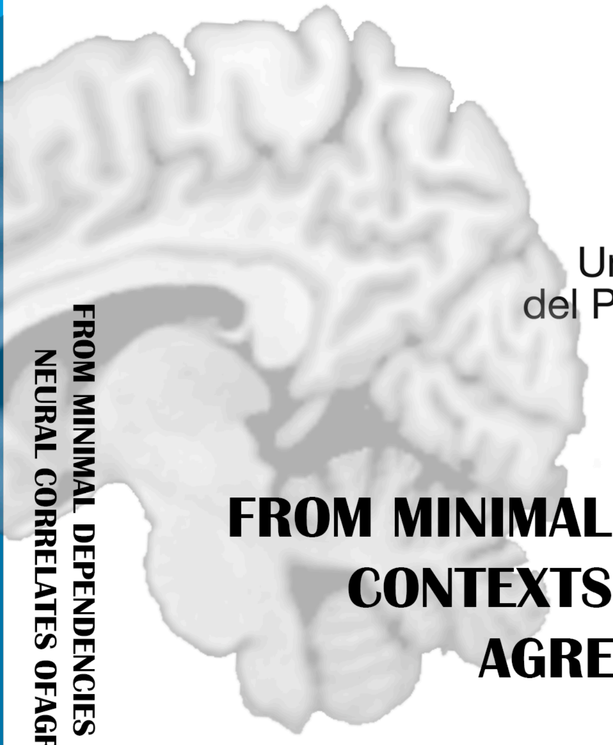
Critically, the current findings highlight the sensibility of the agreement system to syntactic and semantic factors embedded into an agreement relation, opening new windows to the study of agreement computation and language comprehension.

Iliana Quiñones González: Bachelor in Biology (1999-2004), Master in Cognitive Neuroscience (2004-2007). Specialization in electrophysiological and neuroimaging thecniques (2007 - 2010). Phd. in Linguistics (2011-2015).



FROM MINIMAL DEPENDENCIES TO SENTENCE CONTEXTS:
NEURAL CORRELATES OFAGREEMENT PROCESSING.

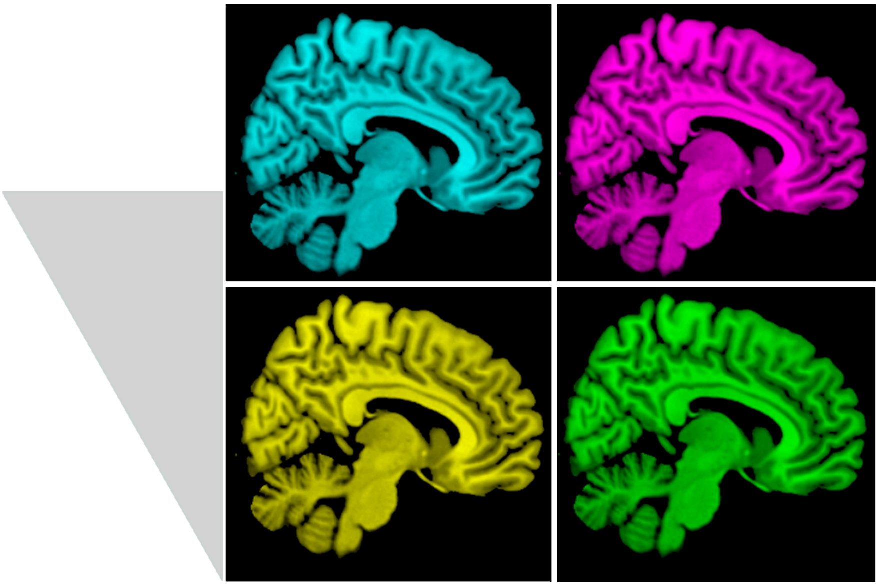
San Sebastián, 2015



eman ta zabal zazu

Universidad del País Vasco
Euskal Herriko Unibertsitatea

FROM MINIMAL DEPENDENCIES TO SENTENCE CONTEXTS: NEURAL CORRELATES OF AGREEMENT PROCESSING.



Iliana Quiñones González

Supervised by Manuel Carreiras and Nicola Molinaro

San Sebastián, 2015

FROM MINIMAL DEPENDENCIES TO SENTENCE CONTEXTS: NEURAL CORRELATES OF AGREEMENT PROCESSING.

The research presented in this thesis was partially supported by grants PSI2012-32350 (*“Aprender un nuevo idioma”*) and PSI2012-31448 (*“Procesamiento en lengua de signos”*) from the Spanish Ministry of Economy and Competitiveness and by grants 295362_ERC_ ADG_2011_ BILITERACY and FP7-SSH-2013-1-GA613465 ATheME from the European Union.

BCBL

Basque Center on Cognition, Brain and Language

Paseo Mikeletegi, 69, Donostia-San Sebastián, Spain

November, 2015

bcbl
BASQUE CENTER
ON COGNITION, BRAIN
AND LANGUAGE

eman ta zabal zazu
Universidad del País Vasco
Euskal Herriko Unibertsitatea

FROM MINIMAL DEPENDENCIES TO SENTENCE CONTEXTS: NEURAL CORRELATES OF AGREEMENT PROCESSING.

By Iliana Quiñones González

A dissertation submitted to the Department of Linguistic and Basque Studies
of the University of the Basque Country in candidacy for the
Degree of Doctor in Linguistics

Thesis Supervised by Dr. Manuel Carreiras Valiña and Dr. Nicola Molinaro

San Sebastian, 2015

A todos los que han contribuido en mi formación durante todos estos años, especialmente a Antonieta y a Mitchell.

A Berti por estar ahí y todo lo demás…

Preface

Eskuetan, bizitza eskuetan
eskuetan daude gure hitzak
Eskuetan, bihotza eskuetan
gure esku dago mundu bizi bat.

Eskuetan, bizitza eskuetan
eskuetan daude gure hitzak.

Eskuetan bihotza eskuetan
gure esku dago mundu berri bat.
……
Eskuetan, bihotza eskuetan
gure esku dago mundu bat… eskuetan.

Pirritx, Porrotx eta MariMotots

Esta tesis es el resultado de cuatro años de trabajo en el *Basque Center on Cognition, Brain and Language* (BCBL), ocho años de trabajo en el *Centro de Neurociencias de Cuba* (CNC) y un cúmulo de personas y circunstancias. Sin estos años previos de aprendizaje, donde he tenido la suerte de conocer a algunas personas que han incidido, y en algunos casos, determinado, mi futuro académico, esta tesis no hubiera sido posible. Por esto, antes de entrar en cuestiones técnicas que pueden ser difíciles de seguir y aburridas en ocasiones, quiero dar las gracias a todas las personas que de una u otra forma han contribuido en este proceso.

En primer lugar quiero dar las gracias a todos los profesores e investigadores que han contribuido al proceso de mi formación. Pero muy especialmente, quiero dar las gracias por mi educación y formación a mi familia, no sólo a los que están unidos a mí por lazos de consanguinidad, sino también a mi familia política. En este grupo quiero agradecer muy especialmente a mis padres, Francisco e Ileana, quienes no sólo inculcaron y fomentaron en mí el interés por los estudios, sino que durante mucho tiempo lo facilitaron. A mi madre por transmitirme su amor por el trabajo y a mi padre por inculcarme la necesidad de superarme a mí misma. A Ada por enseñarme "a palos" lo que significa amar a alguien y dejarse amar. Quiero que sepas que sé que hubieras dado todo por compartir con nosotros este momento.

Quiero agradecerle muy especialmente también, a Antonieta Bóbes León y a Mitchell Valdés Sosa, por abrirme las puertas del CNC y acogerme casi como parte de su familia. A ellos les dedico este trabajo porque las incontables horas que dedicaron a mi formación, son las que han determinado mi tránsito por el BCBL, y por ende, la realización de este trabajo. No olvidaré nunca nuestras maratones nocturnas de procesamiento de datos. Esos momentos cargados de adrenalina, que con la aparición de los primeros resultados se convertían en ataques intempestivos de euforia colectiva y compartida…

Me gustaría expresar mi gratitud a Pascal Belin, por abrirme las puertas de su laboratorio y hacer que esos siete meses en Glasgow fueran intensos, fructíferos y muy agradables. Por hacer que mi carrera profesional despegara, despertando en mí el deseo por conocer el mundo.

Quiero dar las gracias a Simona Mancini, quién no consta dentro de los directores de esta tesis, pero que ha fungido como tal. Por haber influido directamente en esta investigación. Por dedicar tantas horas a enseñarme Psicolingüística *(ya puedes preguntarme la definición de "discourse roles" o "anchoring", bueno, mmmm…, mejor no!!!)*. Por sus comentarios, consejos, tiempo y dedicación, no sólo a esta investigación, sino también a este documento. Por las largas horas de discusión.

Con especial énfasis, quiero dar las gracias a todas aquellas personas que colaboraron con los experimentos, a los que participaron como sujetos experimentales y al "BCBL lab team", especialmente Clara, Larraitz, Oihana y David. A todo el personal administrativo del BCBL (*"The Big Sisters"*), Eider, Ana, Leire, Vanesa y Maider, por hacer tan fáciles y expeditas las cosas que en otros lugares pueden ser tan difíciles. Sin todos ellos, este trabajo tampoco hubiera sido posible.

Quiero dar las gracias a todos los "BCBLianos" que con sugerencias o comentarios también han contribuido al desarrollo de esta tesis, a Sendy, Brendan, Saioa, Kepa, Cesar, Juan Andrés y muy especialmente a Jon Andoni.

A todos los que han sido revisores anónimos o no de este documento, que con sus sugerencias, preguntas y comentarios han enriquecido considerablemente este trabajo, abriendo puertas a investigaciones futuras.

Quiero agradecer también a los compañeros y amigos del CNC, especialmente a Eduardito, Lester, Iturria, Pedrito, Maye, Tin, Lídice, Lourdes, Yanelys, Yuriem, Anabel, Greysi, Alejandro, Lorna, Belkis, Jorge y Yaise, por los muchos momentos y batallas compartidas. A mis amigos de siempre, Belkis, Indo, Durlo y Nany, que con sus *¿qué bola miji, hasta cuando vas a seguir con esto?*, le han puesto un poco de presión al asunto. Por intentar y a veces conseguir hacer más llevaderos los momentos difíciles. Por aguantar mis idas y venidas de olla. A los amigos nuevos, Eneko, Alejandro, Acebo, Cristina, Ainhoa, Gari, Noemi, Brendan, Saioa, Jon Andoni (*"The Taxi Driver"*), Mikel, Myriam y Aina, por haber intentado y muchas veces conseguido hacer de mi paso por San Sebastián toda una aventura, en ocasiones ininteligible, pero divertida. En especial a Aina y a Myriam, por los muchos momentos, *"secretos"* y estados de ánimo compartidos.

Quiero dar las gracias a mi amiga Inma, por no dejarme olvidar que un mundo mejor es posible. Por sus palabras en los momentos difíciles. Por su paciencia en los momentos más estresantes. Por intentar y a veces conseguir hacerme cambiar de opinión.

Quiero dar las gracias a Berti por toda la ayuda que me ha brindado, por la portada, por el trabajo con el EndNote, por ayudarme con el diseño de las figuras. Pero sobre todo, quiero agradecerle por seguirme allá donde vaya, por su empeño en hacerme feliz y por muchísimo más…

Finalmente, quiero dar las gracias a mis tutores, Manuel Carreiras y Nicola Molinaro. Los he dejado para el final porque no sé cómo resumir todo lo que quisiera poder decirles. A ellos les agradezco, no sólo por haberme dirigido de forma excepcional el trabajo de tesis, sino por haberme hecho sentir todo este tiempo como parte de un equipo. A Manolo por ponerme el límite en el infinito. A Nicola por apoyarme en cada una de mis decisiones, fueran buenas o malas.

A todos ellos y a quienes haya podido, sin querer, olvidar, les reitero mi más sincero agradecimiento.

Abstract

Language comprehension is incremental, involving the integration of formal and conceptual information from different words, together with the need to resolve conflicting cues when unexpected information occurs. However, despite the extensive amount of findings regarding how the brain deals with these information, two essential and still open questions are [1]whether the neural circuit(s) for coding syntactic and semantic information embedded in our linguistic code are the same or different, and [2]whether the possible interaction(s) between these two different types of information leaves a trace in the brain response.

The current thesis seeks to segregate the neuro-anatomical substrates of these processes by taking advantage of the Spanish agreement system. This system comprised those procedural mechanisms concerning the regular assignment of the number [singular, plural], person [first, second and third] and/or gender [feminine, masculine] information, associated with different sentence constituents. Experimental manipulations concerning different agreement features and the elements involved in an agreement relation, allowed us to characterize the neural network underlying agreement processing. This thesis comprised five experiments: while experiments I and II explored nominal dependencies in local as well as non-local relations, experiments III, IV and V explored subject-verb relations in a more complex sentence context. To distinguish between purely syntactic mechanisms and those where semantic and syntactic factors would interact during language comprehension, different types of agreement relations and/or agreement features were manipulated in well- and ill-formed constructions. The interaction effect between the different factors included in each experiment was always the critical comparison.

In general, our results include firstly a functional dissociation between well-formed and ill-formed constructions: while ill-formed constructions recruited a bilateral distributed fronto-parietal network associated to conflict monitoring operations, not language specific, well-formed constructions recruited a left lateralized fronto-temporo-parietal network that seems to be specifically related to different aspects of phrase and sentence processing. Secondly, there was an anterior to posterior functional gradient associated to the middle and superior temporal cortex that consistently appears across experiments. Specifically, while the posterior portion of the left MTG-STG seems to be related to the storage and retrieval of lexical and morpho-syntactic information, the anterior portion of this region was related to syntactic-combinatorial building mechanisms. Critically, in the most anterior part of the left temporal cortex, corresponding with the middle and superior temporal pole, form-to-meaning mapping processes seems to be represented. Thirdly, the response of the left temporal cortex appears to be controlled by left inferior frontal regions (LIFG). Finally, left parietal regions such as the angular gyrus showed increased activation for those manipulations involving semantic factors (e.g., conceptual gender and Unagreement constructions), highlighting its crucial role in the processing of different types of semantic information (e.g., conceptual integration and semantic-discourse integration). Overall, these findings highlight the sensitivity of the agreement system to syntactic and semantic factors embedded into an agreement relation, opening new windows to the study of agreement computation and language comprehension.

Laburpena

Hizkuntzaren ulermena areagotzen doa, izan ere, beharrezkoa da hitz ezberdinen formari eta kontzeptuari buruzko informazioa bateratu eta, aldi berean, bat-bateko informazioa jasotzen denean kontrajarriak diren pistak ebaztea. Alabaina, aurkikuntza ugarik garunak informazio hori nola erabiltzen duen erakutsi duten arren, bi galdera erantzun gabe daude oraindik. Bata, kode linguistikoaren informazio sintaktikoa eta semantikoa kodifikatzeko zirkuitu neural berbera(k) erabiltzen diren ala ez, eta bestea, bi informazio ezberdin horien artean egon litezkeen interakzioek (bat edo gehiago) garunaren erantzunean eraginik ote duten.

Tesi honen helburua prozesu horien substratu neuro-anatomikoak banantzea da, horretarako gaztelaniaren komunztadura sistemaz baliatuta. Sistema horren prozedurazko mekanismoek zenbakiari [singularra, plurala], pertsonari [lehenengoa, bigarrena, hirugarrena] edo/eta generoari [femininoa, maskulinoa] buruzko informazioa era erregularrean ematen dute, esaldiaren bestelako osagaiei lotuta dagoena. Komunztadura-osagaien manipulazio esperimentalen eta komunztadura-harremanaren osagaien manipulazio esperimentalari esker, komunztaduraren prozesamenduaren atzean dagoen sare neuralaren ezaugarriak zehaztu ditzakegu. Tesi honetarako bost esperimentu egin ziren; I eta II esperimentuek lotura lokal eta ez lokaletako izenen menpekotasunak aztertu dituzte; eta III, IV eta V esperimentuek esaldi konplexuagoetan subjektuaren eta aditzaren arteko erlazioa aztertu dute. Hizkuntza ulertzerakoan parte har lezaketen alderdi semantiko eta sintaktikoak, guztiz sintaktikoak diren mekanismoetatik bereizteko, egitura zuzen eta akastunetan komunztadura lotura motak edo/eta komunztaduraren osagaiak manipulatu ziren. Esperimentu bakoitzean aurkitutako alderdien arteko elkarreraginak alderatzea izan da beti punturik erabakigarriena.

Lortutako emaitzek lehenik, egitura zuzen eta akastunen artean ezberdintasun funtzionala dagoela erakutsi dute. Egitura akastunek, arazoak kontrolatzeko, eragiketei lotutako sare aurre-parietalaren banaketa aldebikoa sortzen duten bitartean, hizkuntzak

berezkoak ez dituen egitura zuzenek ezkerraldean kokaturiko sare aurre-parietala osatzen dute. Badirudi, azken horiek perpaus eta esaldien prozesamenduko alderdiekin zehazki erlazionatuta daudela. Bigarrenik, esperimentuetan behin eta berriro erdiko eta gaineko kortex tenporalari loturik dagoen aurretik atzerako gradiente funtzionala agertu zen. Emaitzen arabera, ezker MTG-STGaren (Midal eta Superior Temporal Gyrus) atzealdeak zehazki informazio lexikal eta morfosintaktikoa gordetzearekin eta berreskuratzearekin du zerikusia, eta aurrealdeak, aldiz, sintaktiko-konbinatorialak eraikitzeko mekanismoekin. Ezker kortex tenporalaren gunerik aurreratuenean (erdiko eta gaineko polo tenporalari dagokiona), formatik esanahirako mapping prozesuak irudikatzen direla ikusi da. Hirugarrenik, ezker kortex tenporalaren erantzuna ezkerreko azpiko eremu frontalek kontrolatzen dute (LIFG). Azkenik, ezkerreko eremu parietalek, tartean giro angularrak, aktibazio handiago erakutsi zuten aldagai semantikoarekin lotutako manipulazioetan (adib., genero kontzeptuala eta komunztadurarik gabeko egiturak). Horrek argi uzten du informazio semantikoa prozesatzerakoan funtsezko funtzioa betetzen duela (esaterako, kontzeptuak integratzea eta diskurtso semantikoa integratzea). Orokorrean, aurkikuntza horiek komunztadura sisteman eragiten duten alderdi sintaktiko eta semantikoen garrantzia azpimarratzen dute, eta horrek komunztadura konputazionalari eta hizkuntza ulermenari buruzko ikerketan ateak irekitzen ditu.

Contents

List of Figures

List of Tables

Resumen en castellano

Una vez nos insertamos en el mundo de las palabras, nos acostumbramos a procesar información lingüística de forma automática. Este proceso, ya sea por vía auditiva (a través del lenguaje oral) o visual (a través del lenguaje escrito), permite transmitir información (ej.: ideas, conceptos o intenciones) entre individuos, a través de la aplicación de reglas gramaticales pre-establecidas y aprendidas. Esta característica es común a todas las lenguas y dialectos existentes en la actualidad, independientemente de la gran variabilidad estructural presente entre ellas. Estas reglas y los mecanismos que controlan la forma en que estas reglas operan se denominan *Sintaxis*, permitiendo la construcción de frases y/o oraciones (por ejemplo: *"El Señor de las Moscas" en lugar de "de las señor el moscas"*) (Chomsky, 1955a, 1955b, 1995; Petersson & Hagoort, 2012; Radford, 1997, 2004). De igual forma, el significado de las palabras y los mecanismos que controlan la forma en que la representación ortográfica o fonológica de una palabra, es correlacionada con su referente en el mundo externo (por ejemplo: "El Señor de las Moscas", una novela famosa de William Golding), se denomina *Semántica* (Carnap, 1948; Chierchia & McConnell-Ginet, 2000; Chomsky, 1955b; Dapretto & Bookheimer, 1999; Lyons, 1995).

La distinción entre procesos sintácticos y semánticos y su implicación en mecanismos generales de comprensión, han sido el foco de atención de muchas investigaciones en los últimos años (Binder & Desai, 2011; Binder et al., 2009; Crosson et al., 1999; Graves et al., 2010; Humphries et al., 2006, 2007; Kuperberg, 2007; Kuperberg et al., 2000; Kuperberg et al., 2003; Kuperberg, West, et al., 2008; Lau et al., 2013; Zhang, Y. et al., 2013; Zhang, Y. et al., 2010). Sin embargo, a pesar de la gran cantidad de evidencias experimentales que tratan de explicar cómo el cerebro procesa los diferentes aspectos, sintácticos y semánticos, contenidos dentro de la información lingüística, las regiones neurales involucradas en dichos procesos y la dinámica funcional que se establece entre ellas, es aún un tema controvertido. A pesar de estas contradicciones, a partir de las evidencias experimentales derivadas de estos estudios, se han postulado distintos modelos cognitivos que tratan de desentrañar las distintas etapas de este proceso. En especial, intentan distinguir entre mecanismos de naturaleza puramente sintáctica y aquellos que requieren de una integración sintáctico-semántica, necesarios durante la comprensión de información lingüística. Son varios los modelos postulados a este respecto y a la vez disímiles los supuestos en que se sustentan y las predicciones que se derivan de los mismos.

El procesamiento de la *concordancia gramatical* entre los elementos que forman la frase (como por ejemplo: el sujeto y el verbo o el artículo y el sustantivo), constituye una herramienta clave para dilucidar cómo nuestro cerebro lidia con los diferentes aspectos contenidos dentro de la información lingüística. La concordancia gramatical pone de manifiesto relaciones de dependencia entre diferentes constituyentes de la oración. Estas relaciones operan, generalmente, a través de categorías morfológicas, que indican de forma redundante, la persona (primera, segunda y tercera), el número (singular, plural) y/o el género (femenino, masculino) asociados con distintos constituyentes gramaticales (p. ej.: sustantivos, pronombres, verbos, artículos y adjetivos). Los tipos de constituyentes que intervienen en una determinada relación gramatical, dan lugar a dos tipos diferentes de concordancia: concordancia nominal (entre artículo y sustantivo, sustantivo y adjetivo, entre otros) y concordancia verbal (entre sujeto y verbo).

En general, el procesamiento de la concordancia gramatical requiere de mecanismos cognitivos complejos, que nos permiten entender de quien se está hablando, quien está realizando la acción o quién es el objeto de dicha acción, de ahí su papel primordial en la comprensión de frases y oraciones. Los diferentes tipos de relaciones de concordancia, así como también las categorías morfológicas involucradas en estas relaciones, influyen en menor o mayor grado sobre el proceso de comprensión. Por este motivo, manipulaciones concernientes al tipo de relación de concordancia, o al tipo de categoría morfológica implicada en dicha relación, permitirán desentrañar los mecanismos neuro-cognitivos subyacentes al procesamiento de la concordancia gramatical.

En los últimos años el número de estudios dedicados a la caracterización de estos mecanismos ha ido en aumento. A los estudios pioneros sobre esta temática, centrados en evidencias conductuales, se han sumado estudios que han tratado de caracterizar la dinámica espacio-temporal del procesamiento de la concordancia utilizando técnicas de neuroimagen (electrofisiología y resonancia magnética funcional). Las investigaciones realizadas se han basado fundamentalmente en la comparación entre construcciones gramaticales donde los distintos constituyentes muestran los mismos marcadores morfológicos (construcciones gramaticalmente correctas) y construcciones que incluyen incongruencias gramaticales, que pueden resultar en violaciones sintácticas (por ejemplo: “el mesa”) o no (por ejemplo: “Unagreement” en el español). Sin embargo, a pesar de que algunos estudios han documentado la implicación de algunas regiones cerebrales, la correspondencia entre dichas regiones y los procesos cognitivos subyacentes, está aún por dilucidar. A día de hoy no existe ningún modelo neuro-anatómico que caracterice el proceso de concordancia.

La presente tesis tiene como objetivo investigar las bases neurales de la concordancia gramatical, haciendo énfasis en la distinción entre mecanismos puramente sintácticos (como puede ser la evaluación de la concordancia a partir de marcadores morfosintácticos) y mecanismos que requieren de una integración sintáctico-semántica. Para ello, hemos incluido como parte del trabajo de tesis cinco experimentos, cada uno de los cuales se describe en un capítulo. Los experimentos difieren en el tipo de relación de dependencia manipulada en cada caso (nominal o verbal), así como también en el tipo de categoría(s) morfológica(s) usada(s) para manipular la gramaticalidad (género, número o persona). Los cinco experimentos están dirigidos a responder esta pregunta teórica desde un punto de vista neuro-anatómico, investigando las regiones cerebrales involucradas en dichos procesos, así como también las relaciones funcionales que se establecen entre ellas. La tarea de los participantes en todos los estudios fue realizar un juicio de gramaticalidad dado un set de oraciones o pares de palabras que podían ser gramaticalmente correctas o no. Este factor intentamos mantenerlo constante para evitar posibles efectos relacionados con la tarea experimental.

A continuación se presenta un resumen metodológico de cada uno de dichos estudios (ver Tabla 1.1):

Estudio I: “Is our brain sensitive to gender-marking cues during the computation of local agreement relations?”

Este experimento investiga los mecanismos sintácticos involucrados en el procesamiento de la concordancia nominal desde una perspectiva neuro-anatómica. Para ello manipulamos la congruencia gramatical, utilizando parejas artículo-sustantivo (parejas congruentes o incongruentes), en las que el sustantivo podía presentar la marca morfológica de género transparente (*"-a"* femenino ó *"-o"* masculino: sustantivos transparentes como "mesa" o "faro") o no (sustantivos con marcas opacas como "reloj" o "lápiz"). Los factores semánticos involucrados en el procesamiento de la concordancia fueron silenciados utilizando sustantivos con género gramatical donde las relaciones de concordancia son establecidas mediante marcadores morfosintácticos. Este tipo de manipulación nos permitió distinguir aquellas regiones involucradas en el procesamiento de relaciones de concordancia de naturaleza sintáctica, donde la integración sintáctico-semántica no juega un papel fundamental.

<u>Estudio II:</u> "Parietal circuit distinguishing between living and non-living entities: an fMRI study of gender agreement processing."

Este estudio fue diseñado para investigar a) cómo la información semántica contribuye al establecimiento de relaciones de concordancia gramatical, b) si esta información semántica interactúa con el procesamiento de la información morfosintáctica y c) si esta(s) posible(s) interacción(es) entre la información conceptual y formal, dejan una huella en la respuesta neural. Para ello, manipulamos la concordancia de género entre sustantivos y adjetivos, utilizando oraciones de cuatro palabras. Los sustantivos en español poseen la peculiaridad de exhibir dos tipos diferentes de género: el género conceptual [fenómeno intrínseco de la representación semántica de la palabra] y el género formal [fenómeno sintáctico expresado a través de marcadores morfológicos y/o presente en la representación léxica]. Además, manipulamos el tipo de género de los sustantivos con el fin de potenciar la interacción entre los factores semánticos y sintácticos, durante el procesamiento de la concordancia. Este diseño nos permitió segregar mecanismos subyacentes al procesamiento de la concordancia gramatical. Específicamente, dentro de la red neural involucrada en dicho proceso, distinguimos aquellas regiones funcionalmente sensibles a factores semánticos y sintácticos.

Estudio III: “Nominal and verbal agreement: Two sides of the same coin.”

En los dos primeros estudios investigamos los procesos neuro-cognitivos implicados en el procesamiento de la concordancia gramatical, teniendo en cuenta solamente relaciones de concordancia nominal, entre artículo y sustantivo o entre sustantivo y adjetivo. En el experimento 4 investigamos si los mecanismos subyacentes al procesamiento de la concordancia nominal y verbal son similares. En este caso, la concordancia de número fue manipulada en parejas de artículo – sustantivo y sujeto – verbo. Este diseño nos permitió determinar que la concordancia gramatical, sea nominal o verbal, involucra fundamentalmente las mismas regiones cerebrales. Sin embargo, los mecanismos subyacentes a este proceso, son lo suficientemente sensibles, como para distinguir entre los dos tipos de concordancia.

Estudio IV: “Who is doing what? Left temporal involvement for verbal agreement processing.”

En los experimentos V y VI investigamos la concordancia entre el sujeto y el verbo. La concordancia entre sujeto y verbo implica extraer información gramatical, que posteriormente es asignada a diferentes representaciones semántico-pragmáticas sobre el tipo de participantes (1^{era} persona = participante, 2^{da} = destinatario, 3^{era} = no participante) y su numerosidad (una sola entidad versus un grupo). En este estudio investigamos la concordancia entre sujeto y verbo mediante la comparación de violaciones gramaticales de concordancia de persona y de número. Las oraciones gramaticalmente incorrectas se contrastaron con oraciones gramaticalmente correctas, para determinar si las regiones cerebrales involucradas en el procesamiento de ambas categorías morfológicas eran o no las mismas. Este estudio nos permitió distinguir regiones cerebrales que muestran sensibilidad al tipo de categoría morfológica involucrada en una relación de concordancia. Regiones anteriores del giro temporal medial izquierdo mostraron respuestas significativas cuando las oraciones contenían una violación de persona. Sin embargo, estas regiones no mostraron sensibilidad para violaciones gramaticales de número.

Estudio V: “Where agreement merges with disagreement: fMRI evidence of subject-verb integration.”

En el presente estudio nos centramos en el procesamiento de la concordancia gramatical de persona entre sujeto y verbo. En este caso comparamos incongruencias gramaticales de persona que pueden resultar en oraciones gramaticalmente incorrectas con otras, que por el contrario, resultan en oraciones gramaticalmente correctas. Para esto sacamos provecho de una característica específica de la lengua española, el fenómeno de “Unagreement” (por ejemplo: *Los Pintores*$_{3p.pl.}$ *trajimos*$_{1p.pl.}$...). La comprensión de este tipo de construcciones gramaticales implica un cambio en la interpretación semántica del sujeto (pasando de la tercera persona a primera persona), lo que posibilita que la frase “Los pintores” sea re-interpretada como “Nosotros los pintores”. Este diseño nos permitió distinguir entre las regiones cerebrales encargadas de la evaluación de la concordancia morfosintáctica (involucradas en el procesamiento de la violación de persona y del “Unagreement”) y aquellas encargadas de la integración sintáctico-semántico (involucradas en el procesamiento de las oraciones gramaticalmente correctas que presentan un patrón típico de concordancia y del “Unagreement”). El procesamiento de la concordancia del “Unagreement” evidenció la implicación de regiones parietales asociadas a la integración sintáctica-semántica.

Tabla I. Resumen metodológico de cada uno de los estudios contenidos en la presente tesis.

Estudios	Tipo de estímulo	Tipo de Concordancia (Dependencia)	Categoría morfológica manipulada	Diseño Experimental
Estudio I	Pares de palabras	Nominal (Artículo – Sustantivo)	Género	Gramaticalidad x Transparencia
Estudio II	Oraciones de 4 palabras	Nominal (Sustantivo – Adjetivo)	Género	Gramaticalidad x Tipo de Género [Conceptual – Formal]
Estudio III	Pares de palabras	Nominal (Artículo – Sustantivo) Verbal (Sujeto – Verbo)	Número	Gramaticalidad x Tipo de Dependencia
Estudio IV	Oraciones de 8 a 10 palabras	Verbal (Sujeto – Verbo)	Número – Persona	Gramaticalidad x Tipo Violación [Número – Persona]
Estudio V	Oraciones de 8 a 10 palabras	Verbal (Sujeto – Verbo)	Persona Unagreement	Gramaticalidad x Tipo de Violación [Persona – Unagreement]

Los estudios anteriormente descritos han tratado de caracterizar las bases neurales del procesamiento de la concordancia gramatical, poniendo especial atención a la distinción entre mecanismos sintácticos y semánticos. Los principales resultados derivados de estos estudios se resumen a continuación.

- En primer lugar, encontramos una disociación funcional entre construcciones gramaticales correctas e incorrectas. Por un lado, el procesamiento de construcciones gramaticalmente incorrectas involucró una red neural fronto-parietal bilateral, que fue asociada a operaciones no específicas del lenguaje, previamente relacionadas al control y monitoreo de posibles conflictos entre la señal de entrada y la conducta correspondiente a la realización de la tarea. Por otro lado, el procesamiento de construcciones gramaticalmente correctas activó una red neural fronto-temporo-parietal, lateralizada al hemisferio izquierdo. Esta red fue relacionada con procesos específicos del lenguaje, previamente asociados a diferentes aspectos del procesamiento de frases y/o oraciones.

- En segundo lugar, las manipulaciones experimentales utilizadas evidenciaron un gradiente funcional antero-posterior, asociado a la corteza temporal medial y superior, incluyendo el polo temporal. Específicamente, la parte posterior del giro temporal medial y superior, izquierdo, parece estar relacionada con el almacenamiento y la recuperación de información léxica y morfosintáctica. Mientras que la porción anterior de esta región, mostró relación con los mecanismos de construcción sintáctica y procesos de combinación morfosintácticos. Además, la parte más anterior de la corteza temporal izquierda, incluyendo el polo temporal medial y superior, mostró incrementos en su activación asociados a procesos de integración sintáctico-semántico.

- En tercer lugar, la respuesta de la corteza temporal izquierda parece estar controlada por regiones frontales, específicamente por el giro frontal inferior izquierdo. Todos los experimentos contenidos en la presente tesis, evidencian un acoplamiento funcional de las regiones temporales y frontales. El gradiente funcional que muestra la región temporal medial y superior izquierda replica el gradiente funcional previamente descrito para el giro frontal inferior izquierdo.

- En cuarto lugar, regiones parietales izquierdas, como el giro angular, mostraron mayor sensibilidad a aquellas manipulaciones que implicaron modulaciones de factores semánticos (por ejemplo: género conceptual y construcciones complejas como el *Unagreement*), evidenciando el papel primordial que esta región tiene en el tratamiento de diferentes tipos de información semántica (por ejemplo: procesos de integración conceptual o procesos de integración semántico-discursiva).

- Por último, el patrón de respuesta de las regiones frontales, temporales y parietales, del hemisferio izquierdo, subyacentes al procesamiento de frases y/o oraciones, evidenció incongruencias en relación a los modelos teóricos (neuro-anátomicos y neuro-cognitivos) que tratan de explicar cómo este proceso tiene lugar. Los resultados derivados de estos siete estudios están en desacuerdo con la diferenciación entre rutas ventrales y dorsales asociadas a mecanismos sintácticos y/o semánticos respectivamente. La red neural resultante de estos estudios ha mostrado muchas regularidades. Sin embargo, también ha evidenciado su carácter peculiar, mostrando variaciones en función del tipo de relación de dependencia involucrada, el tipo de categoría morfológica manipulada, así como también el patrón de gramaticalidad.

Finalmente en el capítulo de discusión general proponemos un modelo neuro-anatómico, que da cuenta de los resultados obtenidos en los diferentes estudios, poniendo énfasis en la distinción entre factores sintácticos y semánticos subyacentes al proceso de evaluación de la concordancia.

Chapter 1.

General Introduction

When we are reading a text such as *"...como si sobre sus cabezas hubiera caído la gota de agua que forman las estalactitas..."* (literally: "…as if on their heads$_{\text{plural}}$ had$_{\text{singular}}$ fallen [the drop of water][1]$_{\text{singular}}$ that form$_{\text{plural}}$ stalactites…") (Lezama Lima in Paradiso, page 486-487) with apparent incongruities between different sentence constituents, we become aware of the constant computation of grammatical relations (i.e., agreement) that is necessary to combine the different words and grasp the idea that the author wants to convey. The influence of this phenomenon on the existing languages varies over a very wide range, from languages where this phenomenon is highly present to languages where it is almost absent (see Corbett, 2006 for an extensive revision of the variability of this phenomenon across languages). However, independently of the intrinsic complexity and the structural diversity across languages (Miyagawa, 2010; Miyagawa et al., 2014), the basic core of all these systems falls on the common need to transfer information between individuals (e.g., ideas, concepts, intentions, etc.), following some specific rules.

These rules and the mechanisms controlling the way in which these rules operate, structuring words into phrases and sentences (e.g., *"flies the of lord"* versus *"lord of the flies")*, have been defined as *Syntax* (Chomsky, 1955a, 1955b, 1995; Petersson & Hagoort, 2012; Radford, 1997, 2004). In the same way, the meaning of each specific word and the mechanisms controlling the way in which the orthographic or the phonological representation of a word is mapped with its referent in the external world (e.g., *"Lord of the flies[2]", a famous* novel by William Golding) have been defined as *Semantics* (Carnap, 1948; Chierchia & McConnell-Ginet, 2000; Chomsky, 1955b; Dapretto & Bookheimer, 1999;

---

[1] The brackets comprise the noun-phrase structure.

[2] Out of context, it is a semantically incongruent sentence.

Lyons, 1995). The distinction between syntactic and semantic processes and their specific roles guiding language comprehension has been the focus of many investigations in the last seventy years (Binder & Desai, 2011; Binder et al., 2009; Crosson et al., 1999; Graves et al., 2010; Humphries et al., 2006, 2007; Kuperberg, 2007; Kuperberg et al., 2000; Kuperberg et al., 2003; Kuperberg et al., 2007; Kuperberg et al., 2006; Kuperberg, Sitnikova, et al., 2008; Lau et al., 2013; Zhang, Y. et al., 2013; Zhang, Y. et al., 2010). However, despite the extensive amount of evidence on how the brain deals with this kind of information, three essential and still open questions are [1]does the brain have a circuit specialized in the computation of the grammatical relations among words, [2]whether this neural circuit, if it is indeed found, is fine-tuned to the syntactic or semantic signals embedded in our linguistic code, and [3]whether the interaction between these two different types of information leaves a trace in the brain response.

A convenient arena to study these questions is offered by the Spanish agreement system (see MacWhinney et al., 1989, for a discussion of the importance of agreement cues across languages). How could the investigation of this phenomenon contribute to distinguish between purely syntactic mechanisms and those where semantic and syntactic factors interact during language comprehension? The agreement phenomenon, as the example by Lezama Lima illustrates, is apparently nourished by different formal (e.g., the numerosity of the different sentence constituents – singular or plural –) and conceptual information that is encoded in the same linguistic representation. The mapping of these apparently divergent signals into a coherent meaning is an automatic process that develops in less than a second. However, during this second, different mechanisms can be temporally distinguished (Friederici, 1995, 2004, 2011; Molinaro, Barber, et al., 2011). Thus, taking advantage of the diversity of the Spanish agreement system it is possible to tune down some of these factors and, as a consequence, boost others, allowing us to disentangle the different mechanisms sub-serving the agreement processing. The neuro-cognitive characterization of the agreement phenomenon constitutes the broad goal of this thesis. Each one of the experimental chapters will address different aspects of this phenomenon underneath the common prism of the neuroimaging techniques.

Before looking at this phenomenon from a neuro-cognitive perspective, we want to offer some key concepts about agreement, putting more emphasis on the Spanish agreement system, which is the focus of this thesis.

1.1 Agreement

Agreement, one of the pillars of language structure was defined by Steele in1978 as follows:

> *"The term agreement commonly refers to some systematic covariance between a semantic or formal property of one element (the controller) and a formal property of another (the target)..."* (Steele, 1978 page 610).

According to this concept, the critical role of agreement computation is to highlight the mutual dependence between different sentential elements. The establishment of these relations is carried out through agreement features (a certain property of an element, according to the concept of Steele, 1978), the basic building blocks of this process. Agreement features have been defined as partial descriptions of linguistic objects directly involved in agreement computation, whose function is to capture regularities between sentential/phrasal elements by signaling referents and their roles to the reader/hearer (Corbett, 2003, 2006). For instance, in Spanish, agreement features are morpho-syntactic[3] categories that signal the person, number, and gender (but also see Corbett, 2006 for differences across languages) information associated with different sentence constituents (Mancini et al., 2013a, 2013b). These agreement features express their morpho-syntactic values (e.g., in Spanish: number [singular, plural], person [first, second and third] and gender [feminine, masculine]) according to language specific rules. Getting back to the agreement concept, an agreement relation involves a controller and a target. The controller element specifies the feature value it imposes on the target. The values of a morpho-

---

[3] Agreement features having a role in both syntax and morphology.

syntactic feature may be selected according to contextual or formal criteria (semantic or formal properties, according to the concept of Steele, 1978).

Thus, agreement comprises those operations concerning the regular assignment of agreement feature values, driving the agreement information flow required for the proper interpretation of a sentence/phrase. However, the devices used to signal these systematic relations among words differ across languages (see MacWhinney et al., 1989, for a discussion of the importance of agreement cues across languages). For example, languages such as Japanese identify participants in the event, their roles (e.g., agent, patient) and their attributes (e.g., definiteness) through discourse-based devices such as topic-marking, i.e. by morphologically marking the element that represents the topic of the sentence. On the other hand, Romance languages like Spanish or French efficiently rely on agreement and agreement features: the gender, number and person information carried by nouns is displayed in several other sentence parts. As exemplified in (1) below, in Spanish, nouns must agree in gender and number with determiners, adjectives and pronouns, in local as well as non-local relations and similarly, verbs must agree in number and person with predicative subjects, objects and pronouns.

(1) Los$_{\text{3.pl.masc}}$[4] libros$_{\text{3.pl.masc}}$ que ella$_{\text{3.sg.fem.}}$ quiere$_{\text{3.sg.}}$ son$_{\text{3.pl.}}$ míos$_{\text{3.pl.masc}}$.
The books$_{\text{3.pl.masc}}$ that she$_{\text{3.sg.fem}}$ wants$_{\text{3.sg}}$ are$_{\text{3.pl}}$ mine.

However, what makes the Spanish agreement system so special to disentangle the operation of syntactic and semantic processes? The key of this question relies on how these morpho-syntactic features are structured and accessed in Spanish, which determines how agreement information is processed in a given dependency (see Molinaro, Barber, et al., 2011 for an extensive review of agreement processing)[5]. From a linguistic perspective, in

---

[4] Most agreement feature values are glossed with a symbol built from a subset of the following three elements: an Arabic number expressing the person feature value (1, 2, or 3), an abbreviation expressing the number feature value (sing. singular, or pl. plural), and a different abbreviation expressing the gender feature value (masc. masculine, or fem. feminine).

[5] These authors demonstrated that agreement processing is sensitive to both the type of morpho-syntactic feature and the type of sentence constituent involved in the resolution of an agreement relation.

Spanish it is possible to distinguish between two different types of grammatical relations: verbal and nominal agreement (agreement and concord, according to some theoretical frameworks, Pollard & Sag, 1994; Wechsler, 2009; Wechsler, 2011; Wechsler & Zlatić, 2000; Wechsler & Zlatić, 2003). They occur in different syntactic domains and involve different features and different interpretive properties (i.e., the semantic-pragmatic information concerning the argument referent). Thus, verbal agreement usually involves subject-verb dependencies (henceforth, subject-verb or verbal agreement), while nominal agreement takes place in the noun-phrase (NP) domain, i.e. within the same constituent. Moreover, subject-verb agreement usually involves only one (i.e., only the verb such as *Duerme*$_{3.sg}$, Sleeps) or two elements, that is, the verb and its argument(s) (e.g., *El gato*$_{3.sg}$ *duerme*$_{3.sg}$ [The cat sleeps][6]), while nominal agreement generally applies to several different elements in several syntactic positions, which can be in a local as well as a non-local relation with the lexical head: determiners, adjectives and nouns (e.g., *La*$_{fem.sg}$ *casa* $_{fem.sg}$ *roja*$_{fem.sg}$ *que estaba abandonada* $_{fem.sg}$ *fue vendida* $_{fem.sg.}$ [The red house that was abandoned was sold]). Also, different features are usually involved: in Spanish, subject-verb agreement involves person and number features, while number and gender are implicated in nominal agreement. Finally, the analysis of the two types of configurations implies the decoding of the underlying syntactic and semantic representations that significantly differ in complexity. On the one hand, analysis of a subject-verb agreement relation implies not only the extraction of morpho-syntactic information from the input, but also the projection of a complex representation in which the subject noun is associated with a specific role (e.g., agent, patient) in the unfolding of an event, e.g. *él* [he] in the dancing event described in *Él baila* [He dances]. In contrast, the interpretation of a nominal agreement structure in isolation, such as "*la casa*" [the house] simply implies matching a noun with its real-world referent, without building any thematic representation. As is evident from these examples, the morpho-syntactic expression of a given feature is closely related to its corresponding interpretative properties. This relationship drives the interpretation of the feature and hence

---

[6] Literally translated into English.

impacts the comprehension processes in a different way (but see Mancini et al., 2013a, 2013b; Sigurdsson, 2004, 2009; 2011 for different proposals).

The Spanish agreement system comprises a variety of canonical and non-canonical options (i.e., differing not only in their morpho-syntactic and semantic-pragmatic values, but also in the way in which these two factors interact) where it is possible to distinguish many different, but interlacing, factors embedded in the computation of an agreement relation: syntactic, morphological, semantic, and pragmatic[7]. The current thesis takes advantage of the diversity and richness of the Spanish agreement system, in order to characterize the different mechanisms (e.g., the evaluation of the morpho-syntactic subject-verb consistency and the semantic integration process) supporting successful comprehension of written phrase/sentences from a neuro-anatomical point of view. This diversity will allow us to experimentally manipulate different factors (i.e., type of dependency and type of feature) giving us the opportunity to characterize not only the mechanisms underlying general agreement processing, but also the possible interaction(s) between semantic and syntactic factors constraining the interpretation of an agreement relation. However, before getting into the main questions, I would like to address some general topics relevant to the purpose of the current investigation.

The following section gives a brief overview over the structure of the three different morpho-syntactic features (Gender, Number and Person) used by the Spanish agreement system. They have been organized as follows. First, a general description of the features is exposed, including examples that illustrate how the features express their values across languages. Then, some details about how these features are represented in Spanish are reported comprising all grammatically canonical and non-canonical cases. Finally, a description on how each morpho-syntactic feature operates in the Spanish agreement system is presented including its corresponding semantic-pragmatic interpretation properties.

---

[7] Regarding this point Corbett (2003) Corbett (2003) claims that “Agreement is increasingly recognized as of interest not just for syntax, semantics, and morphology, but also for acquisition, psycholinguistics and computational applications” (Corbett, 2003, p. 109).

1.2 Agreement Features

Gender. The morpho-syntactic category of *Gender* provides a classification of nouns based on a two- (or sometimes three-) way system that comprises feminine and masculine entities. According to the review of Corbett (1991), where more than 200 languages were extensively explored, the gender system of a given language exhibits often two or more classes of nouns. In Romance language, such as Spanish or Italian, this classification comprises a class where the gender corresponds to the biological sex distinction. In contrast, in language such as Qafar, the gender classification is based on phonological and morphological criteria without any conceptual information.

Interestingly, the Spanish gender system distinguishes between two types of nouns. On the one hand, most nouns referring to animate entities are assigned to one of two genders – masculine or feminine – depending on the biological sex of the referent (the conceptual system, according to Corbett, 1991). On the other hand, nouns referring to inanimate entities or abstract concepts are also assigned to one of two genders, but since their referents are not endowed with a sex, the assignment follows morphological and/or phonological criteria, such as whether the noun ends in "–a" or "–o" (i.e., transparent nouns, Akhutina et al., 1999; Bates et al., 1995): Nouns ending in "–o" are usually masculine, while nouns ending in "–a" are usually feminine (the formal system, according to Corbett, 1991 with conceptual gender nouns also following this regularity in most of the cases (abuelomasc./abuelafem. [grandfather/grandmother]). However, this syntactic rule has numerous exceptions. For instance, there are some irregular nouns ending in "–o" or "–a" that are classified as feminine or masculine respectively, which is the opposite gender value that its corresponding ending predict (e.g., *mano* [hand] or *día* [day]). In addition, there are many opaque nouns whose ending ("–l", "–z", "–j", "–e", "–n") does not contain information about the morphological gender value (e.g., *reloj*$_{masc.}$ [watch] or *vejez*$_{fem.}$ [eld]).

Regarding how gender agreement relations are established in Spanish, nouns must redundantly agree in gender with determiners, adjectives, pronouns and verbs, in local as well as non-local relations. For instance, in a headline such as in (2) below, the morphological gender value of a transparent and formal subject-noun controls the gender value of the following adjectives (i.e., "calificado" is an adjective derived from a participle form of a verb). The feature gender value of the subject-noun "artículo" is morphologically signaled by the canonical ending of the masculine gender marker. Although this is a highly canonical example, Spanish gender agreement system is as diverse as the gender types explained above. Examples (3) and (4) illustrate this variability. In these cases, the morphological gender value of an opaque subject-noun controls the gender value of the target elements (i.e., in this case, these elements correspond to a reduce object passive relative clause), which vary between the masculine and the feminine forms. Specifically, in (3) below, the feminine form of "editorial" is refers to a publishing house. However, it is also plausible to find the masculine form of "editorial" (as exemplified in (3) below), which refers to an anonymous article published in the newspaper. The relation between form and meaning, at least in this particular case, seems to be critical to the interpretation of such grammatical relation, and consecutively crucial to the comprehension process.

(2) Artículo$_{\text{masc.}}$ calificado$_{\text{masc.}}$ de conservador$_{\text{masc.}}$.
Paper qualified as conservative.

(3) Editorial$_{\text{fem.}}$ calificada$_{\text{fem.}}$ de conservadora$_{\text{fem.}}$.
Publisher qualified as conservative.

(4) Editorial$_{\text{masc.}}$ calificado$_{\text{masc.}}$ de conservador$_{\text{masc.}}$.
Editoral qualified as conservative.

Number. The morpho-syntactic category of *Number* classifies pronominal and nominal argument according to the cardinality of the referent (Mancini et al., 2013a, 2013b). Some languages such as Spanish, Italian or English have a basic system with a singular-plural distinction. While singular refers to a single entity, plural refers to more than one real-world entities (e.g., *casa*$_{\textit{sing.}}$*/casas*$_{\textit{pl.}}$ [house/houses]). Although, according to Corbett

(2000), there are at least four different number systems. For instance, in Upper Sorbian three different categories can be distinguish, singular, dual and plural, where dual refers to only two distinct real-world referents. It is also possible to find languages with more complex systems, where four or five morphological number values can be distinguished. In most of the modern languages, nouns are frequently morphologically marked for number. However, some languages such as Classical Chinese or Kawi do not have plural forms of nouns or pronouns (Corbett, 2000). In these cases, number feature values can be indicated by quantifiers or by conjoining pronouns (according to Becher & Oka, 1974; cite taken from Corbett, 2000). Indeed, it is also possible to find languages with a verbal number system, marking the number of events rather than the number of individuals (Corbett, 2000, 2006). For instance, the examples (5) and (6) used by Corbett (2000, p. 246) illustrates this phenomenon in Chadic. In this example, the number of events is signaled in the verb. In both cases the subject (“Naa” [I]) is singular and the object (“su” [them]) is plural. However, in the latter case (example 6 below) the plural verb (a”aikee) indicates that the number mark of the *sending-event* involved more than one time or more than one place (as example (6) illustrates).

(5) Naa aikee su …
I sent them at the same time to same place.

(6) Naa a”aikee$_{\text{pl.}}$ su …
I sent$_{\text{pl.}}$ them at the different times to same place.
at the same time to different places.
at the different times to different places.

Specifically, Spanish nouns adhering to a binary system can be usually associated with singular and plural number forms (Corbett, 2000). In most of the cases, the plural form of the nouns are morphologically marked by adding an “–s” at the end of the word (e.g., *abuelo*$_{\textit{sing.}}$*/abuelos*$_{\textit{pl.}}$ [grandfather/grandfathers]). However, despite this regularity, there is a group of Spanish nouns, generally abstracts, which are lexically marked for number. They are only singular (e.g., *salud* [health] or *honestidad* [honesty]) or plural (e.g., *añicos* [smithereens] or *víveres* [provisions]). In Spanish, as in many others languages, it is possible to semantically categorize the nouns as countable or uncountable (count-mass distinction in Corbett, 2000). While the countable nouns refer to entities that have a singular and a plural form (*manzanas*$_{pl.}$/*manzana*$_{sing.}$ [apples/apple]), the uncountable ones refer to entities that have only the singular form (*azúcar*$_{sing.}$ [sugar]). The uncountable nouns frequently correspond with things that are too small or too amorphous to be counted. Regarding Spanish number agreement, at least in its canonical form, nouns must agree in number with determiners, demonstratives, adjectives, verbs, possessives, and pronouns, in local as well as non-local relations. All these sentence constituents should also be morphologically marked for number (e.g., determiners (*el*$_{sing.}$/*los*$_{pl.}$ [the/the]), demonstratives (*este*$_{sing.}$/*estos*$_{pl.}$ [this/these]), possessives (*mío*$_{sing.}$/*mios*$_{pl.}$ [my/mine), adjectives (*blanco*$_{sing.}$/*blancos*$_{pl.}$ [white/white]) and verbs (*baila*$_{3p.sing.}$/*bailan*$_{3p.sing.}$ [dances/dance]).

Person. According to Corbett (2006), *Person* is not only a morphological inherent feature of the pronouns, but also a contextual feature of the verbs. This morpho-syntactic feature reflects the basic structure of a speech act relative to the speaker (Benveniste, 1966; Mancini et al., 2013a, 2013b; Siewierska, 2004), pointing out the relation between a given argument and its discourse role (Speas, 2004a, 2004b). Most modern languages involve a three-way distinction of speaker, hearer and third party, distinguishing between first, second and third person (Siewierska, 2004). A first person pronoun or a first person verb are typically linked to the presence of a speaker; similarly, second person is associated with an addressee, while third person invokes the individual(s) being talked about by the speaker and addressee, hence non-participant(s) in discourse (Benveniste, 1966; Harley & Ritter, 2002). Despite this generalization, according to Siewierska (2004) who compares the structure of the morphological category of person across 700 languages, there are at least four different person paradigms which did not distinguish between the three person feature values: 1) the first and the second persons may be homophonous and distinguished from the third [1=2≠3]; b) the second and the third persons may be homophonous and distinguished from the first [2=3≠1]; c) the first and the third persons may be homophonous and distinguished from the second [1=3≠2] and d) the same value may be used for all the three persons [1=2=3] (see Siewierska, 2004 for more details about the structure of person paradigms, page 75-119).

Regarding how Spanish person agreement operates, the systematic covariance of person feature between different sentence constituents is exemplified in (7) and (8) below. This example illustrates the typical person agreement relation in which the person feature of the subject-noun controls the person information of the verb and the following pronouns.

(7) Tú$_{2p.}$ repasabas$_{2p.}$ cada día la materia escolar.
You reviewed every day the school subject.

(8) [Los estudiantes]$_{3p.}$ repasaban$_{3p.}$ cada día la materia escolar. Por eso, <u>ellos</u>$_{3p.}$ obtenían$_{3p.}$ buenos resultados.
The students reviewed every day the school subject. That is why, they got good results.

The following table presents a summary of the information concerning the morpho-syntactic expression of gender, number and person according to Spanish agreement system. A distinction between formal and conceptual gender is included due to its difference in terms of the morpho-syntactic and interpretive values set by the Spanish agreement system.

Table 1.1. Summary of the morpho-syntactic and semantic-pragmatic values corresponding to three different features (Gender, Number and Person). The assignment of the feature values was carried out according to a binary system.

Features	Expression (Example)	Morpho-syntactic values	Semantic-pragmatic values
Formal Gender	Feminine (*La Mesa*)	[+feminine, -masculine]	[-Feminine, -Masculine]
	Masculine (*El Libro*)	[-feminine, +masculine]	[-Feminine, -Masculine]
Conceptual Gender	Feminine (*La Abuela*)	[+feminine, -masculine]	[+Female, -Male]]
	Masculine (*El Abuelo*)	[-feminine, +masculine]	[-Female, +Male]
Number	Singular (*La Mesa*)	[+singular, -plural]	[+One, -Many]
	Plural (*Las Mesas*)	[-singular, +plural]	[-One, +Many]
Person	1rst (*Yo bailo*)	[+1rst, -2nd]	[+Speaker, -Addressee]
	2nd (*Tú bailas*)	[-1rst, +2nd]	[-Speaker, +Addressee]
	3rd (*Él baila*)	[-1rst, -2nd]	[-Speaker, -Addressee]

1.3 Linguistic Theoretical Frameworks of Agreement

From a theoretical point of view, two divergent perspectives can be identified trying to explain how agreement processing occurs. On the one hand, under a *strictly syntactic approach*, syntactic operations are regarded as modular machinery which control a finite set of formal procedures through a unique operation, called *Agree* (Chomsky, 1955a, 1995, 2000, 2001). According to this approach, this process is unidirectional and asymmetrical, in the sense that the first element of a sentence controls the information flow to the next element that inherits the feature value of the previous one. This theory suggested that the interaction between syntactic and semantic information occurs only at the output level, after the syntactic building-up processes. In processing terms, this theoretical framework proposes that the system would extract the morpho-syntactic feature value from the controller without differentiating among person, number, and gender (i.e., without inflection, such as person, number and gender features on determiners, adjectives and verbs). This proposal implies a unified account of verbal and nominal agreement. In verbal agreement, a noun phrase (e.g., *el gato* [the cat]) enters the process with valued person and number features (3rd person, singular number), which will be properly copied by Agree onto the unvalued verb (e.g., *el duerme* [he sleeps]). This perspective suggests that nominal agreement does not require any specialized mechanism compared to verbal agreement (Carstens, 2000, 2001). According to this proposal, initially *Agree* operation would be blind to the discourse and thematic functions of the sentential/phrasal elements involved in an agreement dependency.

On the other hand, a *lexicalist approach* proposes that the word meaning could modulate our formal linguistic code (Pollard & Sag, 1994; Wechsler, 2009; Wechsler, 2011; Wechsler & Zlatić, 2000; Wechsler & Zlatić, 2003). For these authors, features' values are stored in the lexicon and assigned directly from semantics, implying that syntactic and semantic information equally contribute and also interact during the comprehension process. These authors emphasize the intrinsic differences characterizing nominal and verbal grammatical relations. In their view, there exist two different types of features: *index* *features,* which contain semantic information concerning the referent of a noun, and *concord features* (i.e., purely morpho-syntactic features). Crucially, each type of feature is accessed by different sets of syntactic processes (Wechsler & Zlatić, 2003). Index features, with referential properties, permit the identification of an argument referent: whether it is a male or female individual, a single entity or a multitude, a speaker, an addressee or a non-participant. In contrast, concord features do not involve referential indices, but only morpho-syntactic properties: first, second or third person morphology, singular or plural, masculine or feminine gender marking. According to this theoretical framework, this distinction gives rise to two grammatically different processes: concord agreement, which applies to subject-verb and anaphor-antecedent agreement, and nominal agreement, which operates within noun phrases and relies on their set of morpho-syntactic features. Compatible features between the members of index and concord relations are then *unified*.

These two divergent theoretical frameworks have a marked influence on the subsequent neuro-cognitive investigations regarding the phrase/sentence comprehension processing. The vast majority of these studies have evaluated the veracity of the different assumptions comprised in these two theories. The symmetry, the directionality, the sequentiality, and/or the influence of lexico-semantic aspects over the processing of formal information, have been used as critical points to contrast or to corroborate the linguistic theoretical accounts. This debate has also permeated the neuro-cognitive models of sentence comprehension, with proposals extensively pervaded by the *strictly syntactic approach* and proposals clearly guided by the *lexicalist account.* On the one hand, the neuro-cognitive model suggested by Friederici (Friederici, 2011, 2012) illustrates the first case; whereas on the other hand the Memory, Unification and Control Model (MUC) provided by Hagoort (Hagoort, 2003a, 2005, 2013) illustrates the second case.

So far, the previous sections provided an overview of the insights gained from the linguistic theoretical aspects of agreement, with a special focus on how syntactic and semantic factors might mediate the interpretation of an agreement relation and therefore the comprehension process. The following sections attempt to provide a description of the mechanisms underlying agreement processing from a neuro-cognitive point of view.

1.4 Neuro-cognitive Mechanisms Underlying Agreement Processing: ERP Evidence

In the second half of the 19th century psycholinguistics studies were mainly prompted by the introduction of behavioral analyses (i.e., difference in decision times and error rates between experimental conditions) as measures reflecting how a (a) certain cognitive mechanism(s) is(are) implicated during the processing of linguistic inputs. Empirical evidence derived from behavioral studies laid the bedrock of the pioneer neuro-cognitive models of language comprehension and production (for some comments about this topic see Box 1.1). Since the overarching aim of this thesis is to disentangle the neural correlates of agreement processing, we will not devote special attention to behavioral findings in this general section. Those major behavioral findings relevant to some of the experiments included in this thesis will be presented and discussed in the corresponding experimental chapter. Keeping this in mind, we will organize the subsequent sections as follows. Firstly, we will present the major electrophysiological findings focusing on the chronology of the different processing stages of agreement computation. Secondly, we will discuss the main experimental evidence concerning how agreement processing is mapped onto the brain circuits. Finally, we will return to the most relevant neuro-anatomical models that have been put forward in this regard.

One of the most extensively used experimental techniques with high temporal resolution is that of Event-Related Brain Potentials (ERPs). This electrophysiological method measures small changes (occurring about <=1 ms) in the electrical activity of the post-synaptic neurons, time-locked with a sensory stimulus or a cognitive event (Handy, 2005; Rugg & Coles, 1995; Rugg et al., 1986). As a consequence, it allows the characterization of the temporal dynamics of a given neuro-cognitive mechanism. In particular, agreement processing has been extensively studied using ERPs. The combination of behavioral and ERP data have provided a critical inflection point in the agreement literature. The vast majority of these studies investigated agreement comprehension processing by comparing well-formed with ill-formed constructions – which present *agreement feature* mismatches – (see Friederici, 2011, 2012; Friederici et al., 2003; Molinaro, Barber, et al., 2011 for some revisions of this topic). For instance, De Vincenzi et al. (2003) contrasted semantic and syntactic subject-verb agreement violations in Italian combining ERPs and reading-time data. The electrophysiological and the behavioral results reported by these authors converge, suggesting that the two types of agreement violations – semantic and syntactic – differed in their temporal dynamics. Both techniques showed that the detection of a syntactic violation is faster than the semantic violation. ERP responses allowed authors to temporally characterize the processing of syntactic and semantic agreement violation. While syntactic anomalies elicited a left anterior negativity effect followed by a conspicuous positive effect occurring around 600 ms, semantic anomalies elicited a negative effect that started later than the negative component associated with syntactic anomalies.

This new approach allowed researchers to disentangle agreement comprehension processing in a fine-grained way. In general terms, the empirical ERP evidence highlighted that in agreement comprehension three[8] distinct processing stages can be functionally distinguished (see Molinaro, Barber, et al., 2011 for a review). Each one of these stages responds to different agreement manipulations. Specifically, in an earlier time interval (between 300 and 500 ms) two effects have been reported. The first is a negative effect with a typical left anterior topographical distribution (Left Anterior Negativity, LAN; Barber & Carreiras, 2005; Friederici, 1995; Friederici et al., 1996; Hagoort et al., 2003; Munte et al., 1993; Zhang, Y. et al., 2010) that has been associated with the detection of morpho-syntactic violations (Friederici, 2011, 2012; Molinaro, Barber, et al., 2011; Silva-Pereyra & Carreiras, 2007). The LAN effect differs from a more posteriorly distributed effect found in a similar time interval, the N400 component (Clements-Stephens et al., 2012; Kutas & Federmeier, 2000; Kutas & Hillyard, 1983). This negative effect is usually thought to reflect lexical-semantic processing difficulties, as well as contextual and world-knowledge predictability (Hagoort et al., 2004; Kutas & Hillyard, 1984; Molinaro et al., 2012; Molinaro et al., 2010).

---

[8] Among others language related components such as ELAN and sLAN that appear to be very inconsistent, varying as a function of the task, the type of stimuli, the stimulation modality and the experimental manipulation (Bornkessel-Schlesewsky & Schlesewsky, 2009; Friederici, 1995; Friederici et al., 1996).

In a subsequent temporal interval, agreement mismatch-related processing has normally been found to give rise to a positive deflection, arising about 600 ms post-stimulus onset (P600) (Barber & Carreiras, 2005; Mancini et al., 2011a, 2011b; Silva-Pereyra & Carreiras, 2007). Several lines of evidence have indicated that the P600 is related to integration efforts between the presently-processed elements and the previous context, based on both semantic and syntactic information (Friederici, 2011; Kaan et al., 2000; Kim, A. & Osterhout, 2005; Kolk et al., 2003; Kuperberg et al., 2007), re-analysis processes (Barber & Carreiras, 2005; Carreiras et al., 2004; Molinaro, Barber, et al., 2011), or access to discourse-related information (Brouwer et al., 2012; Kaan & Swaab, 2003). From a domain-general perspective, the P600 has been functionally interpreted as indexing conflict-monitoring processes aimed at detecting errors, and triggering corrective actions when there is a mismatch between the predicted and the observed event (van de Meerendonk et al., 2011; van de Meerendonk et al., 2009; van de Meerendonk et al., 2010).

The functional distinctions between these three ERP components (Figure 1, LAN – N400 – P600) have been extensively discussed in the last 20 years. In general terms, based on this functional distinction some authors have suggested that agreement comprehension comprised three distinct processing phases (Mancini et al., 2013a, 2013b; and see Molinaro, Barber, et al., 2011 for a review of this topic):

I) ***Feature consistency checking.*** During this stage, the feature consistency (i.e. consistency in the person, number and/or gender values) between different elements is evaluated at the morpho-syntactic level. This operation has been associated with the LAN effect (Barber & Carreiras, 2005; Friederici, 1995; Friederici et al., 1996; Hagoort et al., 2003; Munte et al., 1993).

II) ***Integration of incoming information*** [i.e., *Form-to-meaning mapping*; (see Bianchi, 2006; Sigurdsson, 2004, 2009, 2011) or *Semantic* or *Syntactic Unification* according to Hagoort (Hagoort, 2003a, 2005, 2013)]. During this stage the formal properties of a sentence/phrasal constituent is linked to its meaning in order to assign an interpretation to the agreement dependency.

This operation has been associated with the N400 effect (see Lau et al., 2008 for a review of this topic) or with the early phase of the P600 component (Brouwer et al., 2012; Brouwer & Hoeks, 2013; Hoeks & Brouwer, 2014; Molinaro, Barber, et al., 2011).

III) ***Reanalysis/repair processing*** [i.e., *Control* according to (Hagoort, 2005, 2013) or *Conflict monitoring resolution* in the functional Magnetic Resonance Imaging (fMRI) literature (van de Meerendonk et al., 2011; van de Meerendonk et al., 2009; van de Meerendonk et al., 2010)]. If during the processing of an agreement relation a conflict between the expected and the perceived input is detected the system should trigger a mechanism responsible for the implementation of attentive mechanisms that permit the detection of possible behavioral mistakes and if it is possible repair the error (cf. van de Meerendonk et al., 2009 for a review of conflict-monitoring mechanisms in language processing). This operation has been typically associated with the P600 effect (van de Meerendonk et al., 2011; van de Meerendonk et al., 2009; van de Meerendonk et al., 2010).

Indeed, the temporal characterization of agreement processing enabled researchers to propose strong claims such as those suggested by Molinaro, Barber, et al. (2011): *"The product of agreement computation is the syntactic structure of the message, but this product could be achieved by also accessing non-syntactic cognitive representations"* Molinaro, Barber, et al. (2011, p. 927). However, despite the large amount of empirical evidence supporting this generalization, there are also ERPs and behavioral findings that are difficult to reconcile with this perspective. For instance, these three ERP components (LAN – N400 – P600) have also been correlated with a variety of tasks involving different experimental manipulations (Bornkessel-Schlesewsky & Schlesewsky, 2009). Table 1.1 illustrates this controversial scenario. This disagreement concerns mainly the N400 and the P600 effects (see Table 1.1) questioning the functional-specificity of these language-related neural responses. A potential solution to address this issue has been offered by neuroimaging techniques. Having information about the neural network(s) (i.e., not only the brain regions, but also the functional relations between them) underlying a given cognitive mechanism could be critical to better understand the comprehension process.

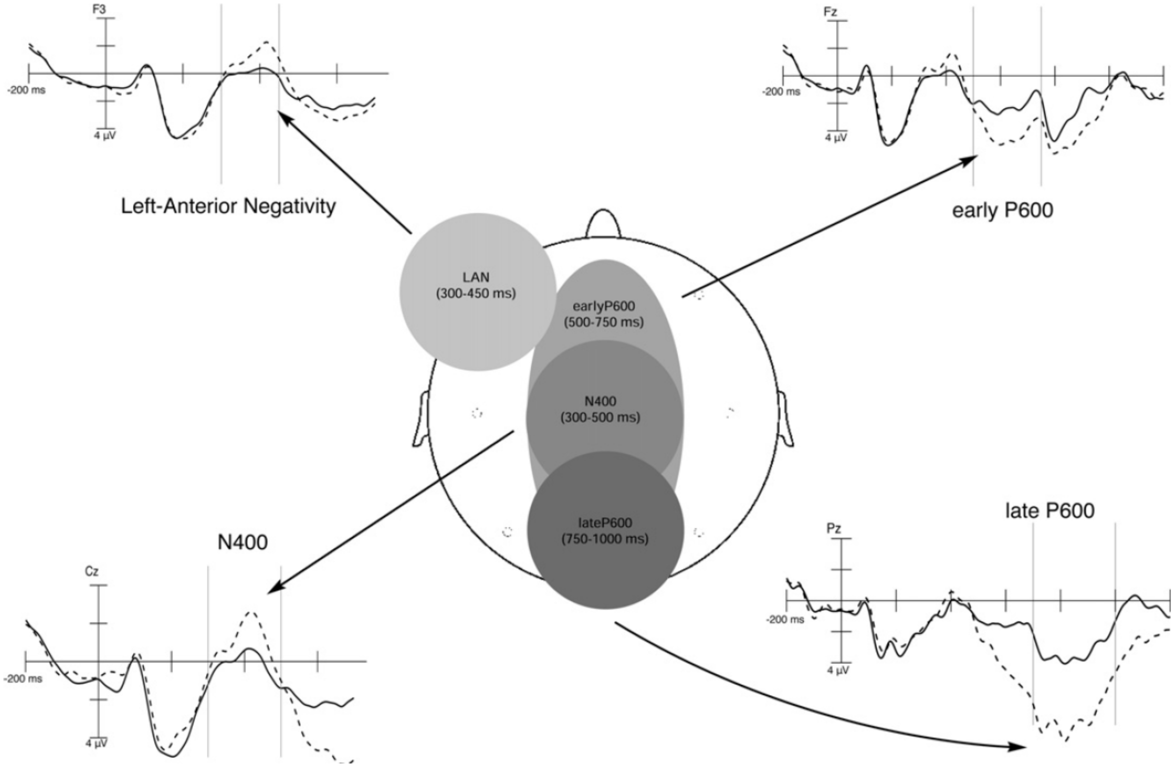


Figure 1.1. Illustration of the latency and topographic distribution of the typical ERP components associated with agreement operations. Taken from (Molinaro, Barber, et al., 2011, p. 915).

Box 1.1[9]**. Behavioral approach.** Most of the behavioral literature on agreement addressed how agreement information is accessed and retrieved during language production (Berg, 1998; Bock et al., 2001; Bock & Miller, 1991; Vigliocco et al., 1996; Vigliocco & Franck, 1999; Vigliocco & Hartsuiker, 2002; Vigliocco et al., 2002). Behavioral evidence on agreement processing in comprehension is very scarce and not very conclusive (e.g., Blackwell, 1996; Gibson & Pearlmutter, 2000; Gibson et al., 1999; Hagoort et al., 1993; Osterhout & Mobley, 1995; Pearlmutter, 2000; Pearlmutter et al., 1999; Pearlmutter & Mendelsohn, 1999).

One of the most used paradigms to evaluate how agreement information is computed during the comprehension process has been the *acceptability judgment task* (see Carreiras et al., 1993; Carreiras & Gernsbacher, 1992; Garnham, 1981, 1984; Garnham & Oakhill, 1985 for a different approach). In this approach, participants are required to judge whether sentences are well-formed. Manipulations regarding the acceptability of the sentences included either syntactic or semantic mismatches between different sentential elements, so that sentences could be grammatical or ungrammatical (see examples (1) and (2) below). Despite the variability in the methodological approaches used by these studies (i.e., different languages, tasks and experimental manipulations), changes in response times and error rates suggest that readers are sensitive to agreement information (Kail et al., 2010; Nicol et al., 1997; Pearlmutter, 2000; Pearlmutter et al., 1999; Pearlmutter & Mendelsohn, 1999).

(1) Syntactic violations: **[The boy]*$_{sing.}$ *are*$_{pl.}$ *throwing the ball.* (Hagoort et al., 1993; Osterhout & Mobley, 1995; Pearlmutter, 2000; Pearlmutter et al., 1999; Pearlmutter & Mendelsohn, 1999).

(2) Apparent but not real violations: *[The key]*$_{sing.}$ *to [the cabinets]*$_{pl.}$ *was*$_{sing.}$ *rusty from many years of disuse.* (Nicol et al., 1997; Pearlmutter, 2000; Pearlmutter et al., 1999; Pearlmutter & Mendelsohn, 1999).In this particular case the distance between the subject-noun and the agreeing verb was manipulated including a prepositional phrase with inconsistent number values.

---

[9] The boxes included in the manuscript provide some additional information relevant to the topic in question.

Table 1.1. ERP components typically associated to language processing and the functional domains that they have been related to. Modified from Bornkessel-Schlesewsky and Schlesewsky (2009, p. 296, Table 16.1 in the original document).

Component	**Domains of occurrence**											
					Sentence-level composition							
	Lexical factors	Morpho-syntactic factors	Word-level composition	Constituent structure	Gramm. Relations	Thematic roles	Linking	Word order	Semantic interpretation	Well-formedness	Complexity	Working memory
ELAN				√								
LAN		√	√				√					
sLAN								√				√
SCR NEG								√				
N400	√		√			√	√	√		√		
P345					√	√						
P600		√	√	√	√			√	√	√	√	√

1.5 Neuro-anatomical Bases of Agreement Processing

In the last few years, the neuro-anatomical mechanisms of sentence comprehension have also been investigated using functional neuroimaging techniques to disentangle syntactic and semantic processing correlates in the brain. A coupling between inferior-frontal and temporal regions in the left hemisphere has been consistently associated with different mechanisms underlying sentence processing (see Figure 1.2 for an illustration of these neural regions; Friederici, 2011, 2012; Hagoort, 2013, 2014; Kuperberg, Sitnikova, et al., 2008; Pallier et al., 2011). Each one of these two critical zones has been parcellated combining cytoarchitectonical and functional criteria (see Friederici, 2011 for a revision of this topic). However, the findings related to the functional clusterization and characterization of each critical node within this circuit is far from conclusive.

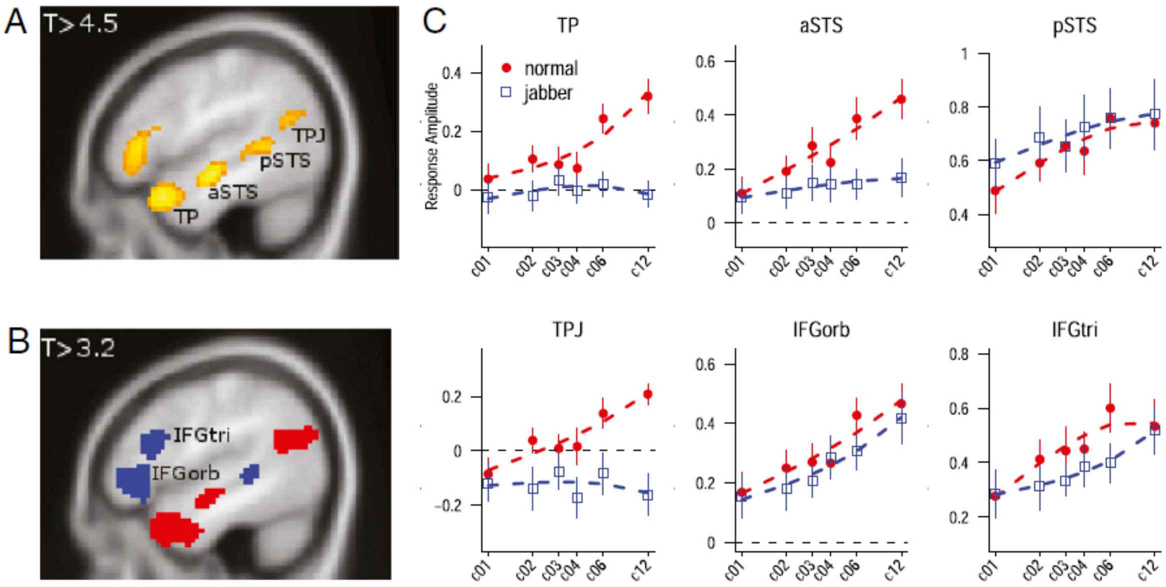


Figure 1.2. Illustration of the fronto-temporal circuit associated with the processing of sentences. This circuit encompasses areas surrounding the sylvian sulcus. The line graphs represented in the right part of the figure illustrate the sensitivity of these regions to the processing of sentential constructions (i.e., these areas results from the comparison between

meaningful sentences and sequences of unrelated words). TP: temporal pole; aSTS: anterior part of the superior temporal sulcus; pSTS: posterior part of the superior temporal sulcus; TPJ: temporo-parietal junction; IFGorb: pars orbitalis within the inferior frontal gyrus; IFGtri: pars triangularis within the inferior frontal gyrus. Adapted from Pallier et al. (2011, p. 2526; Figure 2). Original figure caption: *"Brain regions showing a significant increase in activation with constituent size. (A) fMRI results from the normal-prose group who read sequences with actual French words (group analysis thresholded at T > 4.5, P < 0.05 FWE, spatial extent > 10). (B) Areas in blue show a significant constituent size effect in the jabberwocky group listening to delexicalized stimuli, whereas regions in red show a significant group by constituent size interaction (reflecting a stronger effect of constituent size in normal prose than in jabberwocky) (maps thresholded at T > 3.2, P < 0.001 uncorrected, spatial extent > 50). (C) Amplitude of activations across conditions in the six regions of interest (error bars represent ± 1 SEM). Conditions c01 to c12 are organized according to a logarithmic scale of constituent size, thus a line on this graph indicates a logarithmic increase of activation. The fitting lines are from a regression analysis including linear and logarithmic predictors."*

For instance, semantic operations (e.g., storage, activation and lexico-semantic retrieval) have been mapped in the anterior part of the superior and middle temporal cortex (STG-MTG) (Kuperberg, Sitnikova, et al., 2008) as well as in the most posterior part of this region (Acheson & Hagoort, 2014; Baggio & Hagoort, 2011; Hagoort, 2003a; Lau et al., 2008). Similarly, the characterization of the neural representation of syntactic building operations within the left temporal lobe is highly inconsistent (see Bornkessel-Schlesewsky & Schlesewsky, 2013 for a review) but also see (Rogalsky & Hickok, 2009). In contrast, as far as the inferior frontal gyrus is concerned, the situation seems to be more consistent. Empirical findings concerning the specific functional role of each node within this region in the analysis of semantic and syntactic information are highly convergent. In general, the pars opercularis, within the IFG appears to underlie syntactic processes (phrase structure building (Friederici, 2012; Grodzinsky & Friederici, 2006) and/or syntactic complexity processing (see Grodzinsky, 2000 for a syntactic movement manipulation), whereas the pars triangularis and orbitalis seem to be involved in the processing of semantic-related information (see Friederici, 2011; 2012 for a revision of this topic).

Only a few fMRI studies have investigated agreement processing (Kuperberg et al., 2003; Kuperberg, Sitnikova, et al., 2008; Newman et al., 2003; Ni et al., 2000). Although manipulations have always involved grammatical violations between different sentence constituents (e.g., subjects and verbs), contradictory conclusions have been reported across these studies. For instance, Ni et al. (2000) investigated whether the brain distinguishes between the processing of grammatical information and meaning. Participants listened to sentences that were either grammatically correct or contained a verb finiteness violation (e.g., *"Trees can grew…"*) or a semantic violation (e.g., *"Trees can eat…"*). A dissociation between syntactic and semantic processing was found: while the former violations increased activity in the left inferior frontal gyrus, the latter activated several other regions in both hemispheres including the middle and superior frontal gyrus and the superior temporal and parietal regions.

On the other hand, a study by Newman et al. (2003) attempt to specify the contribution of the inferior frontal cortex during syntactic and semantic processing of sentences using a grammaticality judgment task. They compared sentences with number mismatches between the subject and the second verb of a coordinated structure (e.g., *"The lady praises the sister and meet the artist in the night"*) against sentences including an extra verb (e.g., *"The woman thanked the barber and paid the receptionist knew at the desk"*). In this study, syntactic violations triggered significant activity in the pars opercularis within the inferior frontal gyrus, whereas semantic violations induced significant response in the pars triangularis. Additionally, they observed increased activation in the left posterior temporal region for both types of processing. Nonetheless, since the nature of the violations used, which involve the extra verb, is difficult to determine, the activation observed in this study may not exclusively reflect subject-verb processing difficulties.

With the same goal, Kuperberg et al. (2003) carried out an fMRI study in which they presented participants with three different type of sentences: grammatically correct (e.g., *"We couldn't sleep at night because the baby would cry."*), finiteness anomaly (e.g., *"...because the baby would cries."*), or pragmatic violation (e.g., *"...because the baby would remember."*). These authors found that, relative to the grammatically correct sentences, similar neural regions are recruited by morpho-syntactic and pragmatic information, but with different activation patterns. In a follow-up study these authors reported similar results (Kuperberg, Sitnikova, et al., 2008). The design used was the same, however they added a distinction between two different types of semantically anomalous sentences: real-world pragmatic violations (e.g., *"Every morning at breakfast the boys would plant the flowers."*) and animacy semantic-thematic violations (e.g., *"Every morning at breakfast the eggs would eat toast and jam."*). The common neuro-anatomical network recruited by both, finiteness and animacy semantic-thematic violations, relative to grammatically correct sentences included a widespread bilateral fronto-parieto-temporal response. Some of these regions exhibited more activity in response to the finiteness violations than to the animacy semantic-thematic violations (left inferior parietal lobule, bilateral anterior cingulate cortex and medial frontal gyrus). In this study, the authors introduced the idea that this fronto-parietal network could reflect the detection of conflict monitoring processes that would prevent comprehension errors (Kolk et al., 2003; Kuperberg, Sitnikova, et al., 2008; Vissers et al., 2006). However, since they provided no explanation as to why the recruitment of this monitoring network is not triggered by animacy semantic-thematic violations, this hypothesis was only partially borne out.

Overall, these controversial results illustrate the idea that the regions implicated in the processing of agreement computation and its specific role in sentence comprehension are still uncertain. Different factors can be identified that potentially contribute to these discrepancies. Firstly, although in the case of the four previous studies detailed above, the violations always involved the verb; different aspects of verb inflection and sentence structure have been manipulated to create anomalies across studies. While the finiteness of the verb following the modal auxiliary was violated both in the Ni et al. (2000) and

Kuperberg et al. (2003) studies, Newman et al. (2003) introduced a number mismatch between the subject and the second verb of a coordinate structure. It follows that differences in the nature of the subject-verb grammatical violation may generate the involvement of divergent neural regions concerned with different aspects of sentence processing.

Secondly, limitations and differences in the experimental designs adopted can be found. For instance, in the Ni et al. (2000) design, different types of violations (syntactic and semantic) were presented to participants in separate scanning sessions, which may have caused a high degree of sentence structure predictability. This may have resulted in the adoption of different violation detection strategies compared to the strategies developed in designs such as the Kuperberg et al. (2003) and Newman et al. (2003) studies, in which sentence structure is less predictable. Thirdly, the material presentation modality differs across studies: while in the study by Kuperberg et al. (2003) sentences were presented visually and word by word, in the Newman et al. (2003) study all the words were projected simultaneously. In contrast, Ni et al. (2000) used auditory presentation.

Finally, methodological differences concerning the fMRI analysis can also be found across studies in the way the comparisons between experimental conditions were carried out. For instance, while in Kuperberg et al. (2003) and Newman et al. (2003) the baseline for comparisons was always provided by linguistic material (correct version of the anomalous sentence), Ni et al. (2000) contrasted sentences with a non-linguistic baseline task (pitch judgment). In addition, only in the Kuperberg et al. (2003) studies the comparisons between anomalous and well-formed sentences were carried out considering both directions. This made possible to highlight the neural networks involved in the processing of grammatically correct sentences.

Based on this conflicting scenario, more recently, Nieuwland et al. (2012) investigated the cortical networks involved in the processing of Basque case violations between object and verb. In this study, participants read sentences that contained case violations, number agreement violations, semantic anomalies, or syntactically and semantically correct control sentences. These fMRI findings showed that agreement violation processing stimulates an extensive network of brain regions in both hemispheres beyond the inferior frontal gyrus. Nevertheless, in contrast with previous studies, the left and right anterior inferior frontal gyrus was only sensitive to semantic violations. In addition, case and number violations recruited a largely overlapping neural circuit. These two different types of violations elicited activity increases in a set of parietal regions including the posterior cingulate, the precuneus, the left and right inferior parietal lobules and the right middle frontal gyrus. Besides this commonalities, number violations (i.e., relative to case violations) elicited activity increases in the left middle frontal gyrus (Nieuwland et al. 2012). This study suggested that whereas syntactic and semantic operations are segregated in the brain, case and number violations shared similar neural circuits. However, critically, the results emerging from this study did not provide a significant insight into how the brain process agreement information. Their findings seem to be highly biased by the contribution of domain-general operations probably related to task difficulty effects (i.e., including mainly parietal and prefrontal regions). By removing these effects it would be possible to find differential activity between case and number violations, in inferior frontal and also temporal regions.

Summarizing, despite the variability pointed out in the available information on agreement processing, it is also possible to find some significant commonalities. Firstly, the computation of agreement information consistently engaged a left lateralized fronto-temporal network, where the pars triangularis and opercularis within the IFG and the middle temporal gyrus seem to be crucial nodes. Secondly, the processing of anomalous constructions (relative to the processing of well-formed phrases/sentences) implies changes in the neural responses of some specific regions within this network, suggesting the involvement of different neuro-cognitive mechanisms.

1.6 Neuro-cognitive Models of Sentence Processing

To our knowledge, there are currently no existing neuro-cognitive frameworks that explicitly describe the neural circuitry associated to agreement operations. However, in the last decade several neuro-cognitive models have been proposed trying to integrate the available empirical evidence on sentence processing (Bornkessel-Schlesewsky & Schlesewsky, 2013; Friederici, 2011; Friederici & Alter, 2004; Hagoort, 2003a, 2005, 2013; Hagoort & Indefrey, 2014). All these models are aimed at evaluating how the brain processes and integrates different linguistic information during the on-line comprehension of phrases and sentences. In particular, there are three recent proposals that deserve to be highlighted since they raise, albeit indirectly, questions related with agreement processing. Each one of these models is detailed in depth in the next paragraphs.

The Memory, Unification and Control model (MUC, Figure 1.3 A) was proposed by Hagoort (Hagoort, 2003a, 2005) following a *lexicalist* perspective (see the epigraph *Linguistic Theoretical Frameworks of Agreement*, page 24). In this model, each word in the mental lexicon is associated with its morphological, phonological, morpho-syntactic – including its structural frame(s) – and lexico-semantic representations. According to this author, the posterior portion of the left temporal cortex subserves the storage, access and retrieval processes, i.e. *Memory Component*. Information extracted from the memory system is successively integrated in the so-called "unification workspace" situated in the LIFG, i.e. *Unification Component*. Here, an anterior-ventral to posterior-dorsal unification gradient is found, with BA47 and BA45 contributing to semantic processing, BA45 and BA44 being involved in syntactic processing, while BA44 and BA6 seem to be involved in phonological unification. Crucially, Hagoort (Hagoort, 2003a, 2005) points to the syntactic unification area as the neural substrate supporting the checking of agreement features between elements of an agreement relation. Finally, a network of areas consisting of the anterior cingulate cortex and the dorsolateral prefrontal cortex serves the control function necessary for monitoring processes, i.e. *Control Component*. More recently, Hagoort (Hagoort, 2013, 2014) revisited this theoretical proposal in order to improve the fitting between this model and the new empirical data collected on sentence processing (see also Hagoort & Indefrey, 2014). This new account differs from the previous one in four main points. Firstly, this author proposed the left IFG as a central hub not specific to language but responsible for the unification of different language-related information. According to this view, what is crucial for the proper interpretation of a given phrase/sentence is the functional relationship between the domain-general inferior frontal system and the other nodes of this network. In accordance with this new perspective, this functional coupling will be constrained by the anatomical connections between these perisylvian regions (Figure 1.3 B). Secondly, this author extended the network specialized for the processing of linguistic information including temporal and parietal regions. In this new account, both parietal and temporal regions subserve the *Memory Component* responsible for decoding different types of information (i.e., morphological/phonological, lexical, semantic and syntactic). Thirdly, the functional sub-division proposed for the posterior temporal and parietal areas parallels, in this new account, the functional gradient that has been consistently observed in the left IFG. The recruitment of one specific node within these areas would be dependent on the information required to decode the input. Finally, this new approach highlighted that the functional dynamics established within this left-lateralized network is critical for the processing of linguistic material: the functional interconnections between these three components are the fingerprint of the language specific system.

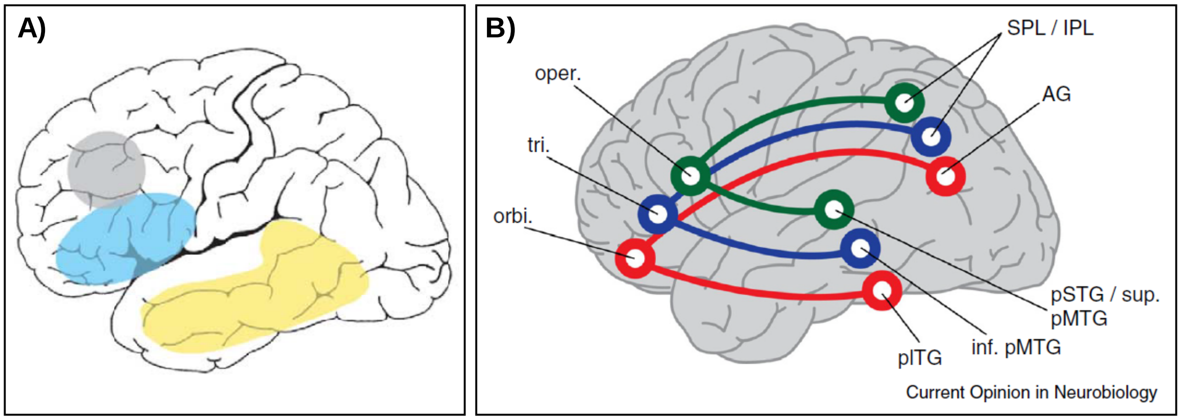


Figure 1.3. Illustration of the three components included in the MUC model. A) The Memory component (left temporal cortex) is represented in yellow, the Unification component (left inferior frontal gyrus) is represented in blue and the Control component (left dorsolateral prefrontal cortex) is represented in grey. Adapted from Hagoort (2005, p. 421, Figure 6). B) Illustration of the connectivity pattern between frontal and temporal/parietal

regions described by Hagoort (2014). Notice that this pattern takes into account the functional gradient characterizing frontal, temporal and parietal regions. Pars opercularis (oper.), pars triangularis (tri.) and pars orbitalis (orbi.), SPL/IPL: superior parietal lobule/inferior parietal lobule; AG: angular gyrus; pSTG: posterior superior temporal gyrus; sup. pMTG: superior posterior middle temporal gyrus; inf. pMTG: inferior posterior middle temporal gyrus; pITG: posterior inferior temporal gyrus. Taken from Hagoort (2014, p. 139, Figure 3).

Based on the experimental findings regarding auditory sentence comprehension, Friederici (Friederici, 2011, 2012) proposed a very different neuro-anatomical framework. This model suggested a functional dissociation between two dorsal and ventral pathways, both functionally divided into two different sub-pathways constrained by anatomical and functional criteria (see Figure 1.4 for a schematic representation of this model). This model proposed that the ventral pathway I is responsible for semantic processing via ventral connections between the middle and posterior superior and middle temporal gyri (STG/MTG) (sometimes extending into the anterior temporal cortex) and the IFG (BA 45/47), while the ventral pathway II is responsible for initial local structure building processes via anterior STG to left frontal operculum projections. According to this model, whereas these two ventral streams work in parallel computing semantic and syntactic relations, the dorsal streams are associated with subsequent higher-order processes. On the one hand, the dorsal pathway I was proposed as a mediator between sensory and motor functions. This pathway connects temporal and premotor regions via the inferior parietal cortex. On the other hand, the dorsal pathway II was proposed as a top-down stream involved in assigning grammatical relations. According to this framework, this pathway connects inferior frontal (BA 44) and temporal regions (posterior STS/STG) that are especially enhanced during the processing of complex structures. In addition, Friederici (2011) proposed that the different nodes of this fronto-temporal network are sequentially recruited during the acoustic processing of a sentence, following four critical stages: 1) acoustic phonological processes around 100 ms after acoustic stimulation [the primary auditory cortex and the planum temporale], 2) initial local structure building processes around 120-200 ms [ventral pathway II], 3) the establishment of semantic [ventral pathway I] and syntactic [dorsal pathway II] relations between 300 and 500 ms and 4) syntactic and semantic integration processes around 600 ms [posterior STG and the basal ganglia] (see Friederici, 2011, p. 1385).

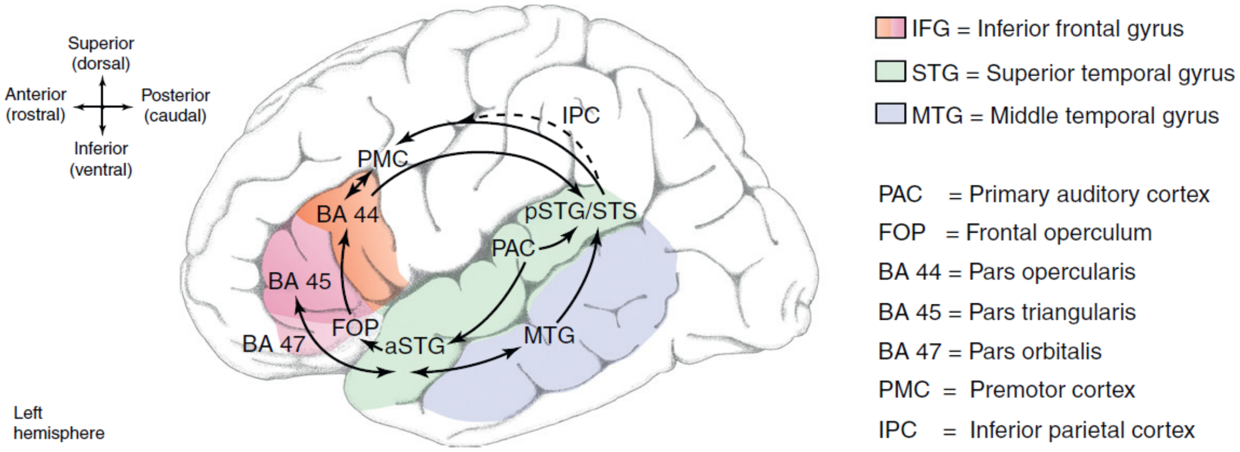


Figure 1.4. Illustration of the dorsal and ventral functional pathways described by Friederici (Friederici, 2011, 2012). Taken from (Friederici, 2012, p. 263, Figure 1). Original figure caption: *“The cortical language circuit (schematic view of the left hemisphere). The major gyri involved in language processing are color coded. In the frontal cortex, four language-related regions are labeled: three cytoarchitectonically defined Brodmann areas (BA 47, 45, 44), the premotor cortex (PMC) and the ventrally located frontal operculum (FOP). In the temporal and parietal cortex the following regions are labeled: the primary auditory cortex (PAC), the anterior (a) and posterior (p) portions of the superior temporal gyrus (STG) and sulcus (STS), the middle temporal gyrus (MTG) and the inferior parietal cortex (IPC). The solid black lines schematically indicate the direct pathways between these regions. The broken black line indicates an indirect connection between the pSTG/STS and the PMC mediated by the IPC. The arrows indicate the assumed major direction of the information flow between these regions…”.*

Finally, Bornkessel-Schlesewsky and Schlesewsky (2013) proposed a new framework of sentence comprehension trying to conciliate the two previous proposals with the empirical evidence across languages. Critically, the general hierarchical organization of the sentence processing previously described by Friederici (Friederici, 2011, 2012) has remained in this new proposal. However, in contrast to the previous model, these authors proposed that a functional dissociation between syntactic and lexico-semantic processing would be supported by a less articulated network consisting of a dorsal and a ventral pathway (Figure 1.5). Specifically, this approach points to the anterior portion of the left temporal gyrus in the ventral stream as the area responsible for the unification of actor-event schemata, i.e., the unification of conceptual information extracted from the elements of a relation, such as for example a subject-verb relation. Such information concerns the event and its participant, i.e., "who does what" in the sentence, while syntactic combinatorial operations (i.e., merging a noun and a verb within the same syntactic frame) are supported by the dorsal pathway, which connects posterior temporal and parietal areas. The output of the dorsal and ventral streams are eventually integrated and evaluated by left inferior frontal regions, in line with the working memory and cognitive control functions associated with this area (Novick et al., 2005; 2005; Thompson-Schill et al., 1997). Therefore, according to this proposal, left-inferior frontal areas should be involved in the evaluation of the grammaticality of a subject-verb or determiner-noun agreement relation. Crucially, however, these authors do not provide any hypotheses concerning whether the neuro-cognitive and neuro-anatomical mechanisms underlying the different kinds of agreement constructions would be similar or not.

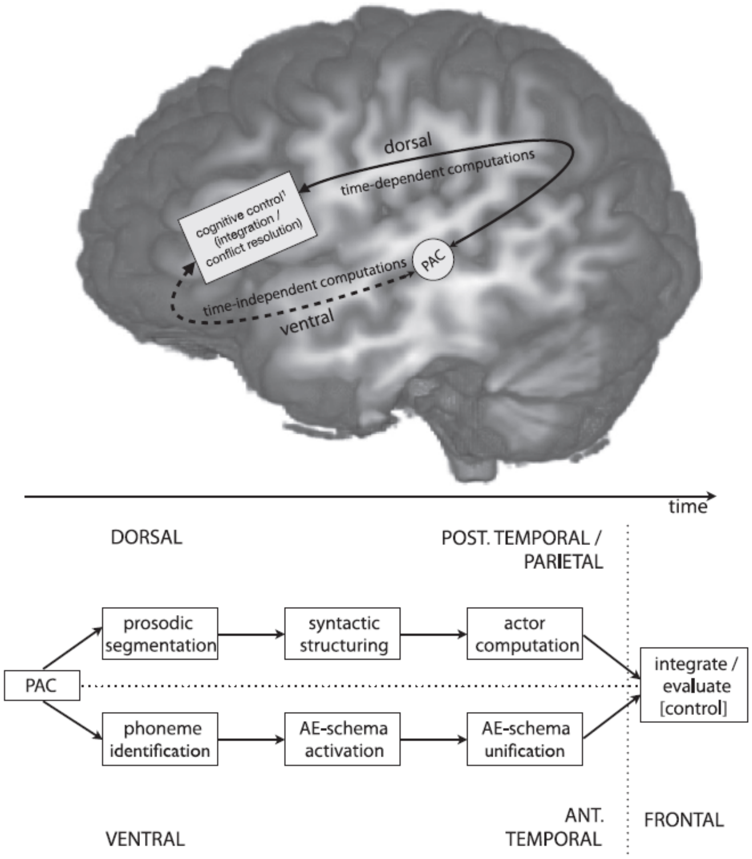


Figure 1.5. Illustration of the dorsal and ventral routes proposed by Bornkessel-Schlesewsky and Schlesewsky (2013). Taken from Bornkessel-Schlesewsky and Schlesewsky (2013, p. 64, Figure 1).

In general terms, these neuro-anatomical models converge in three main aspects. Firstly, all these models include a *Memory-related Hub* from which the underlying morpho-syntactic and lexico-semantic representations associated with the input can be accessed and retrieved. Secondly, they have incorporated an *Integration Hub* that combines the incoming signals with previously encountered information, to ensure the establishment of relations among different sentence constituents. It is noteworthy that all these models coincide in portraying these relations as variable in nature (i.e., syntactic, lexico-semantic, semantic-pragmatic). Finally, these authors agree on the presence of a *Monitoring Hub* responsible for preventing behavioral mistakes. Notably, all these proposals alluded to the cooperation between these *"hubs"* as a key piece for the on-line processing of linguistic inputs. However, as we have illustrated above, despite the theoretical commonalities among them, these models hold significant differences that translate into very dissimilar predictions. Table 1.2 summarized the most significant factors contributing to these discrepancies. Crucially, none of these existing neuro-cognitive models of sentence comprehension explicitly describes the neural circuitry associated to agreement operations. In addition, only scarce evidence on subject-verb agreement processing has been taken into account in these proposals. This overall picture about the neuro-anatomical models of sentence processing will enable the reader to follow the main thread of this thesis. In the following sections we will consider both the similarities and the differences between these models in order to find a place for our experimental data.

1.7 Outline

Following this brief overview of the most recent insights into the neuro-cognition of agreement processing, this manuscript is subdivided into twelve chapters. In the Chapter 2 we will diverge from the main thread to summarize the technical aspects of the neuroimaging method required to comprehend the following sections. Chapters 3 to 7 present the methodological details and the main results of each experiment and some important considerations concerning the respective results. These five chapters are independent from one another. The specific goal(s) of each experimental chapter (from 3 to 7) are detailed in Table 1.3, including the critical experimental manipulations. In general terms, the five experimental chapters are organized according to their syntactic and semantic complexity, i.e. from simpler to more complex syntactic structures (i.e., from nominal and within-constituent agreement to verbal agreement) and from simpler to more semantically complex agreement features (i.e., from determiner-noun transparent gender relations to subject-verb person grammatical relations). The main findings derived from these studies will be discussed at the end of each chapter, paying particular attention to explain how our data contributes to improving the theoretical frameworks and neuro-anatomical models on agreement comprehension.

Following the experimental part, the Discussion section in Chapter 8 provides some general considerations arising from the combination of all the experiments performed (i.e., the regularities and singularities across the experiments). In addition, this chapter discusses possible future directions concerning agreement processing. Finally, Chapter 9 includes critical conclusions derived from the main results. This chapter is followed by a list of the references discussed in the manuscript.

Table 1.2. Different features characterizing the three revisited neuro-anatomical models of sentence processing.

	Neuro-anaotomical Models of Sentence Processing		
	Hagoort et al. (2003; 2005; 2012; 2013; 2014)	**Friederici (2011, 2013)**	**Bornkessel-Schlesewsky & Schlesewsky (2013)**
Linguistic Framework	Clearly framed within *lexicalist approaches*.	Clearly framed within *syntacto-centric approach*es.	Framed within a *lexicalist approaches*. Highly cross-linguistically motivated. Considers a hierarchy between sentences constituents.
Sequentiality	Parallel processing is one of the most notable properties characterizing this model. But it also involves sequential operations.	Highly sequential.	Involves sequential but also parallel operations. Distinguishes between time dependent (syntactic) and time independent (semantic) processes.
Modality-specificity	It is based on visual evidence, but assumes that the systems should be equally represented across modalities.	Mainly auditory	Mainly auditory
Functionality	They differ in the cognitive functions associated with each node/region of the model.		
Domain-specificity	Proposes a close relationship between one language-specific system and two domain-general systems.	Mainly driven by language-specific operations.	It proposes that language-specific and domain-general functions go hand in hand during sentence processing. It is the first model questioning the language specificity of the left IFG.

Complexity	Dissociates the neuro-anatomical regions underlying the Memory, Unification and Control components. Distinguishes between semantic, syntactic and phonological nodes within each component.	It distinguishes between a dorsal and a ventral route, each subdivided into two sub-pathways. It links these different pathways with semantic, syntactic and phonological operations.	From a neuro-cognitive point of view, it distinguishes between a dorsal (time dependent) and a ventral (time independent) stream, which are realized by various neuro-anatomical pathways. It is the first model considering parietal regions within a sentence processing network.
Regional parcellation based on components	Divided into three neuro-functional components (Memory, Unification and Control). Considers the left IFG as a critical domain-general hub. Considers parietal regions as language-specific nodes.	The limits between functional components remain unclear.	Encloses a frontal hub whose function is to control language-specific operations. Even so, the limits between functional components remain unclear.
Distributive vs. functional specialization	It follows a network based approach but the functionality of the nodes is highly localized.	It follows a network based approach but the functionality of the nodes is highly localized. It pinpoints the posterior MTG/STG as a node showing an interaction between syntactic and semantic factors.	It follows a network based approach and the functionality of the nodes is clearly distributive.
Finding a place for agreement operations: the best candidates for each model	It proposes BA44 within the left IFG as the node responsible for syntactic unification. It considers this node sub-serves the checking of agreement features.	It proposes a complex network where the building of relations among sentence constituents is sub-served by different inferior frontal and temporal regions. It suggests that a coupling between the posterior STG and the IFG sub-serves verb-argument relations.	It considers syntactic combinatorial operations are supported by posterior temporal and parietal areas. It proposes the left IFG as the node responsible for the evaluation of grammatical consistencies.

Table 1.3. Specific goal(s) per chapter including a very brief description of the critical experimental manipulations.

Experiments	Experimental manipulations	Main Goals
Experiment I	2 x 2 factorial design including Gender Agreement Congruency and Gender Transparency as factors. Congruency was manipulated using pairs of determiners and nouns.	To investigate a) which brain regions are sensitive to gender agreement within a noun phrase; b) whether the brain processes transparent and opaque nouns in a same way or differently; and c) whether and how different types of gender-marking cues modulate the neural mechanisms underlying agreement processing.
Experiment II	2 x 2 factorial design including Gender Agreement Congruency and Type of Gender [Formal and Conceptual] as factors. The congruency was manipulated between nouns and adjectives using four word sentences.	To investigate a) whether agreement processing system uses conceptual information concerning the noun gender properties during the establishment of gender agreement relations and if so, b) where is this possible interaction between formal and conceptual information mapped in the brain.
Experiment III	2 x 2 factorial design including Number Agreement Congruency and Type of Dependency [Determiner-Noun and Subject-Verb pairs] as factors.	To investigate whether the neural substrates of subject-verb and nominal agreement processing differ as a function of the different syntactic domains and interpretive properties in the processing of a common agreement feature, i.e. number.
Experiment IV	One way design including grammatically correct sentences and sentences which included a person or a number mismatch. The congruency was manipulated between subjects and verbs using eight to ten word sentences.	To evaluate a) whether two different morpho-syntactic features such as person and number differ as a function of its interpretive properties and more importantly b) to establish where is this difference, if it is indeed found, mapped in the brain.
Experiment V	One way design including grammatically correct sentences, sentences which included a person mismatch that result in a grammatical violation and sentences which included a person mismatch that result in a grammatical construction [Unagreement]. The congruency was manipulated between subjects and verbs using eight to ten word sentences.	To isolate the neural substrates involved in agreement computation, with a special focus on both the evaluation of morpho-syntactic feature consistency and semantic integration complexity.

Chapter 2.

Methodological Considerations

Neuroimaging Techniques with special interest in fMRI

Cognitive processes can be characterized according to their temporal dynamics (i.e., “when”) and the neural region(s) underlying these processes (i.e., “where”). There is a variety of techniques and methodological approaches which enable researchers to make inferences about these two dimensions. These techniques differ in terms of their spatial and temporal resolution (see Jaiswal, 2015; Mehta & Parasuraman, 2013; Meyer-Lindenberg, 2010, for some details about the temporal and the spatial resolution across techniques). In particular, language processing and more specifically agreement processing has been extensively explored combining behavioral and electrophysiological techniques (see Molinaro, Barber, et al., 2011 for a review of the ERPs evidence regarding agreement processing). As we previously discussed in the Introduction, the high temporal resolution of the electrophysiological methods (e.g., ERPs Handy, 2005; Rugg & Coles, 1995) provides valuable information about ***when*** a particular cognitive process has occurred. However, the spatial resolution of this technique is relatively low. Therefore, ERP methods alone cannot provide complete evidence for a comprehensive account of the neural representation of a certain cognitive process such as agreement.

One of the most extensively used neuroimaging techniques with high spatial resolution is the functional Magnetic Resonance Imaging (see Box 2.1 for some historical remarks). It provides information about the level of blood oxygenation in the brain with a spatial resolution about 2-3 mm. The high spatial resolution of the fMRI in conjunction with some specific experimental manipulations could allow us to complete the picture and characterize neuro-anatomically the cognitive mechanisms underlying agreement processing. Nonetheless, only few studies have explored agreement processing using fMRI and, more importantly, the evidence derived from these investigations is highly contradictory. Critically, no research to date has investigated how different types of agreement relations and different types of morpho-syntactic features are processed in the brain. In addition, only few experimental findings regarding agreement processing have been taken into account in the existing neuro-anatomical models of sentence comprehension processing.

Given the relevance of the neuroimaging techniques, especially fMRI, to the purpose of the current thesis, this section provides some useful methodological information to better understand the following chapters. We will start with a brief overview about fMRI, including the main concepts and implications. After that, we will explain in more details the physics bases of this technique and some remarkable aspects on the biological mechanisms underlying fMRI.

fMRI. This technique is a specialized MRI application (see Box 2.2 for some details about the physics of the MRI) for studying non-invasively brain functions in human subjects. It measures changes in the level of deoxygenated- and oxygenated-hemoglobin molecules presented in the blood. A ratio of deoxygenated- and oxygenated-hemoglobin was called “blood-oxygen-level-dependent” (BOLD) response (Ogawa, Lee, Kay, et al., 1990; Ogawa, Lee, Nayak, et al., 1990; Ogawa et al., 1998; Ogawa et al., 1993; Ogawa et al., 1992). Critically, deoxygenated-hemoglobin and oxygenated-hemoglobin are associated with different magnetic properties. While oxygenated-hemoglobin is diamagnetic and therefore has no effect on the local magnetic field, deoxygenated-hemoglobin is paramagnetic and thereby disturbs the homogeneity of the magnetic field. The neurophysiological basis of the BOLD signal relies into this physic difference. Changes of the BOLD response in a certain neural region reflect changes of blood flow, volume, and level of oxygenation following neuronal activity (Huettel, 2004, 2012; Huettel, McKeown, et al., 2004; Huettel, Obembe, et al., 2004; Huettel, Song, et al., 2004). The relationship between these physiological responses has been called neurovascular coupling (Bonvento et al., 2002; Dirnagl, 1997; Rosengarten et al., 2001; Villringer, 1997).

Box 2.1. Historical antecedents of MRI: This technique was discovery by two physicists, Felix Bloch and Edward Mills Purcell. They called Nuclear Magnetic Resonance Imaging based on its early implication in the nuclear chemistry. These two physicists shared a Nobel Prize in Physics in 1952 for this discovery. Twenty four years after in Nottingham (specifically in Sir Peter Mansfield's lab), this technique would allow for a 2D image of a human finger. On 1977, Raymond Damadian obtained the first MRI scan of a human body (see the Figure I for a schematic draw of the first MRI scanner).

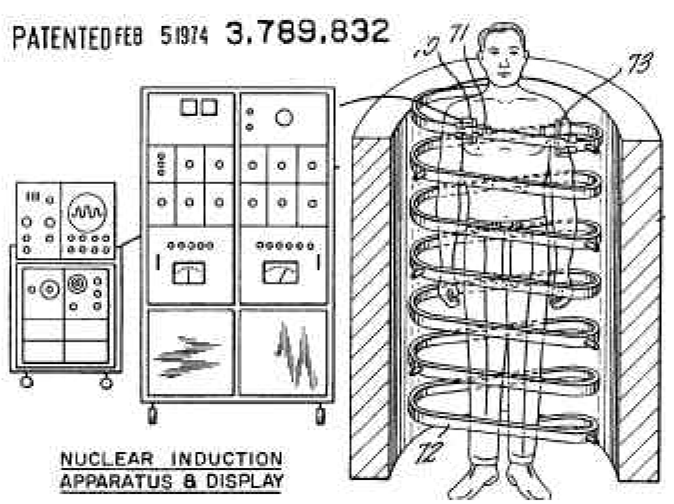
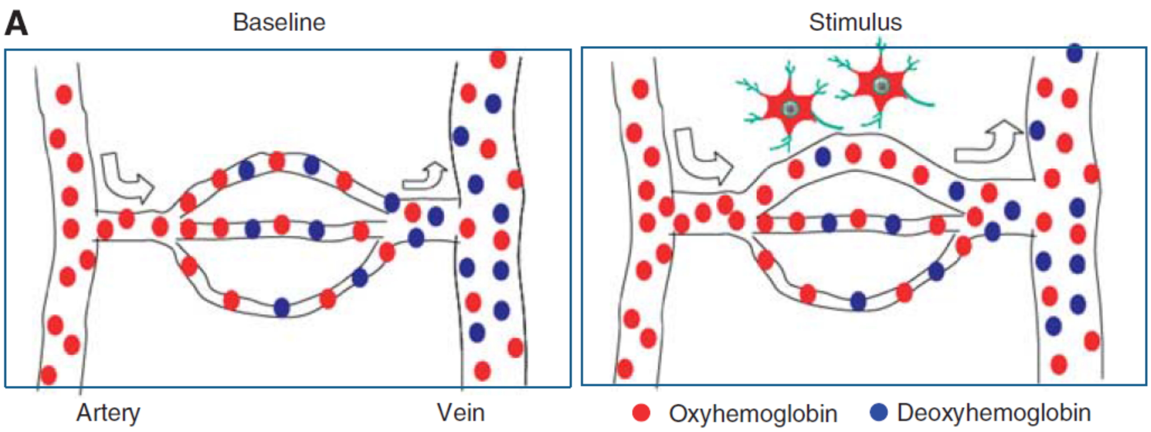


Figure I. Illustration taken from the US Patent and Trademark Office [patent no. 3789832, filed 17 March 1972, issued 5 February 1974], which represents the first MRI scanner designed and patented by Raymond Damadian and colleagues. http://www.nature.com/ijo/journal/v32/n7s/fig_tab/ijo2008242ft.html

Several biophysics models try to explain the metabolic mechanism of the neurovascular coupling (Boas et al., 2008; Buxton, 2012; Buxton, Uludag, et al., 2004; Buxton, Uludağ, et al., 2004; Devonshire et al., 2012; Logothetis, 2002; Logothetis et al., 2001; Uludağ et al., 2004). However, none of these completely explain all the metabolic aspects behind the BOLD signal. One of the most intuitive and simplified interpretation of this signal has been offered by Jueptner and Weiller (1995). These authors suggested that local neuronal activity requires an increased local metabolism with an increased need for glucose and oxygen. This is achieved by a local increase in blood flow and concomitant increase in blood volume, supplying the extra glucose and oxygenated-hemoglobin needed. The amount of oxygenated-hemoglobin delivered is greater than the amount of oxygen extracted, giving a local increase in oxygenated-hemoglobin and thus a local decrease in the concentration of deoxygenated-hemoglobin (but see also Kim, S. G. & Ogawa, 2012, Figure

2.1 illustrates the metabolic changes behind increases in the BOLD signal). In line with this proposal, it has been shown that fMRI results are very consistent with more direct brain mapping techniques such as intracranial evoked potentials and electrocortical mapping (Bizzi et al., 2008). Interestingly, it has been also shown that fMRI activations correlates with increases in neural activity and intracortical processing in a given cortical region (Bartels et al., 2008; Logothetis et al., 2001; Logothetis & Pfeuffer, 2004; Nir et al., 2008; Nir et al., 2007). Nonetheless, despite the empirical evidence supporting this theoretical model, there are still many controversies regarding the relationship between the hemodynamic responses and the underlying neural activity.

Independently of the neurovascular mechanisms controlling the local blood flow, the blood volume, and the balance between the oxygenated-hemoglobin and the deoxygenated-hemoglobin, the relationship between these three factors give rise to two different types of BOLD responses: ***the prolonged positive response*** and ***the prolonged negative response*** (Kim, S. G. & Ogawa, 2012). While the prolonged positive response emerges where the stimulus-induced signal are higher than the baseline signal (i.e., activation), the prolonged negative response appears where the baseline signal are higher than the stimulus-induced signal (i.e., deactivation). According with previous studies, the emergence of these two types of responses and their corresponding physiological basis depends on where we are looking for (i.e., the brain regions) and the process we are trying to characterize (Bianciardi et al., 2011; Harel et al., 2002; Huber et al., 2014; Kim, S. G. & Ogawa, 2012; Kuperberg et al., 2003). In the case of language comprehension, the vast majority of studies have focused on the prolonged positive responses. However, in the last years the investigations about neuro-cognition have paid more attention to the sustained negative bold response and its meaning for different cognitive mechanisms, such as the ones underlying the motor and the visual responses (Bianciardi et al., 2011; Kuperberg et al., 2003; Pasley et al., 2007; Stefanovic et al., 2004). It could be therefore essential for the characterization of the agreement phenomenon to consider both types of responses into account. Thus, throughout the current thesis it is possible to find references to positive and/or negative responses. Both of them will be considered as significant and as a consequence will be discussed.



B Expected stimulus-induced changes in MR-related parameters

	Arterial Blood	Extravascular Tissue	Venous Blood	Cerebrospinal Fluid
Volume Fraction (V)	⬆	⬇	⬆	⬇
Inflow/perfusion Effect (R_1*)	⬆	⬆	⬆	⇔
BOLD Effect (R_2 and R_2*)	⇔	⬇	⬇	⬇

Figure 2.1. Change in the vascular responses associated to increases in the neural activity. Taken from Kim, S. G. and Ogawa (2012). The expected changes associated to the BOLD signal are also represented.

Box 2.2. Physics of MRI: Magnetic resonance imaging (MRI) is a non-invasive imaging technique that uses non-ionizing radiation to create 3D high spatially detailed images (typically between 1.0 and 3.5 mm) of the biological tissues. A MRI scanner uses electromagnets to create a **static and uniform magnetic field of high strength** (1.5 and 3 Tesla are the most frequently use for clinical and research purpose).

This technique is based on the physical properties of the **hydrogen nuclei** which are part of the molecules of water abundantly found in the biological tissues. The nucleus of a hydrogen atom consists of a single proton that spins around its own axis inducing a magnetic field. This magnetic field is characterized by a certain direction and size (called magnetic moment, see Figure II).

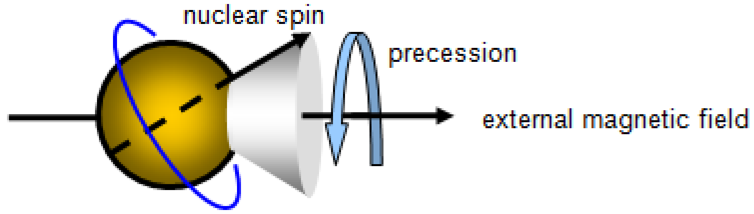


Figure II. Representation of a hydrogen nucleus. Notice that it is aligned with the external magnetic field to which has been subjected. Taken from http://www.schoolphysics.co.uk/.

The static field, by itself, does not produce an MR signal. To obtain the 3D images, the MRI scanner required also a series of **changing magnetic gradients and oscillating electromagnetic fields**. These oscillating electromagnetic fields require radiofrequency coils that generate magnetic pulses. Turning the **radiofrequency pulse** on, changes the magnetization alignment of protons within the magnetic field. When the pulse is turned off, the protons relax to their original equilibrium alignment, which releases energy that is detected by the coils (MR signal).

Spatial resolution is provided by the changing magnetic gradients. The strength of each gradient changes linearly along a single spatial dimension. Thus, three mutually orthogonal gradients are required to localize a signal in three spatial dimensions. Specific manipulations regarding the timing of the radiofrequency pulses and the delays before detecting the MRI signal entails the detection of subtle changes in brain anatomy.

Chapter 3.

Experiment I

Is our brain sensitive to gender-marking cues during the computation of local agreement relations?

Chapter 1 provided the most significant psycholinguistic and neuro-physiological findings concerning agreement processing. It addressed how syntactic, lexico/semantic and semantic/pragmatic information embedded in our linguistic code might modulate the establishment of grammatical relations. Hence, this chapter pointed out the contradictory scenario behind this operation and the different linguistic and neuro-cognitive theoretical frameworks as well. Given the lack of a comprehensive approach that might fit all the empirical findings, and the need for more empirical evidence, the following experimental studies aim to uncover the mechanisms sub-serving agreement processing.

As mentioned in the Introduction, taking advantage of the Spanish agreement system's diversity, it is possible to tune down some of these mechanisms and, as a consequence, boost others. Thus, first of all, in the current chapter we will describe the neuro-anatomical network underlying the establishment of local syntactic relations (i.e., formal gender agreement), tuning down possible confounding factors (i.e., semantic and pragmatic factors) that might affect agreement processing. To do that, we will directly contrast congruent and incongruent determiner-noun pairs in a context where the establishment of a gender agreement relation relies on orthographical/morpho-phonological and/or lexical information. The comparison between transparent and opaque nouns will allow us to investigate whether boosting the access to the lexical representation of a given word could impact the functioning of this agreement network.

This chapter is divided into four sections[10]. Section 3.1 illustrates the major findings on the processing of syntactic gender agreement emphasizing its neuro-anatomical representation. Section 3.2 describes the methodological details concerning the experimental design and the data analysis. Finally, while section 3.3 presents the main results, in section 3.4 the main conclusions emerging from this experiment are outlined and debated.

3.1 Overview

The Spanish formal gender agreement system offers interesting opportunities to investigate to what extend the establishment of grammatical relations would be affected by form-based (i.e., orthographical, morphological and/or phonological) and/or lexical information. As explained in the first chapter, this system is not conceptual in nature and therefore cannot be derived from the biological sex of the referent (i.e., it is independent on the meaning). The nouns within this category can be classified as two main groups, typified by different gender-to-ending regularities (Bates et al., 1995; Harris, 1991). The first group, *transparent nouns*, includes those nouns whose ending has a regular correspondence with a specific gender class ("–a" for feminine and "–o" for masculine, e.g., *libro*$_{mas.}$ [book]; *luna*$_{fem.}$ [moon]). The second group, *opaque nouns*, includes those nouns whose ending is not informative of the gender class to which a given noun belongs (e.g., *lápiz*$_{masc.}$ [pencil]; *vejez*$_{fem.}$ [elderly]).

In Spanish, nouns are typically preceded by their corresponding definite determiners (singular forms: "–la" for feminine and "–el" for masculine, e.g., *el*$_{mas.}$ *libro*$_{mas.}$ [the book]; *la*$_{fem.}$ *luna*$_{fem.}$ [the moon] and plural forms: "–las" for feminine and "–los" for masculine, e.g., *los*$_{mas.}$ *libros*$_{mas.}$ [the books]; *las*$_{fem.}$ *lunas*$_{fem.}$ [the moons]). These two sentential elements should always be grammatically congruent. Investigating how local relations between determiners and nouns are established could provide valuable information about how agreement operates within noun-phrase domain. Although several empirical findings concerning this phenomenon are available (Afonso et al., 2013; Barber & Carreiras, 2003, 2005; Carreiras et al., 2010; Faussart et al., 1999; Hagoort & Brown, 1999; Hagoort et al.,

---

[10] All the experimental chapters follow the same subdivision into four different sections.

2003; Molinaro et al., 2013; Molinaro, Vespignani, et al., 2008; Wicha et al., 2003; Wicha et al., 2004), several questions still remain unclear. How does our brain manage different gender-marking cues during the computation of agreement relations? Does the brain integrate the form-based and the lexical cues embedded in the nouns during agreement processing? The comparison between grammatical and ungrammatical determiner-noun pairs will be the starting point of the current thesis, seeking to identify the brain regions sensitive to local agreement information. Afterwards, by turning the spotlight on the gender-to-ending regularities characterizing transparent and opaque nouns, we will be also able to investigate how our brain manages different gender-related cues during agreement computation.

There have been several studies exploring how gender related information is represented and accessed during the processing of nouns (Bates et al., 1996; Bates et al., 1995; Cacciari et al., 2011; Cacciari & Padovani, 2007; Caffarra & Barber, 2015; Caffarra et al., 2014; Caffarra et al., 2015; De Martino et al., 2011; Gollan & Frost, 2001; Hernandez et al., 2004; Padovani et al., 2005; Schiller et al., 2003b). The vast majority of these studies have taken advantage of the different gender-to-ending rules characterizing transparent and opaque nouns. Despite the variability in the methodological approaches (i.e., different tasks, languages and stimulation modality) adopted by these studies, a major claim has been derived from the comparison between transparent and opaque nouns (Bates et al., 1995; see De Martino et al., 2011 for a comparison across tasks in both comprehension and production; and see also Gollan & Frost, 2001; Hernandez et al., 2004; Holmes & Segui, 2004, 2006; Padovani et al., 2005): the form-based gender-marking cues might affect the processing of a given noun, even in those tasks where participants have not been required to explicitly identify the gender (but see Bates et al., 1996; De Martino et al., 2011; Gollan & Frost, 2001 [Experiment 1]; Padovani et al., 2005). Generally, transparent nouns are classified more rapidly and accurately as masculine or feminine than opaque nouns (Afonso et al., 2013; Bates et al., 1996; Bates et al., 1995; Desrochers et al., 1989; Gollan & Frost, 2001 [Experiment 1]). Some of these studies have also demonstrated differences in the magnitude of the gender-marking regularity effect as a function of the task requirements: the less explicit the task, the fewer chances to find a behavioral advantage for transparent nouns (De Martino et al., 2011; Holmes & Segui, 2004, 2006).

For instance, Gollan and Frost (2001 [Experiment 1A]) manipulated the gender-to-ending regularities in Hebrew using a gender decision task. They included three different groups of nouns: irregular gender-unmarked, regular gender-marked and regular gender-unmarked nouns. These authors reported a facilitation effect related to the marked-nouns (i.e., lower response times and lower error rates) and suggested that the correlation between the gender values and the morphological gender cues (available only for the gender-marked nouns) can mediate the access to gender information (see also Caffarra & Barber, 2015; Caffarra et al., 2014; Caffarra et al., 2015 for similar ERP results). Interestingly, similar results have been reported using a lexical decision task in French (Colé et al., 2003). These authors contrasted transparent (e.g., *briqu<u>et</u>* [lighter], the “-et” termination in French predicts masculine grammatical gender in 100% of cases) and opaque (e.g., *sty<u>le</u>* [style], the “-le” termination in French predicts masculine grammatical gender in 52% of cases) nouns with high and low lexical frequency. The results of this study replicated the lexical word frequency effect expected for this type of task: higher lexical response times for low frequency words than for high frequency words. However, these authors also revealed an interaction between the lexical frequency and the transparency of the nouns suggesting that gender information has an impact on lexical access. Lexical response times were shorter for transparent nouns than for opaque nouns only in the case of low frequency nouns.

The empirical evidence in this respect is not limited to behavioral findings. Previous neuroimaging studies have also demonstrated how gender-marking cues might affect the processing of a given noun (Hammer et al., 2007; Heim, 2008; Heim et al., 2005; Heim et al., 2006; Heim et al., 2010; Hernandez et al., 2004; Indefrey & Levelt, 2004; Miceli et al., 2002; Padovani et al., 2005). These studies have consistently showed that the processing of transparent and opaque nouns produces different brain responses. For instance, Hernandez et al. (2004) compared the brain response associated with Spanish opaque and transparent nouns using a gender decision task. These authors reported significant activation increases in different frontal regions for opaque nouns including the left pars opercularis within the IFG, the left precentral gyrus, the right and left insula and the right and left anterior cingulate cortex. Based on previous evidence, they argued that classifying opaque nouns as feminine or masculine requires increased demands (i.e., with respect to transparent nouns) on language-related regions previously associated with articulation, phonological and morphological processing, as well as domain-general regions such as the anterior cingulate cortex, previously related to task difficulty effects (see Padovani et al., 2005 for similar results in Italian).

Interestingly, Heim (2008) revisited the available functional neuroimaging literature on syntactic gender processing and provided an extensive review of this topic. This author also proposed a neuro-anatomical model of syntactic gender processing that emphasizes the left pars opercularis and triangularis within the inferior frontal gyrus (BA44 – 45 according to Brodmann) as critical nodes involved in different stages of gender processing. Specifically, this author predicts that while BA44 mediates the extraction of gender features when gender is morphologically encoded, the engagement of BA45 would be dependent on the task requirements. Activity in BA45 has been found only when the task explicitly includes the retrieval of the gender morpho-syntactic feature (e.g., gender decision after generation of the corresponding determiner). Interestingly, this model also predicts that when no morphological cue is available (i.e., as in the case of opaque nouns), gender information is retrieved from the lexicon, which according to this author, should be mapped in the middle part of the left MTG. Importantly, the neuro-anatomical circuit underlying syntactic gender processing included in this framework, fits within a previously described sentence processing model proposed by Friederici (Friederici, 2011, 2012; Friederici & Kotz, 2003). However, Heim's proposal (2008) has attempted to explain how the gender information is accessed and retrieved, but it does not provide clear information on whether the availability of different gender cues might affect syntax-related operations.

In contrast to the large number of studies investigating how gender information is accessed and retrieved, the number of studies exploring how gender cues might affect the establishment of grammatical relations is markedly low (Afonso et al., 2013; Akhutina et al., 1999; Caffarra & Barber, 2015; Caffarra et al., 2014; Caffarra et al., 2015; Faussart et al., 1999; Gollan & Frost, 2001). But, more importantly, results derived from these studies are far from conclusive. In this regard, there are some behavioral and ERPs studies which quantitatively explored whether the transparency of the nouns affects agreement operations exploring the interaction between gender-marking and congruency pattern (determiner-noun and posesive pronoun-noun in Spanish: Afonso et al., 2013; adjective-noun in Russian: Akhutina et al., 1999; determiner-noun in Spanish: Caffarra & Barber, 2015; Caffarra et al., 2014; noun-adjective in Hebrew: Gollan & Frost, 2001; determiner-noun in French: Holmes & Segui, 2004)[11]. The vast majority of these studies have consistently reported differences between transparent and opaque nouns as the literature on gender processing predicts. However, concerning the interaction between transparency and agreement pattern, contradictory results emerge from these studies: while some of them have demonstrated that gender information has no influence on the establishment of grammatical relations (Caffarra & Barber, 2015; Caffarra et al., 2014; Caffarra et al., 2015; Hohlfeld et al., 2004), other studies have suggested precisely the opposite (Akhutina et al., 1999; Holmes & Segui, 2004; Taft & Meunier, 1998).

For instance, on the one hand, Holmes and Segui (2004) qualitatively assessed whether comprehension relies on lexical and sub-lexical gender cues available in French grammar (for similar results see also Bates et al., 1996 [Experiment 3, in Italian]; Colé et al., 2003 [Experiment 3, in French]; Hillert & Bates, 1996 [in German]; Radeau & van Berkum, 1996; van Berkum, 1996 [in Dutch]). In French, apart from the gender-to-ending rules explained above, if the noun begins with a vowel the preceding determiner varied from its full form (feminine [“la”] or masculine [“le”]) to a reduced form (“–l´”) that provides no indication of gender. Thus, these authors manipulated the predictability of the gender value information using not only the noun ending regularities, but also this initial phoneme rule. They contrasted determiner-noun word pairs that could be either grammatically correct or not while participants performed a grammaticality judgment task (see Experiment 1,

---

[11] Previous studies have investigated how gender information is processed during tasks in which participants are required to retrieve a gender-marked determiner from different visually presented objects (Janssen & Caramazza, 2003; Lemhöfer et al., 2006; Schiller & Caramazza, 2003; Schriefers et al., 2002, 2005). Nonetheless, we will not consider these studies, given that the neuro-cognitive mechanisms involved in this type of task might differ from those recruited during the comprehension of phrases/sentences.

“Verification of Grammatical and Ungrammatical Phrases”). In this task, the nouns used could begin with either a vowel or a consonant, and end with either a gender-typical or a gender-neutral suffix. These authors reported different results according to the congruency of its grammatical pattern. For grammatical word-pairs, transparent nouns preceded by its corresponding gender-marking determiner were classified more quickly than opaque nouns. In addition, response times were faster for those pairs where the gender information was redundant (i.e., gender cues were available in both determiner and noun) than for pairs where only the noun contained information about the gender value. Similar but larger effects were found for ungrammatical word-pairs. Critically, the response differences between grammatical and ungrammatical word-pairs were higher for transparent than for opaque nouns in both factors (gender-to-ending regularity and initial phoneme). These authors replicated the main results of this experiment using a different paradigm in which the same factors were manipulated in determiner-noun-adjective phrases (see Experiment 2 in Holmes & Segui, 2004).

Following similar experimental procedure, Caffarra et al. (2014) compared ERP responses elicited by grammatically correct and incorrect written Spanish determiner-noun pairs. These authors also manipulated the gender-marking regularity of the nouns: half of them were transparent and the other half were opaque. In order to investigate how each brain hemisphere contributes to gender agreement processing, these authors used a visual-half field presentation paradigm. Determiners were always presented centrally, followed by a noun displayed on the left or on the right visual field. While for the left hemisphere – right visual field –, main effects of transparency and agreement congruency were found in two critical time windows (350-500 ms and 500-750 ms), for the right hemisphere – left visual field –, only a main effect of agreement congruency emerged between 350 and 500 ms. Interestingly, after 500 ms the right lateralized effect of agreement congruency continued to be significant only for transparent nouns. Planned comparisons demonstrated that the main effect of transparency was directed by increases of the negative effect associated with transparent nouns. According to these authors, the orthographical/morpho-phonological gender mark available only in the case of transparent nouns seems to be processed as early as 350 ms. Despite this fact, no significant interaction between transparency and agreement congruency was reported[12], suggesting that the gender-marking regularities do not modulate the computation of local grammatical relations, at least not in the first stages of the noun-phrase agreement processing (see also Caffarra & Barber, 2015 [determiner-noun pairs in Spanish included in a complex sentence context]; Caffarra et al., 2015 [determiner-noun pairs in Italian included in a complex sentence context] for similar results in sentence context).

Regarding gender agreement computation, some fMRI studies have indicated that morpho-syntactic gender violations produce significant responses in the left inferior frontal cortex (Carreiras et al. 2010; Hammer et al. 2007). In particular, Hammer et al. (2007) found increased activation in left inferior frontal areas when morpho-syntactic gender agreement between pronouns and antecedents was violated (see also Hammer et al., 2006 for similar results). In the same line, Carreiras et al. (2010) showed the engagement of the left inferior frontal areas when participants are asked to read determiner-noun pairs with gender agreement violations. Interestingly, these results align with the previously described neuro-anatomical model of syntactic gender processing proposed by Heim (2008). This author suggested a link between the neural representation of gender agreement and gender retrieval: the access and retrieval of gender-related information of a given noun may require the generation of a morphological gender cue, such as a gender-marked determiner (alternative 3 in the neuro-anatomical model proposed by Bates et al., 1995; Faussart et al., 1999; Heim, 2008). However, so far there is no direct evidence supporting this claim[13].

---

[12] Different methodological factors can be identified that potentially contribute to the lack of significant interaction. For instance, as we mentioned in the introduction section, Caffarra et al. (2014) used a visual-half field presentation approach. This could be one of the most important factors which may have a deeper impact on their results. This type of paradigm is highly valuable for elucidating the contribution of each brain hemisphere in a certain cognitive function. However, it might induce atypical inter-hemispheric dynamics (e.g., a delay in the neural response of the ipsilateral hemisphere might produce a drift in the response pattern of the contralateral one), especially in those task where the coupling between the right and left hemisphere could be critical (Vigneau et al., 2011 for an extensive revision of the right hemisphere contribution during sentences processing). Further investigations must be aimed at disentangling this inconsistency.

[13] There are previous findings demonstrating participants can recover the gender feature value of a given opaque noun – during a gender decision task – through the production of the corresponding gender-marked determiner (Miceli et al., 2002). This strategy was related to increases in the brain response of inferior frontal regions.

Importantly, no fMRI studies have been carried out to investigate whether the processing of different gender-related cues embedded in nouns affects the computation of agreement dependencies. The present fMRI study seeks to investigate how local relations between determiners and nouns are established based on form-based (i.e., orthographical, and/or morpho-phonological) and/or lexical gender cues. By combining behavioural and fMRI data here we investigated a) which brain regions are sensitive to gender agreement within a noun phrase; b) whether the brain processes transparent and opaque nouns in a same way or differently; and c) whether and how different types of gender-marking cues modulate the neural mechanisms underlying agreement processing. In the current experiment we investigated the effects of Gender-marking (*Transparent Nouns* vs. *Opaque Nouns*) and Gender Congruency (*Gender Match* vs. *Gender Mismatch*) using Spanish determiner-noun pairs. The construction of a noun phrase representation requires the access to morpho-syntactic information in both types of pairs (i.e., determiner + transparent noun [$el_{masc.}$ $libro_{masc.}$] and determiner + opaque noun [$el_{masc.}$ $lapiz_{masc.}$]). Moreover, the morpho-syntactic integration of this type of grammatical construction implies the association of the linguistic stimulus (*El libro/El lápiz*) to a referent in the external world. However, different sources of gender information are available depending on the transparency of the nouns (Bates et al., 1995; Gollan & Frost, 2001; Heim, 2008). Gender information in transparent nouns could be accessed based on both form-based and lexical cues. In contrast, gender information in opaque nouns cannot be derived from form-based cues since their ending does not predict the gender values (i.e., whether the noun is feminine or masculine), but relies exclusively on lexical cues. Thus, in order to reveal how these sources of gender information might affect the morpho-syntactic integration processing in a within-constituent domain, we tested the main effects and possible interactions.

Regarding the processing of grammatical relations, a distinction between the neural networks involved in the processing of congruent and incongruent determiner-noun pairs (i.e., a main effect of Gender Congruency) is expected. While congruent determiner-noun pairs should activate regions related to the morpho-syntactic integration processing, incongruent determiner-noun pairs should activate mostly regions related to the monitoring of conflicting information. There are no clear predictions for the regions underlying the morpho-syntactic integration processing in a within-constituent domain. According to previous evidence the pars opercularis within the left IFG seems to be the most plausible candidate for this functional role (Carreiras et al. 2010; Hammer et al. 2007). As we commented above, previous studies have been demonstrated a significant increase in the response pattern of this frontal region associated with ungrammatical relative to grammatical constructions (Carreiras et al. 2010; Hammer et al. 2007). As far as the regions involved in the conflict-monitoring operations are concerned, previous evidence points to the anterior cingulate cortex as the core area of this system (Carter & van Veen, 2007; Taylor et al., 2007; van de Meerendonk et al., 2011; van de Meerendonk et al., 2009; van de Meerendonk et al., 2010). These studies have suggested a coupling between the anterior cingulate cortex, dorsolateral prefrontal regions and superior parietal areas (Kuperberg et al., 2003; 2008; Nieuwland et al., 2012). This network would be in charge of preventing behavioral mistakes by monitoring the occurrence of conflicting information (for a discussion of this topic see van de Meerendonk et al., 2011; van de Meerendonk et al., 2009; van de Meerendonk et al., 2010).

Concerning the gender-marking manipulation we expect differences in the neural correlates underlying the processing of transparent and opaque nouns (i.e., main effect of Gender-marking), as previous studies suggested (see Heim, 2008 for a review of this topic; Hernandez et al., 2004; see also Padovani et al., 2005). According to the neuro-anatomical model proposed by Heim (2008), these differences would cover regions such as the left IFG (pars opercularis and triangularis) and the middle temporal gyrus (see also Indefrey & Levelt, 2004). Finally, if the form-based information available for transparent nouns does not modulate the establishment of grammatical relations, we should expect no interactions between Gender Congruency and Gender-marking. If this is so, similar neural circuits should result from the contrast *Gender Mismatch* versus *Gender Match* for both types of configurations (determiner + transparent noun and determiner + opaque noun). In contrast, if the coding of form-based gender-marking cues affects the agreement processing, we should expect a significant interaction between Gender Congruency and Gender-marking. The left

IFG has the potential to showcase this interaction, since this region is a critical node for both agreement processing and the access/retrieval of gender-related information. However, crucially, this issue has not yet been addressed using fMRI. Hence, no clear prediction can be made as to where this interaction, if present, should emerge.

3.2 Materials and Methods

Participants. Fifty three healthy participants took part in the current study as paid volunteers. All were highly proficient speakers of Spanish and all gave informed consent as stipulated in the ethics approval procedure of the *BCBL*[14] *Research Ethics Committee.* They all have right-handed dominance, normal or corrected to normal vision and no history of psychiatric, neurological disease or learning disabilities. Participants were assessed for handedness through an abridged Spanish version of the Edinburgh Handedness Inventory (Oldfield, 1971). They were also asked about claustrophobia, or any other criteria that could exclude them from participating in an fMRI experiment[15]. After the experimental session, the quality of the fMRI data of each individual was explored using the Artifact Repair toolbox (Gabrieli Cognitive NeuroScience Lab; http://cibsr.stanford.edu/tools/ArtRepair/ArtRepair.htm). Those subjects whose fMRI data exhibited more than 40 % of the scan-to-scan motion estimation higher than 1 mm were excluded from following statistical analysis[16]. After these exploratory analyses, a total of forty seven participants (eleven females), age ranging from 18 to 42 years (mean = 23.1, standard deviation = 6.0), were used to make population inference.

Stimuli and experimental procedure. In the current experiment, participants took part in a single scanner session comprising an event-related 2 x 2 factorial within-subject design, which consisted in a serial presentation of 120 Spanish determiner-noun pairs. The gender agreement between determiners and nouns was manipulated, resulting in grammatical and ungrammatical associations (with a proportion of 1:1). The nouns selected could be either

---

[14] Basque Center on Cognition, Brain and Language

[15] The selection criteria were the same for all the experiments. Thus, these details about the sample will not be included in the next experimental chapters.

[16] These exploratory analyses were similarly applied in the other four experiments.

transparent or opaque (with a proportion of 1:1). Transparent nouns refer to those nouns morphologically marked for gender using the Spanish canonical suffixes "–o" for masculine and "–a" for feminine. Opaque nouns refer to nouns that end with non-canonical suffixes (e.g., "–e", "–n", "–l", "–d", "–z"). The resulting 2 x 2 factorial design comprised Gender-marking [*Transparent Nouns* and *Opaque Nouns*] and Gender Congruency [*Gender Match* and *Gender Mismatch*] as factors (see examples (9) and (10) below). Two different stimulation lists were created with the same nouns. They appeared in association with the feminine/singular determiner "–la" in one list and in association with the masculine/singular determiner "–el" in the other list. Thus, the same noun was presented in both conditions, *Gender Match* and *Gender Mismatch* in different lists. These two lists were counterbalanced between participants in such a way that participants saw all nouns once.

(9) Transparent Nouns

(a) Gender Match: e.g., *La*$_{fem.sing.}$ *película*$_{fem.sing.}$ [The film]

(b) Gender Mismatch: e.g., * *El*$_{masc.sing.}$ *película*$_{fem.sing.}$ [The film]

(10) Opaque Nouns

(a) Gender Match: e.g., *La*$_{fem.sing.}$ *catástrofe*$_{fem.sing.}$ [The catastrophe]

(b) Gender Mismatch: e.g., * *El*$_{fem.sing.}$ *catástrofe*$_{fem.sing.}$ [The catastrophe]

All the nouns included in the current design referred to inanimate and concrete entities (e.g., *mesa* [table] or *balón* [ball]) [mean of concreteness = 5.51 (±0.75)], in such a way that only formal gender information and not conceptual information concerning the biological sex of the referent was present. In each condition, half of the nouns referred to masculine entities, while the other half to feminine entities. In Spanish, opaque nouns constitute a highly restricted subset of the total nouns in the lexicon (Anderson, 1961; Eddington, 2004). Thus, all the opaque and transparent nouns included in the current experiment were selected from the lower side of the whole lexical frequency distribution [mean = 36.85 per million, SD = 34.53]. The length of the opaque and transparent nouns was also controlled, with a maximum of 8 and a minimum of 4 letters [opaque: mean = 5.20, SD = 0.91; transparent: mean = 5.60, SD = 1.65]. All the lexical measures considered were extracted from the Spanish ESPaL database (Duchon et al., 2013). In addition, in order to avoid possible interaction effects between gender and number agreement features, different parameters regarding the number agreement information were also controlled. Only the singular form of the determiners and the nouns was included. All determiner-noun word pairs agreed in number (see Appendix 1 for a list of the stimuli used).

Each trial consisted of a visual presentation of determiner-noun pairs. Word pairs were displayed during 300 ms in white capital letters on a black background. Participants were instructed to answer as quickly and as accurately as possible whether the word pair was grammatically acceptable or not, by pressing one of two different buttons. They had two seconds to respond after the offset of each stimulus. During this time a visual cue was displayed indicating when participants had to respond. In order to optimize the sampling of the BOLD response, an inter-stimulus interval was included. During this period a fixation point (“+”) was presented with different durations across trials, varying between 2 and 8 seconds. This baseline period allows us to counteract possible expectation effects, which might influence the brain response. In addition, this procedure is also useful to improve the estimation of the time course of the BOLD response associated to each experimental condition.

MRI acquisition. The experiment was performed on a 3-T Siemens TrioTrim scanner, using a standard thirty two-channel phased-array surface coil (Siemens, Erlangen, Germany), which provided a high spatial resolution and signal-to-noise ratio. Functional event-related scans consisting of 454 echoplanar images were acquired using a T2*-weighted gradient-echo pulse sequence with the parameters described in Appendix 2A. The first six volumes of each functional run were discarded to insure the steady state tissue magnetization[17]. In addition, a MPRAGE T1-weighted structural image (1 x 1 x 1 mm resolution) was acquired with the following parameters: TE = 2.97 ms, TR = 2530 ms, flip angle = 7° and FOV = 256 x 256 x 160 mm^3. This yielded 176 contiguous 1 mm thick slices.

---

[17] Same procedure was used in all the experiments.

FMRI data analysis. Functional data were analyzed using SPM8 and related toolboxes (http://www.fil.ion.ucl.ac.uk/spm). Raw functional scans were slice-time corrected taking the middle slice as reference, spatially realigned, unwarped, coregistered with the anatomical T1 (Collignon et al., 1995) and normalized to the MNI space using the unified normalization segmentation procedure. Normalized images were then smoothed using an isotropic 8mm Gaussian kernel. Resulting time series from each voxel were high-pass filtered (128s cut-off period) (see Box 3.1 for a schematic representation of the fMRI pre-processing pipeline).

Statistical parametric maps were generated with univariate general linear models, using for each stimulus type a regressor obtained by convolving the canonical hemodynamic response function with delta functions at stimulus onsets, and also including the six motion-correction parameters as regressors. The stimuli onsets included five different components. The first four corresponded to each experimental condition (*Transparent Gender Mismatch* [Tr_MM], *Transparent Gender Match* [Tr_M], *Opaque Gender Mismatch* [Op_MM], *Opaque Gender Match* [Op_M]). The last one corresponded to the fixation cross and it was modeled as a single regressor, independently of the experimental conditions. The next Parameters of the GLM were estimated with a robust regression[18] using weighted-least-squares that also corrected for temporal autocorrelation in the data (Diedrichsen & Shadmehr, 2005; http://www.bangor.ac.uk/~pss412/imaging/robustWLS.html).

A pair-wise contrast comparing activity to each experimental condition relative to the fixation baseline was performed. Resulting statistical parametric maps were then submitted into a second level 2x2 factorial design (i.e., in SPM, Flexible Factorial Design), using Gender-marking and Gender Congruency as within-subject factors. This analysis

---

[18] The head movement of the participant is one of the most common sources of fMRI data noise, but other factors such as physiological responses or motion related to behavioural motor responses can also produce artefactual signals. While some pre-processing steps of the data analysis (e.g., realignment procedure) attempt to resolve the effects of this noise in the estimation of the BOLD signal, significant residual effects often remain in the data. The robust regression using weighted-least-squares is an algorithm that estimates the variance of the noise for each volume included in the functional time series. These variance parameters are used to obtain a weighted least-squares estimate of the regression parameters of a linear model, resulting in a significant increase of the model sensitivity to detect emerging activation sources (Diedrichsen & Shadmehr, 2005).

allows us to determine possible main effects and interactions. These effects were also included in the statistical model. This model considers the variability between different subjects as a source of variance. Population-level inferences were tested adjusting the statistical threshold in such a way that only those peaks or clusters with a p-value corrected for multiple comparisons with family wise error (FWE; Nichols and Hayasaka 2003) and/or false discovery rate (FDR; Genovese, Lazar, and Nichols 2002) were consider as significant – i.e., combining the probability values and the required number of activated voxels within each cluster. All local maxima were reported in the results tables as MNI coordinates (Evans et al., 1993).

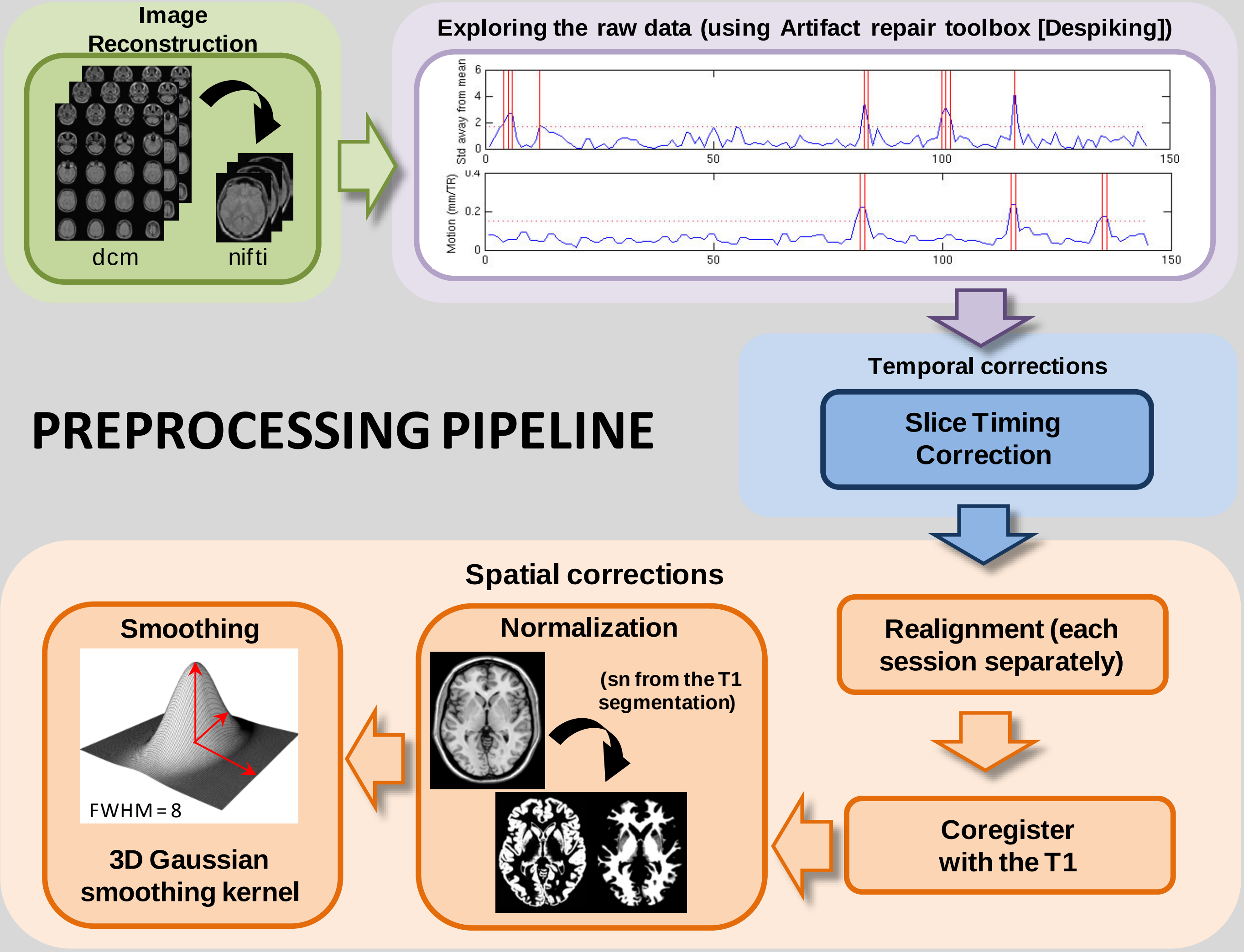


Figure 3.1. Schematic representation of the fMRI pre-processing pipeline. This general procedure will be similarly applied in all the experimental chapters.

3.3 Results

Behavioural results. Statistical analyses of the behavioral responses were performed following the 2x2 factorial design. Because of technical problems with the response recording devices the behavioral data of eigth participants were lost. Furthermore, participants whose mean RTs and/or error rates exceed two standard deviations – above or below – from the mean of the group were excluded from the subsequent analyses[19]. Following these criteria four participants were also excluded, thus a total of forty one participants were considered in the analyses of the behavioral results. Mean RTs and error rates for each experimental condition are presented in Table 3.1, with the corresponding standard error between parentheses.

Table 3.1. Error rates and mean decision times (in ms) for both agreement patterns (match and mismatch) in the two types of nouns (transparent and opaque) with the corresponding standard error between parentheses.

	Mean decision times		**Error rates**	
	Match	**Mismatch**	**Match**	**Mismatch**
Transparent	714.85 (26.92)	809.42 (32.29)	4.31 (0.49)	8.62 (1.16)
Opaque	689.30 (26.83)	825.00 (34.96)	3.23 (0.66)	6.66 (0.96)

For RTs, a significant main effect of Gender Congruency was found [$F(1,40) = 84.27$, $p < 0.005$]. Additionally, a significant interaction between Gender-marking and Gender Congruency emerged from this analysis [$F(1, 40) = 9.84$, $p < 0.005$], suggesting that the congruency differential effect (i.e., difference between *Gender Mismatch* and *Gender Match*) was different for transparent and opaque nouns. In order to test the source of this interaction, the experimental conditions were contrasted in a pair-wise manner. Planned comparisons demonstrated that the *Gender Mismatch* condition was harder (i.e., higher RTs

---

[19] The same procedure was used in the other four experiments. However, the threshold applied to clean the data varied between 2.0 and 2.5 depending on the variability of the sample included in each study.

and error rates) than the *Gender Match* condition, for both transparent [$t(40) = 7.83$, $p < 0.001$] and opaque nouns [$t(40) = 8.90$, $p < 0.001$]. However, the effect was larger for opaque than for transparent nouns [$t(40) = 3.14$, $p < 0.005$]. Additionally, the error rates analysis showed a main effect of Gender Congruency [$F(1, 40) = 13.49$, $p < 0.001$]: the percentage of error rates was larger for *Gender Mismatch* than for *Gender Match* condition. In addition, there was a main effect of Gender-marking [$F(1, 40) = 7.92$, $p < 0.01$], indicating that the percentage of errors was larger for transparent than for opaque nouns. The interaction between these two factors did not reach the significance threshold.

fMRI results: Congruency effect (Difference between Gender Mismatch and Gender Match conditions). We extracted the main effect of Gender Congruency to characterize the functional neuro-anatomical network involved in the processing of grammatical relations. The significant effects included regions with higher responses for the *Gender Mismatch* condition than for *Gender Match* condition and regions that exhibited the opposite pattern, i.e. higher activation for *Gender Match* than for *Gender Mismatch*. Significant response increases in occipital, frontal and parietal regions in both hemispheres emerged from the contrast *Gender Mismatch* > *Gender Match*. This response pattern also comprised regions exhibiting bilateral activation such as the middle and medial superior frontal gyrus, the anterior cingulate, the pre- and postcentral gyrus, the supplementary motor area and the lingual gyrus. This contrast also showed significant left lateralized parietal responses including regions such as the angular gyrus and the posterior cingulate cortex. Interestingly, the statistical activation map resulting from this contrast comprised also the right insula and the right dorsal striatum including the putamen and the caudate nuclei (see Table 3.2 and Figure 3.2 for more details).

On the other hand, the contrast *Gender Match* > *Gender Mismatch* resulted in a bilateral response pattern. This pattern included brain regions such as the pars opercularis and triangularis, within the inferior frontal gyrus, the superior frontal gyrus, the middle cingulate cortex, the anterior part of the supplementary motor area and the inferior and superior parietal gyrus. This contrast, *Gender Match* > *Gender Mismatch*, also showed significant response increases in the left posterior middle temporal gyrus –extended into the middle occipital cortex– and the right superior temporal gyrus (see Table 3.3 and Figure 3.2 for a detailed list of regions and its response pattern).

Table 3.2. Significant activation clusters resulting from the contrast Mismatch > Match, including both Types of Nouns (Transparent and Opaque).

Hemisp.	**Region**	**x,y,z {mm}**	**Peak level**	**Cluster level**
			Z	**Vx**
Left	Medial Orbitofrontal	-4 52 -2	**5.69**	653
	Middle Frontal Gyrus	-26 24 50	**6.42**	839
	Ant Cingulate	-6 38 -6	**4.56**	
	Paracentralobule	-6 -22 60	**5.92**	269
	Precentral Gyrus	-42 -6 32	**4.55**	231
	Postcentral Gyrus	-44 -16 34	4.39	
	Angular Gyrus	-48 -66 42	**5.27**	528
	Precuneus	-4 -48 10	**6.71**	1439
	Post Cingulate	-8 -40 26	**6.11**	
	Sup Occipital/Cuneus	-16 -82 28	**5.78**	
	Lingual	-4 -74 -2	**5.12**	317
Right	Medial Sup Frontal Gyrus	10 52 2	**6.88**	653
	Middle Frontal Gyrus	26 54 6	**5.14**	
	Precentral Gyrus	50 12 42	**5.24**	279
	Insula	34 -2 16	**6.14**	280
	Caudate	14 14 12	**4.69**	
	Putamen	26 8 10	**4.56**	
	Supp Motor Area	2 -16 68	**4.47**	269
	Lingual	8 -70 -4	**4.49**	317

x,y,z {mm} = Coordinates in MNI space of local maxima. Z = Z scores. Vx = Number of voxels significantly activated inside the cluster belonging to each local maximum. Z scores and Vx are reported in bold if they are significant at the cluster level after FWE or FDR correction, if indicated in bold and underline are significant at the peak level after FWE or FDR correction. Post: Posterior; Ant: Anterior; Sup: Superior; Supp: Suplementary.

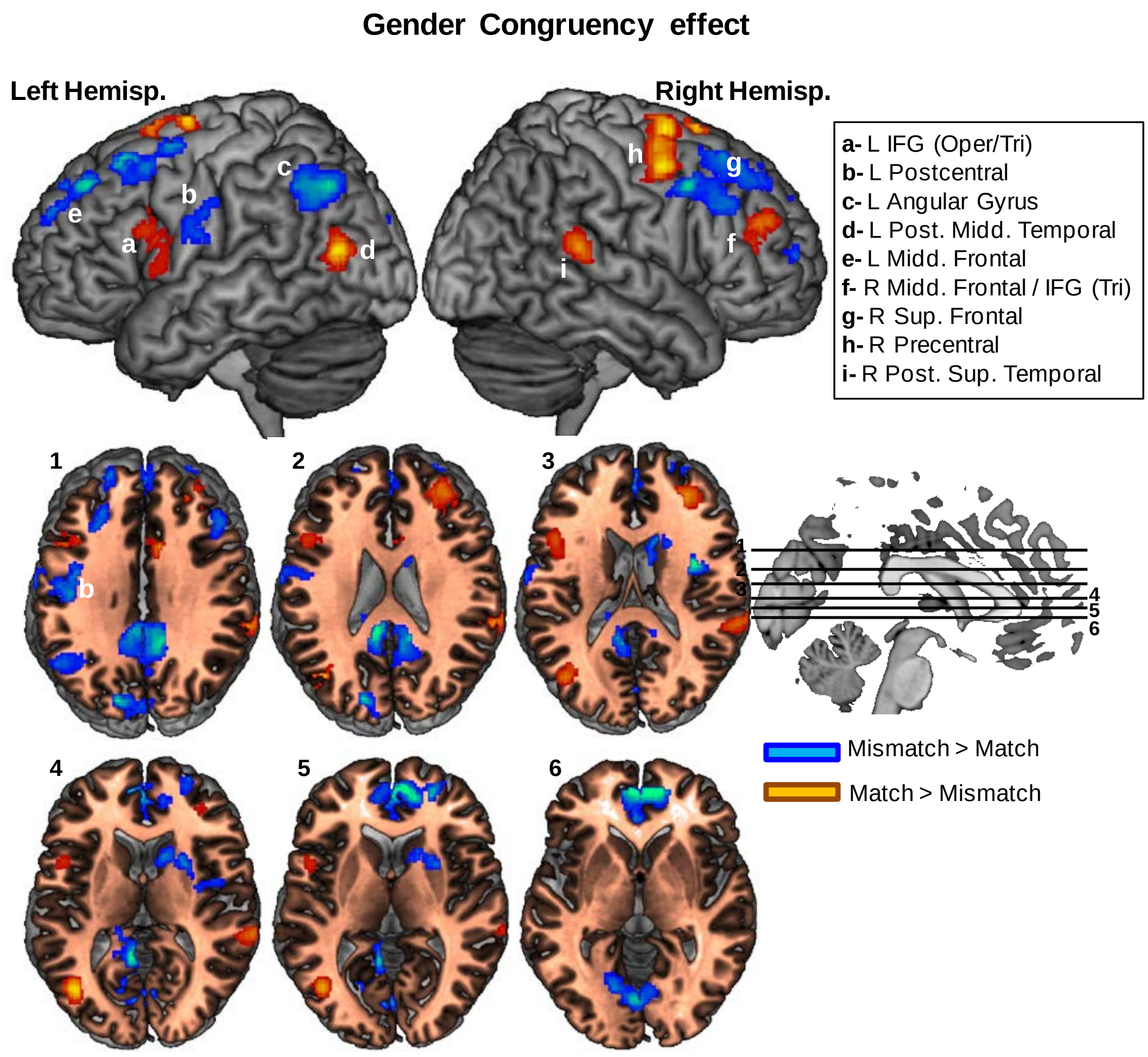


Figure 3.2. Statistical parametric map emerging from the main effect of Gender Congruency was projected on the MNI single-subject T1 image. The two tails of the F-contrast were represented with different colors: *Gender Mismatch* > *Gender Match* in blue and *Gender Match* > *Gender Mismatch* in red-yelow. All clusters depicted were statistically significant with a p-value corrected for multiple comparisons. The sagittal view represented in the right part of the figure display the axial slices used to represent the significant activated clusters. The numbers in this sagittal view correspond with the numbers located in the upper and left side of each axial slice. Hemisp: Hemisphere; IFG: Inferior frontal gyrus; Oper: Opercularis; Tri: Triangularis; Midd: Middle; Inf: Inferior; Post: Posterior; Sup: Superior.

Table 3.3. Significant activation clusters resulting from the contrast Match > Mismatch, including both Types of Nouns (Transparent and Opaque).

Hemisp.	Region	x,y,z {mm}	Peak level	Cluster level
			Z	Vx
Left	Oper Inf Frontal Gyrus	-48 14 22	**4.36**	359
	Tri Inf Frontal Gyrus	-41 16 30	3.61	
	Sup Frontal Gyrus	-24 -4 72	**6.06**	264
	Supp Motor Area	-10 14 68	**4.85**	
	Inf Parietal Gyrus	-50 -28 50	**4.52**	193
	Post Middle Temporal	-38 -64 16	**4.40**	319
	Middle Occipital	-42 -70 14	**6.2**	
Right	Oper Inf Frontal Gyrus	44 10 22	**4.75**	196
	Middle Frontal Gyrus / IFG	36 -2 60	**5.28**	513
	Sup Frontal Gyrus	22 2 66	**6.26**	922
	Supp Motor Area	10 16 68	**5.74**	
	Middle Cingulate	10 12 34	**5.26**	
	Sup Parietal Gyrus	16 -48 56	**5.18**	158
	Sup Temporal Gyrus	66 -36 14	**5.05**	221
	Calcarine	12 -78 18	**4.86**	132

x,y,z {mm} = Coordinates in MNI space of local maxima. Z = Z scores. Vx = Number of voxels significantly activated inside the cluster belonging to each local maximum. Z scores and Vx are reported in bold if they are significant at the cluster level after FWE or FDR correction, if indicated in bold and underline are significant at the peak level after FWE or FDR correction. Sup: Superior; Ant: Anterior; Inf: Inferior; Supp: Suplementary; Tri: Triangular; Oper: Opercular.

<u>fMRI results: Transparency effect (Difference between Transparent and Opaque Nouns).</u> In order to explore whether transparent and opaque nouns would trigger different brain activation patterns, we extracted the main effect of Gender-marking. Several clusters in the two hemispheres were identified, showing a significant main effect. Similarly to the Gender Congruency effect, the main effect of Gender-marking included regions with higher responses for transparent than for opaque nouns and regions that exhibited the opposite pattern (i.e., higher response for opaque than for transparent nouns). On the one hand, opaque nouns compared to transparent nouns produced increased responses in a widespread fronto-parieto-temporal network, bilaterally distributed (see Figure 3.3). This neuro-anatomical network included regions such as, the pars opercularis and triangularis within the

inferior frontal gyrus, the insula, the medial part of the superior frontal gyrus, the posterior part of the middle temporal gyrus, the hippocampus (including the parahippocampal region), the fusiform gyrus and the thalamus (see Table 3.4 for a detailed list of regions). On the other hand, transparent nouns compared to opaque nouns produced increased responses in a more restricted left lateralized network (Figure 3.3). This network included parietal regions, such as the left supramarginal and the left angular gyri, and occipital regions such as the left superior and middle occipital, the cuneus and the calcarine sulcus (see Table 3.5 for more details).

fMRI results: Interaction between Gender Congruency and Gender-marking. Importantly, the main goal of the present study was to investigate whether agreement processing could be modulated by the morphological and/or the lexical information embedded in our linguistic code. Thus, with this aim we tested the interaction between Gender Congruency and Gender-marking. Interestingly, we found significant interaction effects in five different left lateralized clusters including the supramarginal and the angular gyri, the hippocampus, the posterior part of the MTG/STG and the pars triangularis within the IFG. However, planned comparisons revealed that the patterns of response resulting from each of these areas were different depending on the gender-to-ending regularities (Figure 3.4). Specifically, for *Transparent Nouns*, the hippocampus, the pars triangularis within the IFG and the posterior MTG/STG exhibited higher response for *Gender Mismatch* than for *Gender Match*. In contrast, for *Opaque Nouns* the neural responses of these two regions were more conspicuous for the *Gender Match* than for the *Gender Mismatch* condition. Interestingly, neural responses in the parietal areas (i.e., the angular and the supramarginal giri) were similarly modulated: the difference between *Gender Mismatch* and *Gender Match* conditions was only significant for *Opaque Nouns*. While activity in the angular gyrus was maximally enhanced by the *Gender Match* condition, it was the *Gender Mismatch* condition which produced the greatest activity in the supramarginal gyrus (Figure 3.4 and Table 3.6).

Table 3.4. Significant activation clusters resulting from the contrast Opaque Nouns > Transparent Nouns, including both grammatical patterns (Mismatch and Match).

Hemisp.	**Region**	**x,y,z {mm}**	**Peak level**	**Cluster level**
			Z	**Vx**
Left	Oper Inf Frontal Gyrus	-44 14 10	**7.55**	2921
	Insula	-36 20 8	**7.17**	
	Medial Sup Frontal Gyrus	-6 48 20	**5.88**	3446
	Sup Frontal Gyrus	-20 4 48	**4.92**	303
	Precentral	-28 -16 56	**4.73**	
	Paracentralobule	-12 -38 72	**4.64**	284
	Thalamus	-4 -24 6	**4.7**	299
	Post Middle Temporal	-58 -8 -10	**4.56**	176
	Fusiform	-36 -38 -16	**7.44**	341
	ParaHippocampal	-22 -28 -16	**5.29**	
	Lingual	-12 -40 -8	**5.04**	
	Hippocampus	-22 -22 -10	**6.65**	
Right	Tri Inf Frontal Gyrus	40 38 6	**6.93**	1871
	Insula	36 4 14	**6.69**	
	Oper Inf Frontal Gyrus	50 16 20	**5.86**	
	Meiddle Frontal Gyrus	28 22 38	**5.95**	3446
	Middle Cingulate	10 22 40	**5.85**	
	Supp Motor Area	2 6 58	**5.69**	438
	Sup Parietal Gyrus	20 -58 62	**6.15**	629
	Postcentral	34 -42 62	**5.52**	
	Thalamus	4 -24 4	**6.33**	299
	Sup Temporal Gyrus	62 -32 16	**5.93**	1803
	Precentral	54 -2 48	**5.9**	
	Lingual	6 -68 6	**4.93**	481
	Calcarine	10 -80 8	4.16	

x,y,z {mm} = Coordinates in MNI space of local maxima. Z = Z scores. Vx = Number of voxels significantly activated inside the cluster belonging to each local maximum. Z scores and Vx are reported in bold if they are significant at the cluster level after FWE or FDR correction, if indicated in bold and underline are significant at the peak level after FWE or FDR correction. Sup: Superior; Post: Posterior; Inf: Inferior; Supp: Suplementary; Tri: Triangular; Oper: Opercular.

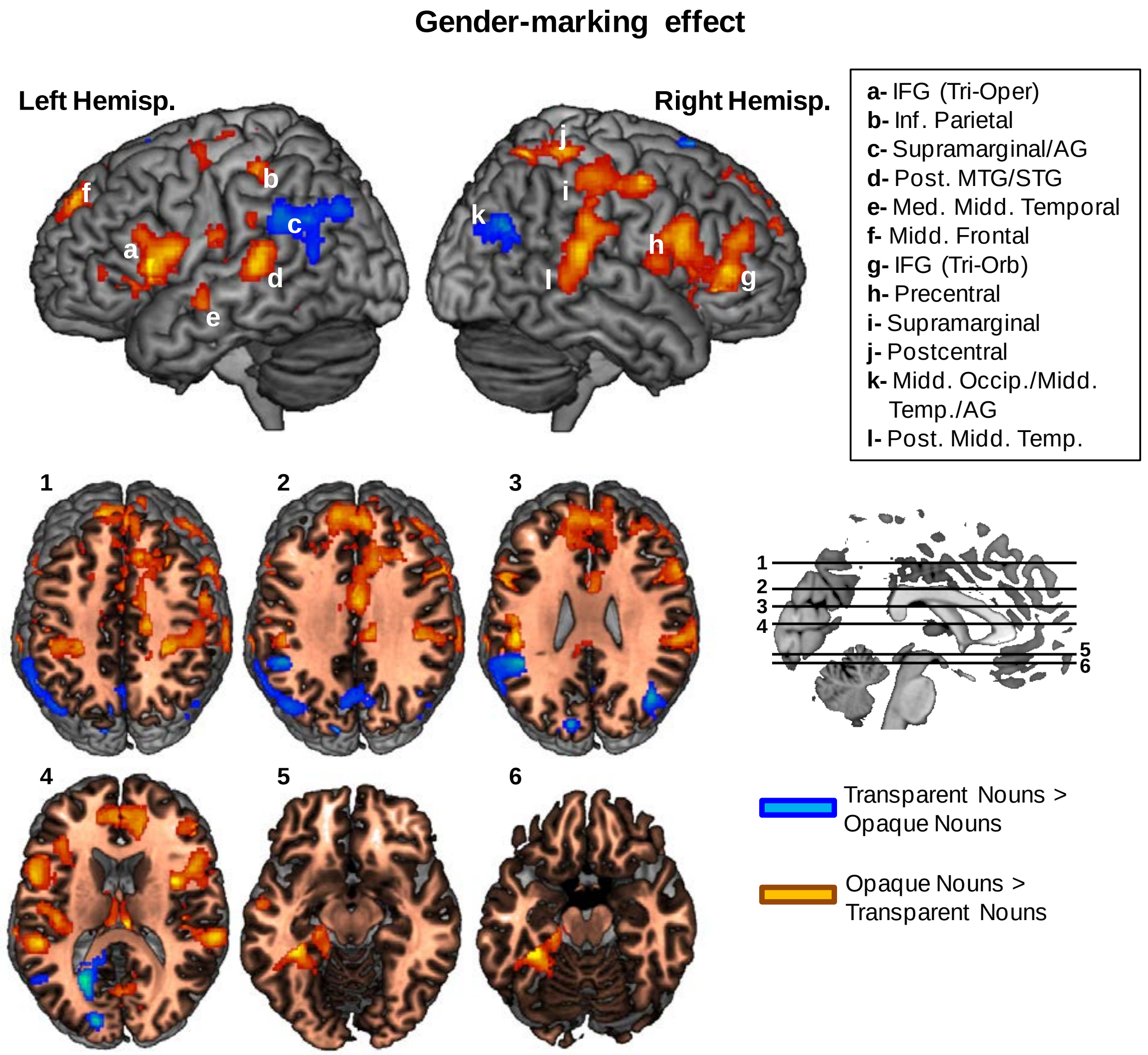


Figure 3.3. Statistical parametric map emerging from the main effect of Transparency was projected on the MNI single-subject T1 image. The two tails of the F-contrast were represented with different colors: *Transparent Nouns* > *Opaque Nouns* in blue and *Opaque Nouns* > *Transparent Nouns* in red-yelow. All clusters depicted were statistically significant with a p-value corrected for multiple comparisons. The sagittal view represented in the right part of the figure display the axial slices used to represent the significant activated clusters. The numbers in this sagittal view correspond with the numbers located in the upper and left side of each axial slice. Hemisp: Hemisphere; IFG: Inferior frontal gyrus; Oper: Opercularis; Tri: Triangularis; Midd: Middle; Inf: Inferior; Post: Posterior; Sup: Superior.

Table 3.5. Significant activation clusters resulting from the contrast Transparent Nouns > Opaque Nouns, including both grammatical patterns (Mismatch and Match).

Hemisp.	**Region**	**x,y,z {mm}**	**Peak level**	**Cluster level**
			Z	**Vx**
Left	Supp Motor Area	-4 16 64	**5.15**	237
	SupraMarginal	-44 -44 32	**5.5**	689
	Angular Gyrus	-60 -58 30	**4.76**	
	Middle Occipital	-44 -72 36	4.29	
	Sup Occipital	-12 -86 22	**6.33**	189
	Sup Occipital	-18 -86 12	**6.14**	
	Calcarine	-22 -60 14	**6.3**	220
	Precuneus	-20 -50 14	**4.57**	
Right	Supp Motor Area	6 18 64	**5.3**	237
	Cuneus	8 -72 36	3.75	220
	Middle Occipital	40 -66 26	**5.51**	221

x,y,z {mm} = Coordinates in MNI space of local maxima. Z = Z scores. Vx = Number of voxels significantly activated inside the cluster belonging to each local maximum. Z scores and Vx are reported in bold if they are significant at the cluster level after FWE or FDR correction, if indicated in bold and underline are significant at the peak level after FWE or FDR correction. Sup: Superior; Supp: Suplementary.

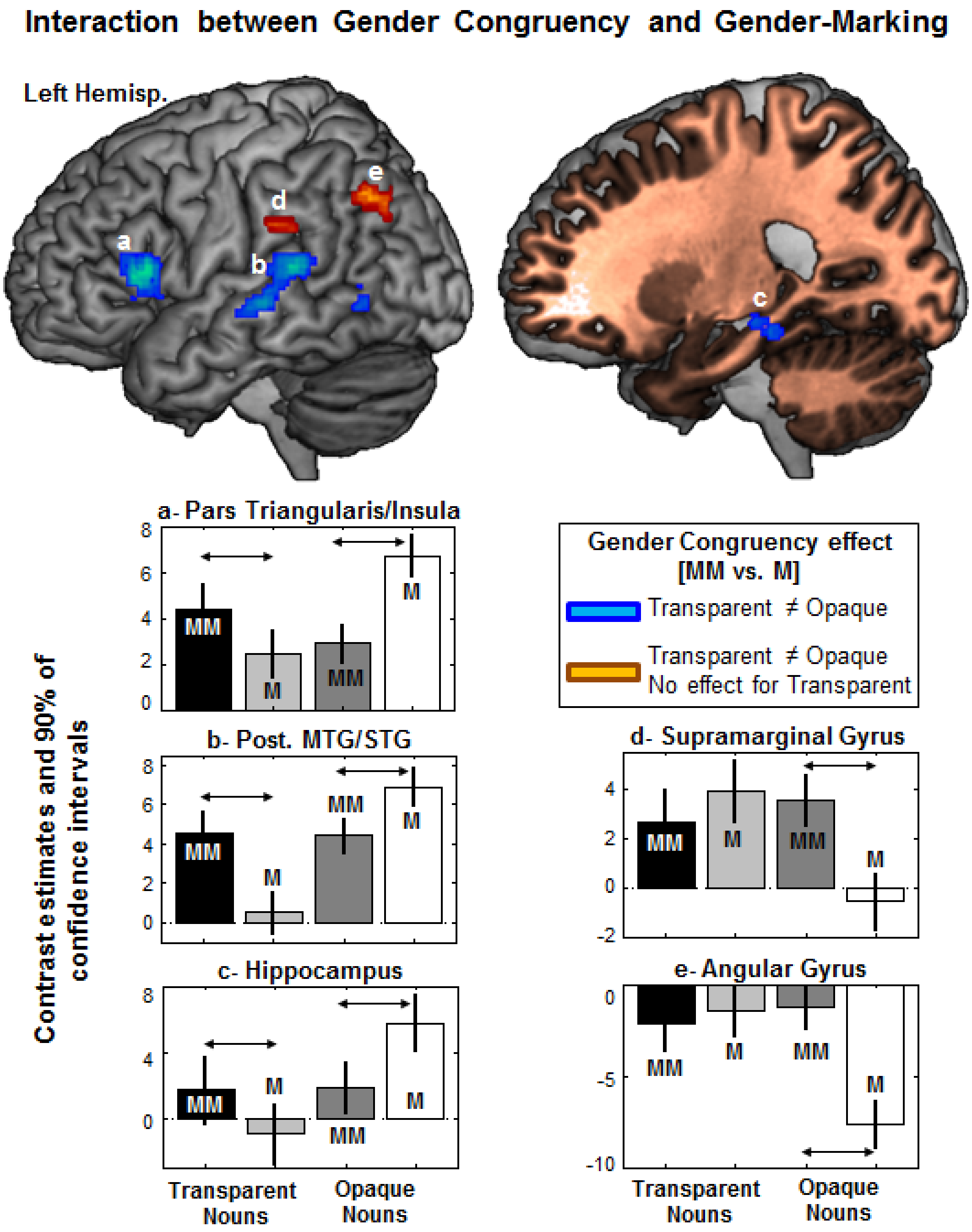


Figure 3.4. Statistical parametric map emerging from the interaction effects between Gender Congruency and Gender-marking were projected on the MNI single-subject T1 image. The sagittal view represented in the upper part of the figure display the significant activated clusters. The lowercase letters signalling each cluster correspond with each neural region represented in the bar graphs. The bar graphs (lowest part) display the contrast estimates and 90% of confidence intervals at the maximum peaks representative of the clusters resulting from the interaction effect.

Table 3.6. Significant activation clusters resulting from the interaction effects between Gender-marking and Gender Congruency.

Region (Left Hemisp.)	x,y,z {mm}	Interaction		Simple effects	
		Peak level	Cluster level	Tansparent	Opaque
		Z	Vx	Z	Z
Tri Inf Frontal Gyrus	-48 20 10	5.58	276	+4.11	-6.09
Post MTG/STG	-62 -26 -2	4.17	316	+5.43	-4.22
Hippocampus	-28 -34 -12	3.24	26	+5.27	-3.32
Supramarginal Gyrus	-64 -30 28	3.61	59	n.s	+4.9
Angular Gyrus	-52 -66 38	4.18	80	n.s	+6.64

x,y,z {mm} = Coordinates in MNI space of local maxima. Z = Z scores. Vx = Number of voxels significantly activated inside the cluster belonging to each local maximum. Z scores and Vx are reported in bold if they are significant at the cluster level after FWE or FDR correction, if indicated in bold and underline are significant at the peak level after FWE or FDR correction. The sign of the Z scores indicates the direction of each interaction. The positive sign indicates that the neural response for the Mismatch condition was higher than for the Match condition. Whereas the negative sign indicates the opossite pattern, higher neural response for Match than for Mismatch. Tri: Triangularis; Inf: Inferior; Post: Posterior; MTG/STG: Middle and superior temporal gyrus;Trans: Transparent.

3.4 Discussion

Taken toghether, the current findings suggested that a specific brain circuit responds according to the agreement congruency between determiners and nouns and more importantly, that the gender-marking regularities fine-tune the neural response of some specific nodes within this circuit. Regarding the first question (i.e., which brain regions are sensitive to gender agreement within a noun phrase), we showed the critical role of the pars opercularis and triangularis within the left IFG and the posterior part of the left MTG/STG during gender agreement computation. But, critically, we also demonstrated that this circuit is not circumscribed to these regions. Bilateral areas such as the superior parietal cortex, the anterior cingulate cortex and the superior frontal gyrus exhibited higher responses for incongruent than for congruent items (Figure 3.2). Concerning the second question (i.e., does the brain process transparent and opaque nouns in a same way or differently), we isolated the brain regions engaged in the processing of transparent nouns from those recruited by opaque nouns. While the network related to transparent nouns is circumscribed to occipital and adjacent parietal areas in the left hemisphere, the network associated to opaque nouns spread to temporal, parietal and frontal regions bilaterally distributed (Figure 3.3). Finally, with regard to the third question (i.e., whether and how different types of gender-marking cues modulate the neural mechanisms underlying agreement processing), the current experimental design allowed us to isolate those regions involved in the processing of gender agreement that are also sensitive to gender-marking regularities. Specifically, significant interaction effects between Gender Congruency and Gender-marking emerged in five left-lateralized clusters, including the pars triangularis within the IFG, the posterior part of the MTG/STG, the hippocampus, the angular and the supramarginal gyri (Figure 3.4). Critically, behavioral data goes in line with the fMRI results: the subjects classified determiner-noun pairs as grammatically correct more easily and accurately (i.e., shorter decision times and lower error rates) than incongruent pairs (for similar behavioral results see Akhutina et al., 1999 [adjective-nouns in Russian]; Caffarra et al., 2014 [determiner-nouns in Spanish]; Gollan & Frost, 2001 [noun-adjectives in Hebrew]; Holmes & Segui, 2004 [determiner-nouns in French]). This differentiation was evident for both transparent and opaque nouns. However, regarding the RTs, the difference between incongruent and congruent items was larger for opaque than for transparent nouns, as indicated by the significant interaction between Gender Congruency and Gender-marking. Overall, the current results constitute a critical piece of evidence suggesting that the neural substrates of agreement processing could be constrained by the available morpho-syntactic cues (i.e., form-based and/or lexical information embedded in the nouns). From now on, the next paragraphs will be focused on discussing the relevance of these three main findings.

In order to establish commonalities and singularities across experimental chapters, it is important to be clear about the main findings provided by each study. Thus, we summarize the main behavioral and neuro-anatomical results in the Table S1. To facilitate the comparison across the studies, this table will be updated at the end of each experimental chapter.

Table S1. Main Findings

	Behavioral results	Neuro-anatomical results	
		Grammaticality effects	Effects related with the critical manipulation
Experiment I (determiner-noun pairs)	**Main effect of Agreement Congruency**: Subjects classified determiner-noun pairs as grammatically correct more easily and accurately than incongruent pairs. This differentiation was evident for both transparent and opaque nouns. **Interaction effect**: Regarding RT, this effect was larger for opaque than for transparent nouns.	***Gender Mismatch* relative to *Gender Match***: the dorsal striatum, the middle and medial superior frontal gyrus, the orbito-frontal cortex, the pre- and post-central gyrus, as well as the anterior cingulate cortex. ***Gender Match* as compared to *Gender Mismatch*:** the pars opercularis and triangularis within the left IFG and the posterior part of the left MTG/STG.	Significant **interaction effects** between Gender Congruency and Gender-marking emerged in five left-lateralized clusters: ▪ Pars triangularis within the IFG ▪ Posterior part of the MTG/STG ▪ Hippocampus ▪ Angular Gyrus ▪ Supramarginal Gyrus
Experiment II			
Experiment III			
Experiment IV			
Experiment V			

Which brain regions are sensitive to gender agreement within a noun phrase [Main effect of Gender Congruency]? In line with our hypothesis and in consonance with previous fMRI evidence, we demonstrated a clear distinction between the neural circuits involved in the processing of gender congruent and incongruent items. Namely, while a bilateral widespread fronto-parietal network was recruited for *Gender Mismatch* relative to *Gender Match* condition, a more circumscribed fronto-temporal network was engaged for *Gender Match* as compared to *Gender Mismatch* (but see also Bambini et al., 2011; Carreiras et al., 2010; Hammer et al., 2007; Hammer et al., 2011; Kerns et al., 2004; Kuperberg et al., 2003; Kuperberg, Sitnikova, et al., 2008; Molinaro et al., 2013; Ni et al., 2000; Novick et al., 2005; van de Meerendonk et al., 2011; van de Meerendonk et al., 2009; Ye & Zhou, 2009). In the former case, the circuit engaged by ungrammatical constructions included cortical and subcortical regions such as the dorsal striatum (see Box 3.1 for some relevant considerations about the involvement of this region during the processing of linguistic information), the middle and medial superior frontal gyrus, the pre- and post-central gyrus, the anterior and middle cingulate cortices, as well as the inferior and superior parietal cortices[20]. In the latter case, the pars opercularis and triangularis within the left IFG and the posterior part of the left MTG/STG were distinguished as critical areas for the processing of grammatically correct associations. These results suggested that when incongruent information (e.g., a grammatical gender violation) is detected, the system certainly shoots up different mechanisms in an attempt to solve the conflicting cues. Combining the current results with what previous findings suggest, it is possible to advance some hypotheses about the role of some of these regions. Specifically, we will focus on the three distinct neuro-cognitive mechanisms that can be differentiated within agreement comprehension processing (see Molinaro, Barber, et al., 2011 for a review): I) feature consistency checking; II) integration of incoming information and III) reanalysis/repair processing or control monitoring resolution (see

---

[20] The anterior and middle cingulate cortices, as well as the inferior and superior parietal cortices, exhibited negative response (de-activation) compared to the fixation baseline condition, with greater de-activation for mismatching than matching constructions. These areas are sensitive to the presence of morpho-syntactic mismatches. Using different tasks (i.e., language related or not), previous studies have showed similar de-activation pattern in these regions. These effects have been frequently associated with the functioning of the default mode network (i.e., regions exhibiting high resting baseline responses) (Gusnard & Raichle, 2001; Kuperberg et al., 2003; Kuperberg, Sitnikova, et al., 2008; Lutcke & Frahm, 2008; Pardo et al., 1990; Raichle et al., 2001; Sohn et al., 2007).

Chapter 1, *Neuro-cognitive Mechanisms Underlying Agreement Processing: ERP Evidence* for more details).

Firstly, our results demonstrate that each type of grammatical construction evokes differentiated responses in the **left middle frontal gyrus**. This frontal region showed similar effects for transparent and opaque nouns, with higher activation for incongruent than for congruent items. In spite of the strong debate about the role of the left IFG during language processing, far less attention has been paid to other regions within the frontal lobe. However, the recruitment of the middle frontal gyrus by phrases/sentences with syntactic incongruities has been consistently reported (Folia et al., 2009; Kuperberg et al., 2003; Kuperberg, Sitnikova, et al., 2008; Newman et al., 2003; Nieuwland et al., 2007). Interestingly, the response of this area has remained invariant when the processing of different types of morpho-syntactic features has been compared (Folia et al., 2009 [gender mismatch between pronouns and antecedents in Dutch]; Kuperberg et al., 2003; Kuperberg, Sitnikova, et al., 2008 [finitness violations in English]; Newman et al., 2003 [finiteness violations in English]; Nieuwland et al., 2012 [verb-object violations in Basque]). Based on these previous findings, it is possible to hypothesize that activity in this region could be reflecting morpho-syntactic feature checking mechanisms equally enhanced regardless of the transparency of the nouns. Supporting this hypothesis, previous electrophysiological studies which investigated gender agreement processing consistently reported a LAN effect with higher amplitudes for gender incongruent than for well-formed constructions independently of their transparency (Barber & Carreiras, 2005; Barber et al., 2004; Caffarra & Barber, 2015; Caffarra et al., 2014; Caffarra et al., 2015; Deutsch & Bentin, 2001; Martin-Loeches et al., 2006; Molinaro, Kim, et al., 2008). In particular, this early electrophysiological response has been consistently related with the early detection of morpho-syntactic mismatches, especially in those manipulations where the access to morpho-syntactic feature values is crucial for the assignment of syntactic roles (Barber & Carreiras, 2005; Friederici, 2011; Friederici et al., 1996; Hagoort et al., 2003; Molinaro, Barber, et al., 2011; Munte et al., 1993; Silva-Pereyra & Carreiras, 2007).

In contrast to this argument, some authors have argued that the middle frontal gyrus response could reflect the involvement of domain-general working memory mechanisms (see Katsuki & Constantinidis, 2012a; 2012b for the involvement of the dorsolateral prefrontal regions in working memory processes) that might be triggered by the evaluation of the morpho-syntactic consistency. Consistently with this idea, previous studies have reported the activation of this frontal region in association with more general aspects of language processing such as verbal fluency (Abrahams et al., 2003) and cross-modal interference effects (see Ye & Zhou, 2009 for the activation of this region in a visual Stroop congruency task). In line with this hypothesis, activity in this frontal region mirrors the behavioral differences emerging between congruent and incongruent items – i.e., the larger the reaction times, the greater the neural response in this area. Unfortunately, based on the current fMRI data it is not possible to discern between these divergence points of view. Nonetheless, demonstrating that in addition to the IFG, other regions in the frontal lobe significantly contribute to the processing of linguistic material may be crucial, not only for basic language research, but also for the investigation of clinical populations. Indeed, it could be critical for further neuro-cognitive models of sentence processing to investigate in a more exhaustive way the role of this region. Hence, we will return to this debate in the next experimental chapters.

Secondly, in consonance with previous evidence, we identified **the pars opercularis and triangularis within the left IFG and the posterior part of the left MTG/STG** distinguishing between incongruent and congruent items. These regions have been previously identified as crucial epicenter of the language-specific network (Friederici, 2011, 2012; Hagoort, 2005, 2013, 2014; Price, C. J., 2010, 2012). A harmonic engagement between these left-lateralized perisylvian regions seems to be critical for decoding linguistic information, not only in the context of sentence comprehension but also in the context of single word processing (Friederici, 2002; Friederici & Alter, 2004; Friederici & Kotz, 2003; Friederici et al., 2003; Grodzinsky & Friederici, 2006; Jefferies, 2013; Lau et al., 2008; Molinaro et al., 2013; Novick et al., 2005; Petersson et al., 2012; Petersson & Hagoort, 2012; Rodd et al., 2010; Zhu et al., 2012). However, despite the huge amount of evidence concerning this topic, it has not been possible to reach a consensus about the functions carried out by each of these areas during sentence processing (Bornkessel-Schlesewsky & Schlesewsky, 2013; Friederici, 2011, 2012; Hagoort, 2003a, 2005; 2013 for three different perspectives about this topic). In this particular case, where the syntactic gender consistency was manipulated between determiners and nouns, the harmonic engagement of these regions could be mediating the operations behind the integration of the two syntactic elements in a noun-phrase structure (Brouwer et al., 2012; Brouwer & Hoeks, 2013; Hagoort & Indefrey, 2014; Lau et al., 2008; Molinaro et al., 2013; Molinaro et al., 2015). While the MTG/STG seems to underlie the mechanistic procedures required for decoding the inputs (e.g., the access/retrieval of the morpho-syntactic and lexical information, the structure building processing and the form-to-meaning mapping), the IFG seems to reflect a processing cost that shoot up when the system tries to integrate different sources of information (Baggio & Hagoort, 2011; Hagoort, 2013; see Hagoort, 2014 for a discussion of this topic; Hagoort & Indefrey, 2014).

Finally, regarding the third processing stage, **the anterior cingulate cortex** has been pointed out as the neural epicenter of an amodal conflict-monitoring system responsible for distinguishing between a conflict associated with the input signal and a processing error (Du et al., 2013; Olichney et al., 2010; van de Meerendonk et al., 2011; van de Meerendonk et al., 2009; van de Meerendonk et al., 2010; Vissers et al., 2006; Ye & Zhou, 2009). In line with our predictions and in consonance with previous evidence, this system seems to be reinforced after the detection of conflicting information such as the gender agreement violation included in the current design. Interestingly, a close relationship between this system and attentional mechanisms has been previously demonstrated, suggesting that such attentional mechanisms are biased by this conflict-monitoring system through bottom-up control processes (van de Meerendonk et al., 2011; van de Meerendonk et al., 2009; van de Meerendonk et al., 2010). Supporting this theory, the current differential congruency effect (i.e., difference between *Gender Mismatch* and *Gender Match* conditions) encompassed regions previously related with attentional mechanisms (Corbetta & Shulman, 2011 for a review of this topic). For instance, incongruent items produced increments in regions such as the medial superior frontal gyrus, the insula, the middle and posterior cingulate cortex, as well as the inferior and superior parietal gyrus. This hypothesis finds support in the behavioural results: greater neural responses of these regions were found associated with the *Gender Mismatch* condition which is harder to process (i.e., stimuli that produced more errors and longer reaction times) (for similar behavioral results see Akhutina et al., 1999 [adjective-nouns in Russian]; Caffarra et al., 2014 [determiner-nouns in Spanish]; Gollan & Frost, 2001 [noun-adjectives in Hebrew]; Holmes & Segui, 2004 [determiner-nouns in French]).

Does the brain process transparent and opaque nouns in the same way or differently [Main effect of Gender-marking]? Regarding the neural network sensitive to gender-to-ending regularities, the current fMRI results demonstrated a dissociation between transparent and opaque nouns. Interestingly and in accordance with previous evidence, the statistical parametric map obtained from the main effect of Gender-marking revealed a bilateral pattern of activation including temporal, parietal and frontal regions (Heim, 2008; Hernandez et al., 2004; Miceli et al., 2002; Padovani et al., 2005). From a theoretical perspective, transparent and opaque nouns differ in terms of gender values predictability (i.e., whether the noun is feminine or masculine): while the gender information of transparent nouns could be accessed based on both morphological and lexical cues, the gender information of opaque nouns relies exclusively on lexical information. The differences in the neural responses characterizing transparent and opaque nouns provide conclusive evidence suggesting that the system could be fine-tuned depending on the available gender-related information sources.

On the one hand, *Opaque Nouns* compared to *Transparent Nouns* produced increased responses in a widespread bilaterally distributed fronto-parieto-temporal network. Interestingly, this network included regions such as the pars opercularis and triangularis within the IFG, the insula, the medial part of the superior frontal gyrus, the posterior part of the middle temporal gyrus, the angular gyrus, the hippocampus (including the parahippocampal region), the fusiform gyrus and the thalamus. On the other hand, we found higher neural responses for *Transparent Nouns* than for *Opaque Nouns* in left occipitoparietal regions. These areas included the supramarginal gyrus, the superior and middle occipital cortices, the cuneus and the calcarine sulcus. The difference concerning the hemispheric lateralization characterizing transparent and opaque nouns is very salient: while the left hemisphere is more sensitive to transparent nouns (i.e., in comparison with opaque nouns), opaque nouns (i.e., relative to the transparent ones) recruit regions in both hemispheres (for some empirical evidence showing typical syntactic gender processing in patients with damage in the left hemisphere see Badecker et al., 1995; Cacciari & Cubelli, 2003; but see also Friedmann & Biran, 2003 for contradictory results; Laiacona et al., 2001; Luzzatti & De Bleser, 1999).

As far as the processing of opaque nouns is concerned, our data parallel the neural responses that have been previously observed in other fMRI studies that pointed out the critical role of the left IFG in controlling syntactic gender processing. However, our data extend this finding by suggesting that there is a coupling between the **inferior frontal gyrus** and other **parietal and temporal regions** during the access/retrieval of gender information. This empirical finding supports what is predicted by the neuro-cognitive model proposed by Heim (2008). Accordingly, some authors highlighted the posterior portion of the middle temporal gyrus as a hub for lemma selection and retrieval processes (Bemis & Pylkkänen, 2011, 2012a; Brennan & Pylkkanen, 2012; Gold et al., 2006; Indefrey & Levelt, 2004; Levelt, 2001; Levelt et al., 1999; Pylkkänen et al., 2014; Pylkkänen et al., 2002; Rissman et al., 2003). For instance, Choi et al. (2015) demonstrated that the transcranial magnetic stimulation of the posterior part of the left middle temporal gyrus selectively produced a reduction in the response times in a lexical decision task (see also Braun et al., 2015; Hernandez et al., 2015).

Concerning the processing of transparent nouns, increases in the activation of **left occipito-temporal regions** have been previously reported for Spanish determiner-noun pairs (Molinaro et al., 2013). This study measured the magnetoencephalographic activity of transparent nouns which appeared in association with their corresponding gender-marked determiners (see Dikker et al., 2010 for a different form-based effect in these posterior regions). Based on a large body of empirical evidence, the involvement of these areas was considered as reflecting morphological decomposition processing (Božić & Marslen-Wilson, 2013; Božić et al., 2013; Gold & Rastle, 2007; Lewis et al., 2011; Solomyak & Marantz, 2010). Interestingly, in the current experiment, the recruitment of these regions by transparent nouns is coupled with an increase in the neural response of the supramarginal gyrus. Activity in this parietal region has been strongly linked to phonological decomposition and grapheme-to-phoneme processes (Booth et al., 2004; Buchsbaum & D'Esposito, 2008; Church et al., 2008; Obleser & Kotz, 2009; Petersen & Posner, 2012; Prabhakaran et al., 2006; Raizada & Poldrack, 2007; Seghier et al., 2004; Sharp et al., 2010; Sliwinska et al., 2012; Zevin & McCandliss, 2005). The selective engagement of these occipito-temporal and parietal regions by transparent nouns (i.e., relative to opaque ones) might reflect a processing cost associated with decoding the morpho-phonological information. It is plausible to hypothesize that this process could mediate the access-retrieval of the gender morpho-syntactic feature values required to compute agreement dependencies (Braun et al., 2015).

Crucially, this is the first time that such increased neural activity is reported for transparent as compared to opaque nouns. Probably it is the combination of gender-marking and agreement congruency that boosts the morphological-phonological decoding of transparent nouns. The gender morpho-syntactic information of the determiners might enhance expectations concerning not only the gender morpho-syntactic values of the nouns, but also the presence of a given morpho-phonological gender mark (i.e., canonical Spanish suffixes) (DeLong et al., 2005 for a discussion about this topic). This goes in line with Cafarra et al. (Caffarra & Barber, 2015; Caffarra et al., 2014; Caffarra et al., 2015) who reported greater negative ERP responses for transparent as compared to opaque nouns. This negativity emerged in the left hemisphere as early as 300 ms, similarly to the early supramarginal phonological involvement (at around 200 ms) found by Sliwinska et al. (2012) in a TMS study (see also Božić et al., 2007; Marslen-Wilson & Tyler, 2007; Rolheiser et al., 2011 for relevant functional and anatomical connectivity results). In summary, both the hemispheric differential contributions and the distinctions regarding the areas involved in the processing of transparent and opaque nouns point in the same direccion: the access-retrieval of gender morpho-syntactic values required to compute the agreement relation relies on different sources of information, depending on the transparency of the nouns.

Is our brain sensitive to gender-marking cues during the computation of determiner-noun agreement relations [Interaction effect]? With regard to this issue, the interaction between Gender Congruency and Gender-marking revealed a functional coupling between **the pars triangularis within the left IFG, the hippocampus and the posterior part of the left MTG/STG**. The neural activity of these areas follows the same pattern across conditions: the differences between congruent and incongruent items for transparent and opaque nouns were significant in these three regions. In the former case – transparent nouns –, incongruent determiner-noun pairs exhibited greater response than congruent pairs, whereas in the latter case – opaque nouns –, it was the congruent condition which produced the more conspicuous signal. In contrast with the huge amount of previous studies that have demonstrated the engagement of this left fronto-temporal activity during sentence comprehension, there is only few empirical evidence reporting this coupling during grammatical gender processing (see Heim, 2008 for a review of this topic; see also Miceli et al., 2002; Padovani et al., 2005).

The interaction effect emerging in these areas could be reflecting a lexical processing cost that differently affects the decoding of gender features and the building of local syntactic units (i.e., noun phrases) in transparent and opaque nouns. Interestingly, the difference between conditions emerging in this region could be explained based on the MUC model of sentence processing (Hagoort, 2003a, 2005, 2013). This neuro-cognitive perspective highlighted the posterior part of the left MTG as a hub underlying the access/retrieval of the information stored in the mental lexicon. According to this author, each word in the mental lexicon is associated not only with its lexical representation but also with its syntactic structural frame(s). In accordance with Levelt et al. (1999), it is plausible to hypothesize that in the mental lexicon this information is organized following some hierarchical principles: the deeper the lexical representation of a given noun, the greater the processing cost over this temporal region. The divergence in the congruency differential response found for transparent and opaque nouns could be explained by the hierarchical organization of the lexicon. Activity in these particular regions seem to be sensitive to both the building of the local syntactic unit (i.e., as the difference between congruent and incongruent items suggest) and the "lexical load" distinguishing transparent and opaque nouns. It is important to stress that the middle temporal regions have been functionally related with the hippocampus, a region exhibiting an interaction between Gender-marking and Gender Congruency. The similarities in the response patterns showed by the hippocampus and the posterior MTG/STG constitute a critical piece of evidence supporting the contribution of these regions during the access/retrieval of gender-related information (see Duncan et al., 2012 for a discussion about the hippocampus functioning, see also Box 3.2 for some important findings regarding this issue).

In addition to this fronto-temporal coupling, the interaction effect also showed that the engagement of **the supramarginal and the angular gyri** depends on both Gender-marking and Gender Congruency factors. While in the case of transparent nouns the neural responses for incongruent and congruent determiner-noun pairs did not differ in amplitude, in the case of opaque nouns, the incongruent items produced greater responses than the congruent ones. As mentioned above, the functional characterization of parietal regions during sentence processing has received much less attention than the investigations concerning the role played by inferior frontal and temporal areas. This situation becomes critical when we review the literature on agreement computation. Regarding this issue, some neuro-anatomical models of sentence processing include parietal areas as crucial nodes within this network. However, similarly to the contradictions regarding the functional role associated with frontal and temporal areas, different functions have been related with parietal regions. For instance, Hagoort and colleagues (Hagoort, 2013; Hagoort & Indefrey, 2014) defined parietal regions as critical nodes engaged for the access/retrieval of different types of linguistic information (e.g., morphological, phonological, lexico-semantic and/or syntactic information). In contrast, Bornkessel-Schlesewsky and Schlesewsky (2013) highlighted the critical role played by parietal areas during syntactic combinatorial operations. These authors also pointed that during this process, a close relationship between parietal and posterior temporal regions is boosted. Crucially, according to the current data, both theoretical accounts seem to be plausible. Activity in parietal regions seems to depend on both Gender Congruency and Gender-marking, suggesting that these areas are sensitive to syntactic combinatorial and lexical processes. During the establishment of local grammatical relations, opaque nouns appear to impose a processing cost over the integration of the morpho-syntactic information. This could be affected by a differential "lexical load" distinguishing between transparent and opaque nouns. It is important to stress that this is the first time the engagement of parietal regions has been reported during agreement computation as a function of different lexical and morpho-syntactic factors.

Interim conclusions. To sum up, the current fMRI study demonstrated the preferential role of different left-lateralized perisylvian regions in the establishment of syntactic gender agreement. Crucially, these data illustrated how our brain is sensitive to gender-marking cues during the computation of determiner-noun agreement relations: different gender-related signals associated with nouns may affect the neural circuits involved during the computation of local agreement dependencies. According to the present findings, when gender orthographical/morpho-phonological cues are available (i.e., as in the case of transparent nouns), both form-based and lexical information are used to establish grammatical relations. The circuits underlying these mechanisms involve regions associated with morpho-phonological decomposition (i.e., occipito-temporal and parietal regions exhibiting a main effect of Gender-marking) but also regions associated with lexical processing (i.e., activity in temporo-frontal and parietal regions depending on both Gender-marking and Gender Congruency). In contrast, when no form-based cues are available (i.e., as in the case of opaque nouns), gender information is retrieved from the lexicon. These processes seem to be mediated by a functional coupling between the posterior part of the MTG/STG, the pars triangularis within the IFG and the hippocampus. In addition, parietal areas seem to be critical for the processing of opaque nouns. Activity in these cortical regions could be mediating the fronto-temporal loop (i.e., posterior MTG/STG – pars triangularis within the IFG) enhanced by the integration of different information sources. It is important to highlight that this is the first time that such clear synchrony between posterior MTG/STG, pars triangularis within the IFG and parietal regions has been observed during agreement computation. Critically, these results underpin the previous neuro-anatomical models proposed in the context of both syntactic gender processing (see Heim, 2008) and sentence comprehension (Bornkessel-Schlesewsky & Schlesewsky, 2013; Friederici, 2011, 2012; Hagoort, 2003a, 2005, 2013). But, more importantly, they provide valuable information regarding the role this left-lateralized perisylvian circuit plays during agreement computation. Further studies are required to determine how differences associated with the experimental design, the task and the stimulation material could produce a fine-tuning of this circuit.

Box 3.1. Basal ganglia response associated with the processing of incongruent items.

It is important to point out the involvement of the dorsal striatum (i.e., the basal ganglia included the striatum (caudate nucleus and putamen), the globus pallidus, the substantia nigra, the nucleus accumbens, and the sub-thalamic nucleus), specifically the putamen and the caudate nuclei, during the current grammaticality judgment task. In line with previous evidence, these sub-cortical regions exhibited higher neural responses for incongruent than for congruent items (Fiebach et al., 2002; Kuperberg et al., 2000; Kuperberg et al., 2003; Kuperberg, Sitnikova, et al., 2008; Ni et al., 2000; Price, C. J. et al., 1997). In particular, previous studies have reported the implications of these sub-cortical regions during language acquisition, as well as their involvement in developmental language disorders (Copland, 2003; Mestres-Missé et al., 2014; Mestres-Missé et al., 2008; Mestres-Missé et al., 2012; Mueller et al., 2014; Nadeau & Crosson, 1997; van der Lely & Pinker, 2014).

Supporting these studies, it has been also demonstrated that the arcuate fasciculus, which anatomically links the superior posterior temporal cortex and the inferior frontal gyrus, has branch connecting with the basal ganglia (Leh, Chakravarty, et al., 2007; Leh, Ptito, et al., 2007; Teichmann et al., 2015). However, there is a debate about whether these sub-cortical regions directly support language-specific processes or whether they are implicated in domain-general functions such as executive functions, working memory or attentional control processes, directly linked to language comprehension and production (Kotz & Schmidt-Kassow, 2015; Kotz & Schwartze, 2010; Kotz et al., 2009).

Based on empirical evidence from clinical populations, Kotz and Schmidt-Kassow (2015) suggested that syntactic processing impairments resulting from basal ganglia damages might be a consequence of a more generalized temporal processing deficit. According to these authors, the involvement of the dorsal striatum might be related with domain-general mechanisms triggered by the detection of unexpected information. Nonetheless, the possible connections between this sub-cortical region and the conflict-monitoring system need to be further investigated.

Box 3.2. Is the hippocampus involved during the processing of syntactic errors?

Some authors have proposed that the hippocampus computes the correspondence between the expected and the encountered signals (Duncan et al., 2012; Hasselmo et al., 1995; Kumaran, 2008; Kumaran & Maguire, 2005, 2006, 2007; Lisman & Grace, 2005). In line with this claim, Duncan et al. (2012) labeled one specific sub-region within the hippocampus (i.e., CA1) as a mismatch/match detector.

However, the role this region plays in language comprehension has received much less attention than its general involvement in memory functions. Specifically, an extensive body of research has pinpointed a causal relation between hippocampal damage and vocabulary acquisition and declarative memory deficits (Bayley & Squire, 2002; Maguire et al., 2001; O'Kane et al., 2005; O'Kane et al., 2004; Schmolck et al., 2002). Indeed, patients with hippocampal impairment showed problems for the on-line comprehension of sentences (see Duff & Brown-Schmidt, 2012 for a revision of this topic; see alsoDuff & Kurczek, 2013; Kurczek, 2014; Kurczek et al., 2013). Specifically, Kurczek et al. (2013) demonstrated that hippocampus damage disrupts the pronoun referential processing (e.g., *“Melissa is playing violin for Debbie/Danny… She*$_{\text{[target]}}$ *is …”*) during sentence comprehension, suggesting its critical role in maintaining and integrating language information.

Interestingly, Ullman and colleagues (Ullman, 1999, 2004; Ullman et al., 1997) proposed that a declarative memory system sub-served by medial temporal regions (including the hippocampus) underlies lexical processing (i.e., learning, storage and retrieval) (see also Lum et al., 2012; Lum et al., 2015). Empirical evidence from clinical populations has showed that impairments in this declarative system worsen performance converting irregular verbs (i.e., relative to regular verbs) to their past tense forms (Ullman, 1999, 2004; Ullman et al., 1997).

Chapter 4.

Experiment II

Parietal circuit distinguishing between living and non-living entities: an fMRI study of gender agreement processing.

4.1 Overview

In the previous experimental chapter, we showed that agreement processing is modulated by the form-based and the lexical information embedded in our linguistic code. This effect was tested manipulating the congruency pattern between transparent or opaque nouns and their corresponding Spanish canonical determiners. Interestingly, the Spanish gender agreement system, also offers the opportunity to evaluate whether semantic factors modulate agreement operations. As mentioned in the Introduction, in addition to the formal gender system (i.e., where the assignment of the gender values follows formal rules [i.e., orthographical, morphological and phonological]) explored in the previous experiment, in Spanish it is possible to distinguish a conceptual system (Corbett, 1991). The nouns corresponding with this category are mostly animate entities and the assignment of the gender values – masculine or feminine – depends on the biological sex of the referent. However, interestingly, both the formal and the conceptual gender system share the same termination rule: nouns ending in "–o" are usually masculine, while nouns ending in "–a" are usually feminine. Despite the significant increase in the knowledge of agreement processing, it is still not clear whether and how conceptual information mediates the establishment of grammatical relations. The vast majority of studies have explored the formal and conceptual factors separately, assuming there is no interaction between them.

The current study is aimed at shedding light into this issue, by comparing the neural network underlying the Spanish formal and conceptual gender agreement system.

Only few behavioral/ERP studies have investigated whether semantic factors could modulate syntactic processes during language comprehension (Barber et al., 2004; Deutsch & Bentin, 2001; Gunter et al., 2000; Schiller et al., 2003a; Xu et al., 2013). Interestingly, although similar manipulations have been used across these studies, the results are different and even contradictory. For instance, on the one side, Schiller et al. (2003b) compared ERP responses elicited by German mono-morphemic written nouns conceptually marked for gender to nouns that were not. In this study, participants were required to classify each word according to their grammatical gender, linking each noun with its corresponding masculine or feminine determiner. Both, behavioral (decision times) and ERP (mean peak latency of the N2 component) results showed that the processing of conceptually gender marked nouns was faster than syntactic gender nouns, suggesting that semantic factors can influence grammatical gender processing (see also Vigliocco & Franck, 1999 for contrasting conceptual and formal gender in production). In consonance with this study, Deutsch and Bentin (2001) combined ERP and eye tracking results in a more complex sentence context and tested the interaction between syntactic and semantic factors during agreement processing. Each sentence began with a main clause of three to four words followed by a sentential object complement (e.g., "The woman saw that *the boy*$_{\text{[subject]}}$ *had fallen*$_{\text{[target word]}}$ into the pool"). The gender agreement congruency was manipulated within the object-complement clause between the subject and the predicate. In addition, the animacy (animate or inanimate) of the subject (e.g., *the boy*/*the diamond*) was also a critical factor. These authors found a significant interaction effect between animacy and agreement congruency in a time window between 250 and 550 ms which comprised the N400 component (Experiment 2). The amplitude modulation of the N400 component by the incongruent conditions was only significant for animate subject-nouns. This interaction was replicated focusing on the first-pass duration resulting from the eye-tracking experiment (Experiment 1). Based on these results, these authors argued that syntactic and semantic factors might be processed simultaneously, but also they might interact with each other depending upon the context (Deutsch & Bentin, 2001).

However, on the other side, Barber et al. (2004) compared Spanish conceptually marked gender nouns with nouns that were arbitrarily marked for gender. In order to measure possible interactions between formal and conceptual factors, they also manipulated the gender grammatical congruency between the subject nouns and the predicative adjectives in a grammaticality judgment task, leading to two different types of constructions: well-formed and ill-formed sentences. Comparing ERP waveforms associated with congruent and incongruent sentences, both conceptual and formal gender produced a biphasic LAN-P600 effect typically reported for agreement processing. Interestingly, these authors reported a significant main effect of gender type: conceptual gender nouns elicited higher anterior response than formal gender nouns in a time window from 450 to 700 ms, suggesting that conceptual information would trigger different underlying mechanisms. However, the interaction between agreement congruency and gender type was not significant (for contrasting ERP results see Silva-Pereyra et al., 2012).

Different factors can be identified that potentially contribute to the different findings reported by the studies described above, such as the type of task (i.e., a grammaticality judgment task in Barber et al. (2004) vs. a gender decision task in Schiller et al. (2003b)), and possible differences in the way results are reported. For instance, since Barber et al. (2004) exclusively reported results concerning the amplitude differences, it is difficult to determine the possible source of the null interaction effect. Significant interactions effects could appear in terms of peak latencies, topographical distributions or even in terms of behavioral performance as the ones reported in the previous study of Schiller et al. (2003b).

As we detailed in the Overview section of the previous chapter (Chapter 3, *Is our brain sensitive to gender-marking cues during the computation of local agreement relations?*), the investigation on gender processing has not restricted to behavioral and ERP studies. This research topic has been also addressed using fMRI methods (Folia et al., 2009; Hammer et al., 2007; Heim, 2008; Heim et al., 2005; Heim et al., 2006; Heim et al., 2010;

Hernandez et al., 2004; Indefrey & Levelt, 2004; Miceli et al., 2002; Padovani et al., 2005). Indeed, the empirical findings derived from these investigations have been outlined in a neuro-anatomical model of gender processing (Heim, 2008, see Chapter 3 for a detailed description of this model). However, crucially, this proposal lacks information regarding different types of gender: formal and conceptual systems might engage different neural regions. Concerning how the brain integrates conceptual and/or formal information during agreement comprehension, the empirical evidence is significantly scarce and currently inconclusive (see Hammer et al., 2007; Hammer et al., 2011 for two fMRI studies about anaphoric references). The vast majority of these studies have examined this issue comparing well-formed sentences with sentences including semantic and/or syntactic incongruities (Folia et al., 2009; Huang et al., 2012; Kuperberg et al., 2000; Kuperberg et al., 2003; Kuperberg, Sitnikova, et al., 2008; Newman et al., 2003; Ni et al., 2000; Nieuwland et al., 2012). In general terms, syntactic anomalous constructions typically recruited the middle frontal gyrus, as well as some parietal areas such as the inferior parietal gyrus, the precuneus and the posterior/anterior cingulate cortices (Folia et al., 2009; Kuperberg et al., 2003; Kuperberg, Sitnikova, et al., 2008). In contrast, a coupling between the inferior frontal gyrus and different middle and superior temporal[21] regions in the left hemisphere has been consistently observed for semantic violation relative to well-formed sentences (Friederici, 2011, 2012; Hagoort, 2013, 2014; Hofmann et al., 2007; Hofmann et al., 2003; Kuperberg, Sitnikova, et al., 2008; Pallier et al., 2011). Interestingly, similar results have been reported by Molinaro et al. (2015). These authors evaluated the dynamics of the semantic combinatorial network as a function of the typicality of the relation between a concept and an attribute (e.g., *wet rain* [prototypical semantic combination]; *dry rain* [atypical but composable semantic combination]). Importantly, these authors demonstrated that atypical relative to prototypical combinations enhanced a functional coupling between the anterior temporal cortex and the angular gyrus (see Jefferies, 2013; Lau et al., 2008; Pascual et al.,

---

[21] Previous studies have investigated the role played by the IFG and the superior temporal gyrus in the left hemisphere during gender processing using aphasic patients with brain lesions (Hofmann et al., 2007; Hofmann et al., 2003). These authors claims that while the engagement of the LIFG is critical for phonological tasks, the left superior temporal gyrus seems to be an essential hub for the integration of different information sources (i.e., the integration of phonological and lexical cues) (but see Hagoort, 2003b; Hagoort, 2013, 2014; Hagoort & Indefrey, 2014 for a different perspective).

2015 for convergent results). Consistently with these findings, Price, A. R. et al. (2015) demonstrated the engagement of the angular gyrus during adjective-noun conceptual combinatorial processing in both typical and pathological populations. Crucially, these authors also showed that atrophy of the angular gyrus results in impaired conceptual combination. Taken together, these findings revealed how the brain processes semantic relations during language comprehension. However, how the brain leads with conceptual factors during the building of a syntactic structure has not yet been examined in depth.

The present study was designed to investigate a) whether agreement processing uses the conceptual information concerning the noun gender properties during the establishment of gender agreement relations and if so, b) where is this possible interaction between conceptual and formal information mapped in the brain. In the current study Gender Congruency [*Gender Match* and *Gender Mismatch*] was manipulated between subject nouns and predicative adjectives including both Gender Systems [*Conceptual* and *Formal*]. To avoid possible lexical and/or morphological confounds that could be influencing the appearance of an interaction effect, we controlled the gender predictability of conceptual and formal nouns by selecting nouns whose gender was morphologically marked by either "–a" or "–o" [feminine or masculine]. In addition, the nouns were selected and matched on lexical frequency, number of lexical neighbors and length (Duchon et al., 2013). Finally, the intrinsic variability of these lexical variables was also controlled incorporating the three scores of each item as regressors in the statistical approaches implemented.

From a neuro-anatomical perspective, we expect a neural distinction between grammatical and ungrammatical constructions: while congruent sentences should activate a left lateralized fronto-temporal circuit, ungrammatical constructions should activate a bilateral fronto-parietal network. If conceptual and formal gender agreement systems rely on similar mechanisms, we would expect no interaction between Gender Congruency and Gender Systems. In that case, the processing of correct sentences should give rise to an overlapping fronto-temporal network regardless of the gender type of the noun. Similarly, the detection of a grammatical violation should trigger the activation of similar fronto-parietal activation pattern, with no modulation based on the type of gender agreement. In contrast if during agreement computation word meaning interacts with syntactic information, we would expect a distinctive activation pattern associated to each gender system. According with previous fMRI findings (see Molinaro et al., 2013 for convergent MEG findings; see also Molinaro et al., 2015; Price, A. R. et al., 2015), this neural distinction could involve left parietal regions including the angular gyrus. Supporting this hypothesis, Binder et al. (2009) highlights the crucial role of this highly heteromodal associative parietal region as part as a domain-general semantic network. The link between parietal regions and the left-lateralized language-specific fronto-temporal network (e.g.; the inferior, middle and superior temporal regions and also the pars triangularis and orbitalis within the left inferior frontal gyrus) has been supported by previous anatomical connectivity findings (Catani et al., 2012; Catani & Mesulam, 2008; Catani & Thiebaut de Schotten, 2008; Thiebaut de Schotten et al., 2012). However, no existing evidence explains how these two functional segregated networks interact during agreement processing.

4.2 Materials and Methods

Participants. Fifty three healthy paid volunteers gave written informed consent to participate in this study. After the quality checking of the data, a total of forty nine participants (thirty females), with ages ranging from 22 to 42 years (mean = 28.6, standard deviation = 4.8), were used to estimate the group effects.

Stimuli and experimental procedure. Each subject participated in a single functional run consisting of an event-related 2 x 2 factorial within-subject design. Each trial consisted in a word-by-word visual presentation of four words' sentences that could be grammatically acceptable or not. Words were displayed during 300 ms in white capital letters on a black background. In order to optimize the sampling of the BOLD response, an inter-stimulus interval was included between successive sentences. During this period a fixation point ("+") was presented with different durations across trials, varying between 2 and 8 seconds. This baseline period also allows us to counteract possible expectation effects, which might influence the brain response and also to estimate the time course of the BOLD response associated to the critical word. After each sentence a visual cue indicated participants to distinguish whether the sentence was grammatically acceptable or not pressing one of two different buttons.

The stimuli consisted of 160 sentences, which included 120 critical items and 40 fillers. Each sentence contained a subject noun followed by a verb, which was always followed by a predicative adjective. The gender of the adjective (the critical word) was manipulated to produce agreement or disagreement with the subject noun. While half of the sentences included a gender agreement violation between the subject noun and the predicative adjective, the other half consisted of well-formed sentences. In addition, we also manipulated the gender type of the subject by including nouns with conceptual (e.g., *abuela* [grandmother]) and grammatical (e.g., *teoría* [theory]) gender, in the proportion 1:1. The resulting 2 x 2 factorial design comprised the Gender Type of the subject noun [*Conceptual Gender* and *Formal Gender*] and the Gender Congruency between subjects and predicative adjectives [*Gender Match* and *Gender Mismatch*] as factors (see examples (11) and (12) below).

(11) Conceptual Gender

(a) Gender Match: e.g., *La abuela era* ***sabia*** ([The grandmother]$_{\text{masc.sing.}}$ was wise $_{\text{masc.sing.}}$)

(b) Gender Mismatch: e.g., **La abuela era* ***sabio*** ([The grandmother]$_{\text{masc.sing.}}$ was wise $_{\text{fem.sing.}}$)

(12) Formal Gender

(a) Gender Match: e.g., *La teoría era* ***exacta*** ([The theory]$_{\text{fem.sing.}}$ was accurate $_{\text{fem.sing.}}$)

(b) Gender Mismatch: e.g., * *La teoría era* ***exacto*** ([The theory]$_{\text{fem.sing.}}$ was accurate $_{\text{masc.sing.}}$)

All subject nouns and predicative adjectives included in the critical sentences are morphologically marked for gender using the Spanish canonical suffixes "–o" for masculine and "–a" for feminine. In order to avoid strategies related to the morphological decomposition of nouns and adjectives (i.e., participants would attend only to the suffixes in order to determine whether there is a gender grammatical violation or not), in filler sentences we kept the noun type constant but we included opaque predicative adjectives, i.e. adjectives that end with non-canonical suffixes (e.g., "–e", "–n", "–l"). In addition to gender agreement, in Spanish it is mandatory that subject nouns and adjectives also agree in number. In order to avoid possible interactions between gender and number agreement features, the number agreement was also controlled: a) all the subjects nouns and adjectives agreed in number; b) all subject nouns and adjectives were morphologically marked for number with the canonical Spanish plural suffix ("–s") and c) half of the nouns were presented in their singular form, and the other half in their plural form. All nouns and adjectives were of medium lexical frequency [nouns: mean = 38.37 per million, SD = 54.25; adjectives: mean = 22.67 per million, SD = 61.65] and 4 to 9 letters long [nouns: mean = 5.69, SD = 0.91; adjectives: mean = 6.41, SD = 1.65] (see also Table 4.1) according to the Spanish ESPaL database (http://www.bcbl.eu/databases/espal/) (Duchon et al., 2013) (see Appendix 3 for a list of the stimuli used).

Table 4.1. Mean of the frequency, length and neighbors of the critical word (predicative adjectives) per condition. Mean values for conceptual and formal gender in the two congruency patterns (match and mismatch) were included, with its corresponding standard deviation between parentheses.

	Formal Gender		**Conceptual Gender**	
	Mismatch	**Match**	**Mismatch**	**Match**
Log (frequency)	2.2828 (1.33)	2.5208 (1.54)	1.6333 (1.84)	1.9732 (1.72)
Length	5.5667 (0.63)	5.4333 (0.86)	7.9231 (2.13)	7.5385 (1.70)
Lev Neighbors	1.5433 (0.25)	1.5 (0.36)	1.9981 (0.62)	1.8538 (0.52)

MRI acquisition. The current experiment was performed on the same scanner than Experiment I. Functional event-related scan consisted of 544 echoplanar images were acquired following the T2*-weighted gradient-echo pulse sequence described in Appendix 2B. In addition, a MPRAGE T1-weighted structural image was acquired using the same sequence.

FMRI data analysis. Functional data were analyzed using the same pipeline applied in Experiment I. However, here we inserted an additional step after the normalization procedure. At this point, global effects were removed using a voxel-level linear model of the global signal proposed by Macey et al. (2004). Detrending fMRI time series were then smoothed and high-pass filtered.

Statistical parametric maps were generated by modeling univariate general linear model, using for each stimulus type a regressor obtained by convolving the canonical hemodynamic response function with delta functions at stimulus onsets, and also including the six motion-correction parameters as regressors. The stimuli onsets include five different components. The first one corresponded to the onset of each sentence trial and was modelled as a single regressor, independently of the experimental conditions. The next four corresponded to each experimental condition (*Incongruent Formal Gender* [IGG], *Congruent Formal Gender* [CGG], *Incongruent Conceptual Gender* [ICG] and *Congruent Conceptual Gender* [CCG]) and lasted from the onset of the critical adjective. In addition, we also included in the design matrix three different features of the stimuli used: the frequency, the length and the Levenshtein's distance of each critical word. Similarly to the previous experiment, parameters of the GLM were estimated with a robust regression using weighted-least-squares (Diedrichsen & Shadmehr, 2005). Those trials associated to incorrect behavioral responses were removed from its corresponding condition.

Contrast images for each of the four conditions compared to the fixation baseline were submitted into a second level 2x2 ANOVA using the Gender Type (*Conceptual* and *Formal*) and the Gender Congruency (*Match* and *Mismatch*) as factors. This analysis would allow us to determine possible main effects and interactions. Population-level inferences were tested using a threshold of $p < 0.001$ uncorrected with a voxel extent higher than 100 such that only those peaks or clusters with a p-value corrected for multiple comparisons with family wise error (FWE; Nichols & Hayasaka, 2003) and/or false discovery rate (FDR; Genovese et al., 2002) were consider as significant. All local maxima were reported in the results tables as MNI coordinates (Evans et al., 1993).

A very similar whole brain approach was used in the previous chapter in order to neuro-anatomically characterize the neural regions involved in the establishment of nominal agreement relations. However, this procedure does not give any information concerning the temporal dynamic of the areas within this agreement network. For this reason, in addition to the classical whole brain analysis, in the current experiment we also estimated the time course of the hemodynamic response function (HRF) in a group of Regions of Interest (ROI). Using these ROIs the spatially unsmoothed time series were extracted using the same design matrices described above for the whole brain analysis. To estimate the HRF for each critical event a Finite Impulse Response [FIR] (Burock & Dale, 2000; Dale, 1999) model was used (http://marsbar.sourceforge.net/download.html). The FIR was characterized by its maximum peak of amplitude and the latency corresponding to the location of this maximum. This approach allows us to distinguish whether the temporal characterization of the brain response for each ROI complement in some way the information extracted from the direct comparison between conditions. These analyses also increment the statistical power of each comparison reducing the dimensionality of the problem. The ROIs used were built in MNI space combining a functional and an anatomical criteria such that all voxels: a) were included in the group-level effect of the contrast *Mismatch* vs. *Match* [main effect of Gender Congruency]; b) were connected to a local t maxima; and c) were included in one AAL structural ROI. Repeated measured analyses of variance were preformed independently over the log transformation of amplitude and latency parameters estimated for each type of stimuli following the same statistical design described above for the whole brain analysis.

4.3 Results

Behavioral results. Mean decision times and error rates for each condition are presented in Table 4.2, with the corresponding standard error between parentheses. Trials with incorrect responses and/or reaction times below or above 2.5 standard deviations from the mean were excluded from the latency analysis. Percentage of correct responses was above 96 % for all experimental conditions, indicating that participants judged the well-formed sentences as grammatically acceptable in contrast to the sentences with a gender agreement violation. 2x2 ANOVAs on mean decision times and error rates were performed using Gender Type (*Conceptual* and *Formal*) and Gender Congruency (*Match* and *Mismatch*) as factors. These analyses showed no significant effects among the experimental conditions, neither for accuracy nor for decision times ($p > 0.05$).

These null effects could be reflecting the wrap-up effect previously described for sentence processing: participants require longer decision times to respond when the critical event is located at the end of the sentences (Gibson et al., 2005; Hagoort, 2003b; Hyönä et al., 2002; Igoa et al., 1998; Just & Carpenter, 1980; Silva et al., 2014). Previous studies have showed different behavioral and ERP effects for the processing of sentences including violations in the last word in compared with sentences including violations in intermediate positions (Hagoort, 2003b; Hagoort & Brown, 1999; Weber & Lavric, 2008). This effect seems to reflect a sum of different neuro-cognitive mechanisms triggered by a retrospective processing of the whole sentence (Hagoort, 2003b; Silva et al., 2014).

Table 4.2. Error rates (in %) and mean decision times (in ms) for conceptual and grammatical gender in the two types of sentences (match and mismatch) with standard error between parentheses.

	Mean decision times		**Error rates**	
	Match	**Mismatch**	**Match**	**Mismatch**
Conceptual	648.79 (35.18)	613.56 (30.60)	2.04 (0.62)	3.22 (0.62)
Grammatical	639.33 (33.88)	638.10 (31.73)	2.69 (0.63)	2.26 (0.49)

FMRI data: Congruency effect (Gender Match vs. Gender Mismatch). To characterize the neural circuit underlying agreement computation processes that should be operating for both types of gender (*Formal Gender* and *Conceptual Gender*) we extracted the main effect of Gender Congruency (*Gender Match* vs. *Gender Mismatch*) from the 2x2 Factorial design. The significant effects included regions with higher responses for the *Gender Mismatch* condition than for the *Gender Match* condition and regions that exhibited the opposite pattern, i.e. higher activation for *Gender Match* than for *Gender Mismatch* condition. On the one hand, significant activation increases emerged from the *Gender Mismatch* > *Gender Match* contrast, including regions such as the right and left insula, the left pars orbitalis, opercularis and triangularis within the IFG, the left precentral, the left supplementary motor area, and the left inferior parietal. On the other hand, the contrast *Gender Match* > *Gender Mismatch* produced higher brain response in regions such as the angular gyrus, anterior cingulate cortex, precuneus, middle temporal gyrus (MTG) and orbitofrontal cortex bilaterally and the left occipital and left superior frontal cortex (see Table 4.3 for a detailed list of regions and Figure 4.1 and 4.2 for a representation of its response pattern [activation or de-activation with respect to the fixation baseline]). Note that the hemodynamic response functions of these regions exhibited different patterns. The left anterior cingulate cortex, the left middle temporal gyrus and the left pars opercularis –

within the IFG –, exhibited significant congruency effects between 2.5 and 5.0 seconds, whereas others regions such as the pars triangularis within the IFG, the middle frontal gyrus and the medial superior frontal gyrus exhibited sustained – i.e., between 2.5 and 12.5 seconds – significant differences between congruent and incongruent items (for more details see Figure 4.2).

FMRI data: Interaction between Agreement Congruency and Gender Type. In order to investigate whether the brain regions involved in gender agreement processing vary as a function of the gender type (*Conceptual* and *Formal Gender*) we explored the interaction effect resulting from the 2x2 factorial design. Interestingly, we observed significant interaction effects in two different clusters including the left inferior parietal gyrus and the left angular gyrus (Figure 4.3 and Table 4.4). Significant differential effects emerging from the contrast *Mismatch* vs. *Match* in both regions were found only for *Conceptual Gender*. No significant differential effect was found in these regions for *Formal Gender*. Note that the hemodynamic response functions of these two parietal clusters are very similar; both exhibited an increment in the response pattern between 2.5 and 7.5 seconds with a maximum peak around 5.0 seconds. The interaction effects reported for these regions were only evident when the amplitudes of the maximum peaks were analysed.

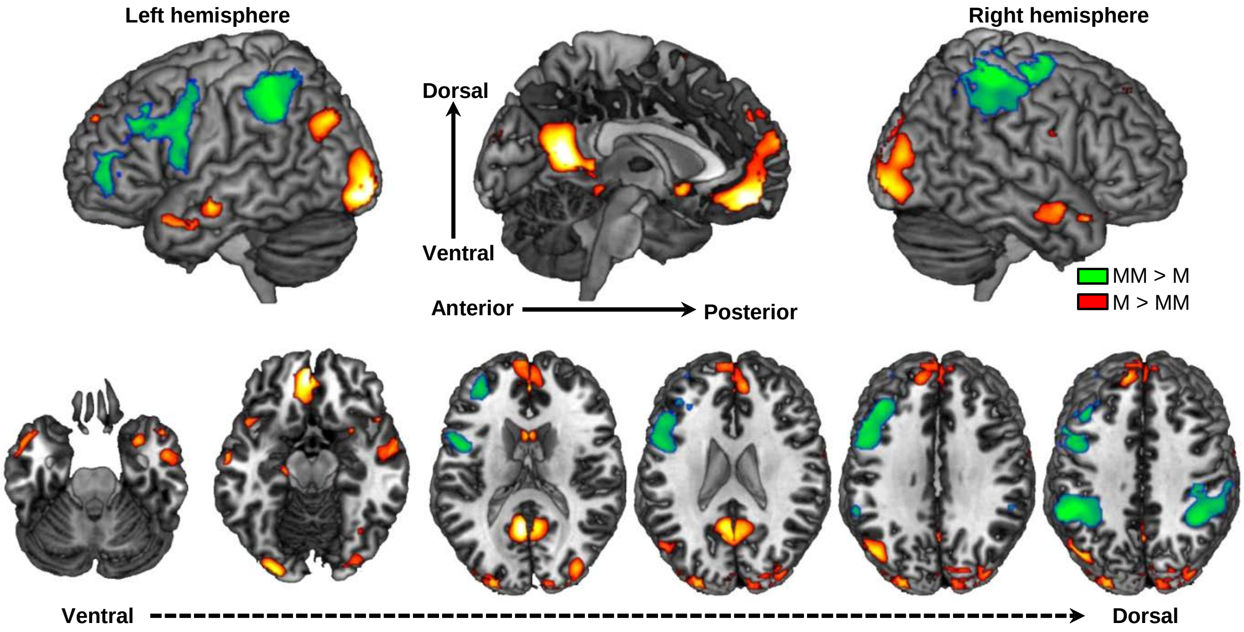


Figure 4.1. Statistical parametric map emerging from the main effect of Gender Congruency was projected on the MNI single-subject T1 image. The two tails of the F-contrast were represented with different colors: *Gender Mismatch* > *Gender Match* in green and *Gender Match* > *Gender Mismatch* in red-yellow. All clusters depicted were statistically significant with a p-value corrected for multiple comparisons. MM: Gender Mismatch; M: Gender Match.

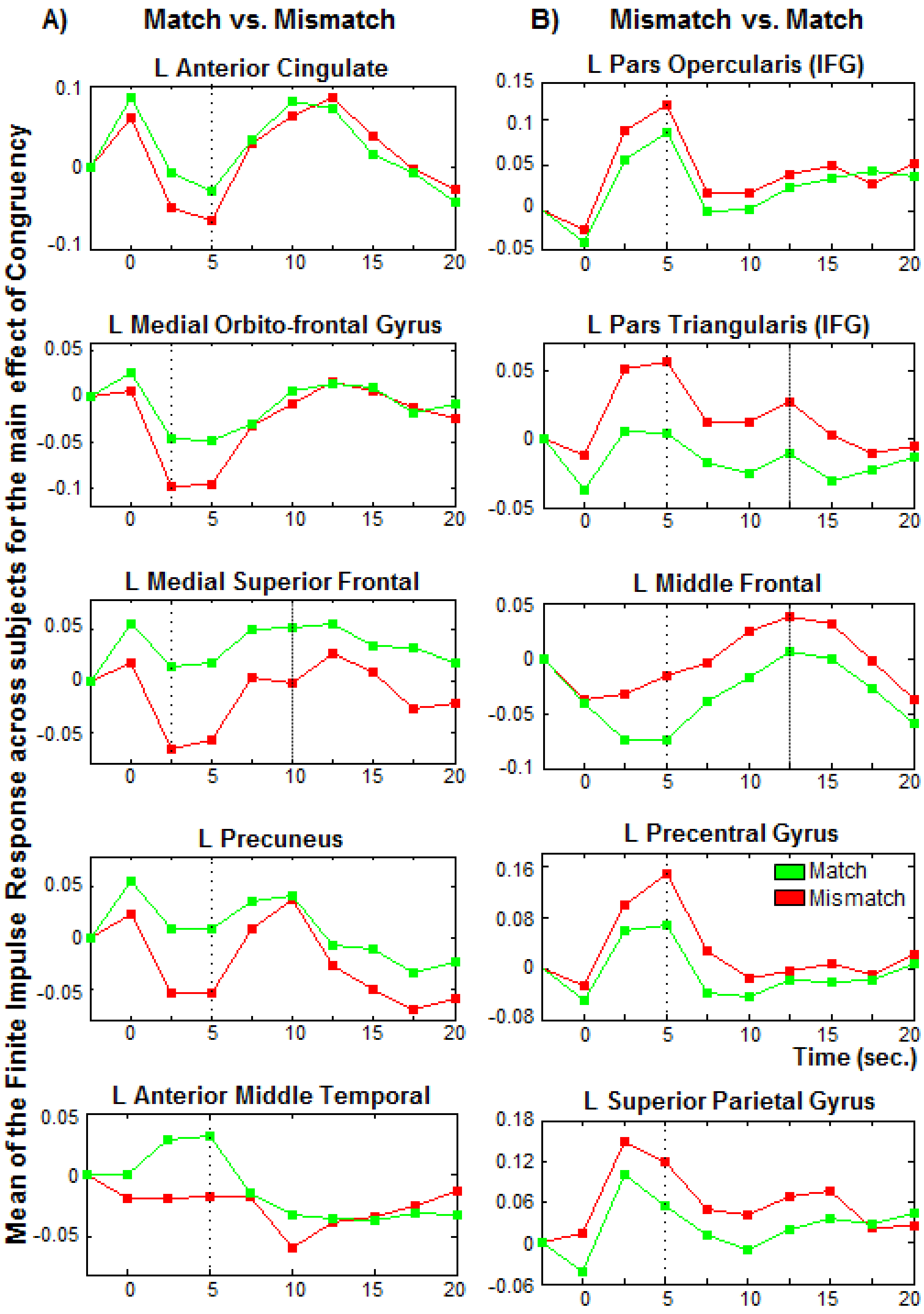


Figure 4.2. Time courses of the HRFs of those regions resulting from the main effect of Gender Congruency. Gender Mismatch and Gender Match are represented with different colors. The vertical dotted lines signal the maximum amplitude peaks and the latency corresponding to the location of this maximum.

Table 4.3. Significant activation clusters resulting from the main effect of Congruency (Match > Mismatch and Mismatch > Match) for conceptual and grammatical gender.

Contrast	Hemisp	Region	x,y,z {mm}	Peak level	Cluster level
				T	No. Vox
Mismatch > Match	**L**	Inferior Parietal Gyrus	-58 -46 38	4.35	**1562**
		Supramarginal Gyrus	-52 -46 38	3.88	
		Angular Gyrus	-33 -50 38	3.13	
		Middle Frontal Gyrus	-40 50 2	3.81	**2384**
		Pars Triangularis (IFG)	-52 20 30	3.75	
		Pars Orbitalis (IFG)	-38 46 0	3.72	
		Pars Opercularis (IFG)	-54 8 24	3.54	
	R	Inferior Parietal Gyrus	50 -34 58	**5.23**	**2717**
		Angular Gyrus	40 -48 40	3.79	
		Supramarginal Gyrus	54 -38 42	3.42	
		Precentral Gyrus	38 -12 58	4.24	
		Postcentral Gyrus	28 -36 68	4.06	
Match > Mismatch	**L**	Superior Frontal	-12 54 36	3.14	83
		Orbitofrontal Medial	-4 46 -12	4.23	**633**
		Superior Frontal Medial	-6 52 6	2.49	
		Precuneus	-6 -56 14	4.35	**867**
		Middle Occipital	-44 -74 34	3.22	167
		Inferior Occipital	-26 -94 -8	4.79	**651**
		Middle Temporal Pole	-52 10 -26	2.92	62
		Superior Temporal Pole	-42 20 -24	2.83	
		Middle Temporal Gyrus	-56 2 -26	2.68	
	R	Superior Frontal Medial	2 56 16	2.69	83
		Anterior Cingulate	8 48 24	2.93	
		Middle Temporal Gyrus	52 0 -24	2.91	214
		Precuneus	6 -56 18	3.42	**867**
		Calcarine	22 -96 -4	3.75	**699**
		Inferior Occipital	32 -88 -8	3.53	
		Middle Occipital	34 -86 12	3.13	

Only those clusters with an effect corrected with FWE or FDR criteria were considered as significant and it was included in the table. x,y,z {mm}= Coordinates in MNI space of local maxima. T = T scores. No.Vox. = Number of voxels significantly activated inside the cluster belonging to each local maximum. T scores at the peak level are reported in bold if they are significant after FWE correction.

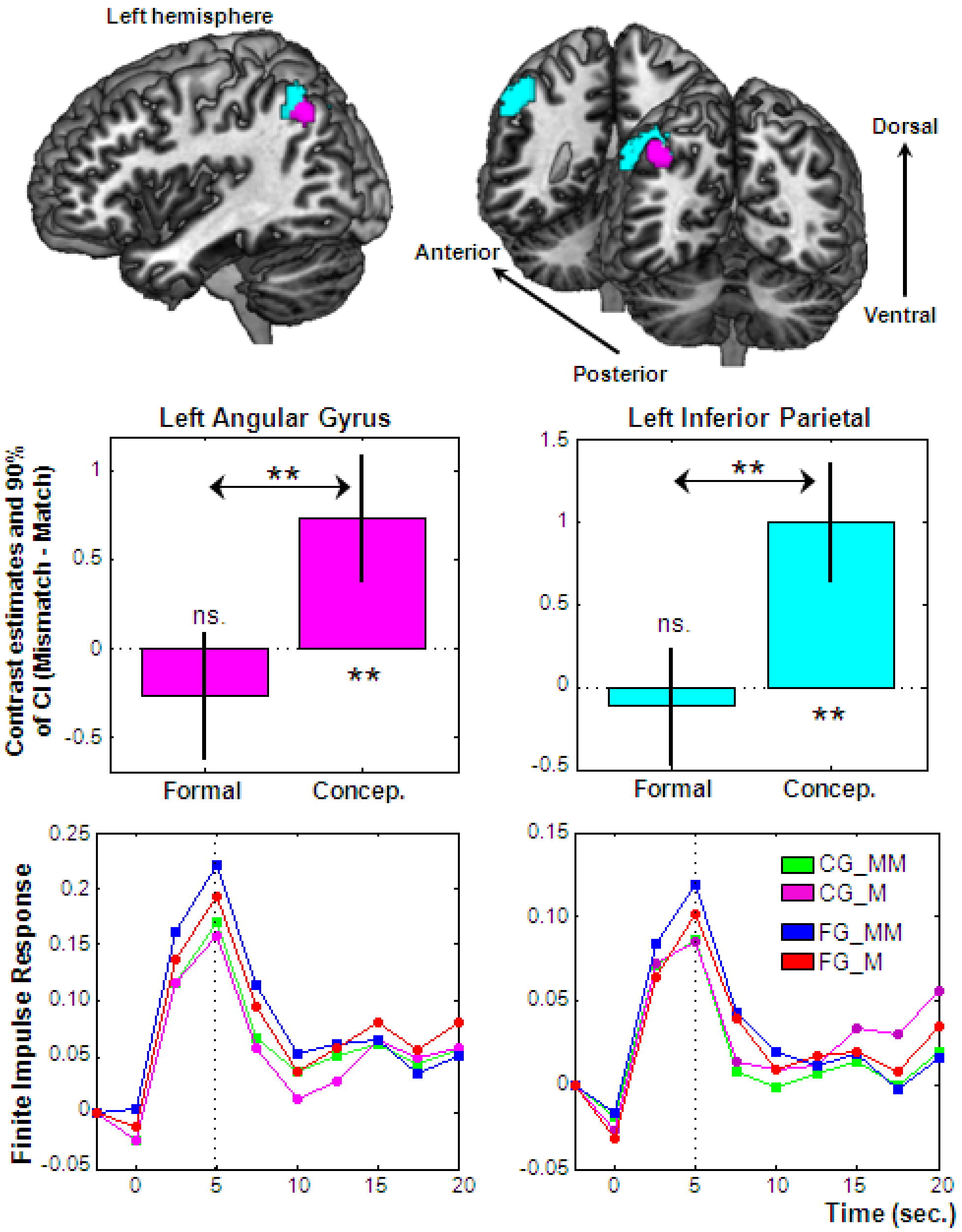


Figure 4.3. Statistical parametric map emerging from the interaction effects between Gender Congruency and Gender Type were projected on the MNI single-subject T1 image. The sagittal and axial views represented in the upper part of the figure display the significant activated clusters. The bar graphs display the contrast estimates and 90% of confidence intervals at the maximum peaks representative of the two clusters resulting from the interaction effect. Time courses of the HRFs are represented in the lowest part of the figure. Each condition is represented with different colors. The vertical dotted lines signal the maximum amplitude peaks and the latency corresponding to the location of this maximum. MM: Mismatch; M: Match. CG: Conceptual Gender; FG: Formal Gender.

Table 4.4. Interaction between Congruency Pattern (Match and Mismatch) and Type of Gender (Conceptual and Formal).

Region	Interaction			Match vs. Mismatch for Conceptual Gender		
	x,y,z {mm}	T	No. Vox.	x,y,z {mm}	T	No. Vox.
Inferior Parietal (L)	-46 -56 48	4.12	**998**	-56 -46 40	**5.76**	**506**
Angular Gyrus (L)	-40 -62 40	3.05		-42 -54 44	**4.57**	**65**

Only those clusters with a significant interaction effect (p<0.001 uncorrected) were resported. x,y,z {mm}= Coordinates in MNI space of local maxima. Vx = Number of voxels significantly activated inside the cluster belonging to each local maximum. T = T scores. T scores are reported in bold if they are significant at the peak level after FWE or FDR correction.

4.4 Discussion

As we pointed out in the Overview section, it remains unclear whether and how the conceptual knowledge associated to certain grammatical elements affects the building of a syntactic structure. The empirical evidence with regard to this phenomenon is scarce and even contradictory, making difficult to draw any theoretical conclusion. The current study was designed to investigate a) whether the building of a syntactic structure hinges on the conceptual information embedded in our linguistic code and if so b) where is this dependency mapped in the brain. To examine this, we took advantage of the Spanish gender agreement system, where it is possible to distinguish two different gender types depending on the animacy of the nouns – i.e., conceptual (mostly living entities) and formal (mostly non-living entities). Interestingly, the assignment of the gender values – masculine or feminine – in both gender types follows the same morpho-phonological rule (i.e., regardless of their animacy, nouns ending in "–a" are usually feminine and nouns ending in "–o" are usually masculine). This property allowed us to determine how our brain processes agreement information distinguishing between merely syntactic dependencies – e.g., formal gender agreement in Spanish – and more complex agreement relations, where the interplay between form-based and conceptual signals could be an important constraint – e.g., conceptual gender agreement in Spanish. Critically, it also enabled us to explore the possible interactions between these formal and conceptual factors, controlling the syntactic complexity of the grammatical units.

In consonance with the previous experimental chapter (Chapter 3), the current findings revealed that a specific brain circuit responds according to the gender agreement congruency between determiners and nouns. The pars opercularis and triangularis within the left IFG, the left middle frontal gyrus, as well as the left MTG/STG emerged as critical hubs for the computation of grammatical relations. In addition, we also demonstrated that others fronto-parietal areas in both hemispheres (e.g., the superior parietal cortex, the anterior cingulate cortex and the superior and middle frontal gyri) are actively engaged in contributing to this operation. The response patterns of these regions varied as a function of the congruency between the different elements involved in such grammatical relations. This empirical finding indicated that the neural circuit responsible for agreement operations is not circumscribed to the left prerisylvian regions that have traditionally been the key focus of the sentence processing literature (Friederici, 2011, 2012; Friederici & Gierhan, 2013; Hagoort, 2003a, 2005). However, even more important is the result concerning the interaction between conceptual and formal information during the establishment of local grammatical relations. Regarding this question, we isolated a parietal cluster in the left hemisphere which included part of the angular gyrus and the inferior parietal cortex showing a significant interaction between Congruency Pattern (*Match* and *Mismatch*) and Type of Gender (*Conceptual* and *Formal*). These two parietal areas exhibited greater response for incongruent than for congruent items (i.e., *Mismatch* > *Match* contrast). However, crucially, this difference was only significant for *Conceptual Gender*. In addition, the methodological approach used here enabled to better characterize the neural circuit underlying agreement operations providing chronological details about its functioning.

Taken together the current results (Table 1S shows an updated summary of the principal results enabling a comparison between the findings derived from Experiment I and II) provide crucial evidence concerning how our brain deals with agreement information.

The interplay between one of the main hubs of the domain-general semantic network (i.e., the angular gyrus and adjacent areas) and the neural circuit involved in agreement computation suggests that for the processing of grammatical relations a complex circuit, which include language-specific and domain-general areas, is boosted. The fine-tuning of this system seems to be constrained by the available conceptual and/or formal information. From now on, the next paragraphs will be focused on discussing the relevance of these main findings.

Table S1. Main Findings

	Behavioral results	Neuro-anatomical results	
		Grammaticality effects	Effects related with the critical manipulation
Experiment I (determiner-noun pairs)	**Main effect of Agreement Congruency**: Subjects classified determiner-noun pairs as grammatically correct more easily and accurately than incongruent pairs. This differentiation was evident for both transparent and opaque nouns. **Interaction effect**: Regarding RT, this effect was larger for opaque than for transparent nouns.	***Gender Mismatch* relative to *Gender Match***: the dorsal striatum, the middle and medial superior frontal gyrus, the medial orbito-frontal cortex, the pre- and post-central gyrus, as well as the anterior cingulate cortex. ***Gender Match* as compared to *Gender Mismatch****:* the pars opercularis and triangularis within the left IFG and the posterior part of the left MTG/STG.	Significant **interaction effects** between Gender Congruency and Gender-marking emerged in five left-lateralized clusters: ▪ Pars triangularis within the IFG ▪ Posterior part of the MTG/STG ▪ Hippocampus ▪ Angular Gyrus ▪ Supramarginal Gyrus
Experiment II	**Null effects** for RT and error rates.	***Gender Mismatch* relative to *Gender Match***: the pars triangularis, orbitalis and opercularis within the left IFG, the middle frontal gyrus, as well as the inferior parietal gyrus and the supramarginal and the angular gyri. ***Gender Match* as compared to *Gender Mismatch****:* the medial superior frontal gyrus, the medial orbito-frontal cortex, the anterior cingulate cortex, as well as the anterior part of the left MTG/STG and the superior and middle temporal pole.	Significant **interaction effects** between Gender Congruency and Type of Gender emerged in two left-lateralized clusters: ▪ Inferior Parietal ▪ Angular Gyrus

Experiment III			
Experiment IV			
Experiment V			

Interplay between a left lateralized prerisylvian circuit and a bilateral fronto-parietal network. Critically, the computation of agreement dependencies, an essential operation required to comprehend phrases or sentences has been neglected for a long time, especially if we talk about neurocognition. Despite of the scarcity of empirical evidence, all the studies relating to this topic share an important result: the brain areas involved in computing agreement relations concur with the regions pinpointed as crucial nodes of the network underlying sentence comprehension. The IFG and the anterior and posterior MTG-STG, essential nodes within the left lateralized perisylvian circuit responsible for decoding linguistic inputs, have also been identified as critical areas recruited during agreement computation (Kuperberg et al., 2000; Kuperberg et al., 2003; Kuperberg, Sitnikova, et al., 2008; Newman et al., 2003; Ni et al., 2000; Nieuwland et al., 2012). The current results nicely support this claim, but critically, they also fit well with recent theoretical models that have proposed that the processing of linguistic material is not circumscribed to this language-specific circuit (Hagoort, 2013, 2014; Hagoort & Indefrey, 2014). In contrast, the need to consider the interplay between this circuit and other domain-general networks has become increasingly apparent.

Regarding this point, the current results reveal that while regions such as the IFG (i.e., encompassing the pars opercularis and triangularis), the middle frontal gyrus and the superior parietal cortex exhibited higher responses for the ill-formed constructions than for their correct counterpart, other areas such as the anterior cingulate cortex, the superior frontal gyrus, the medial orbito-frontal cortex, the precuneus, as well as well as the anterior part of the left MTG/STG and the superior and middle temporal poles showed the opposite pattern. Consistent with what we proposed in the previous chapter, these results indicate that during the building of a syntactic structure at least two different functional modules can be identified: 1) a left lateralized language-specific perisylvian network – i.e., including regions such as the IFG, the middle frontal gyrus[22] and the middle and superior temporal cortices – and 2) a domain-general module responsible for the monitoring of conflicting signals – i.e., comprising areas such as the anterior cingulate cortex, the superior frontal gyrus and the superior parietal gyrus.

---

[22] See the Discussion of the previous chapter for two plausible hypotheses about the role of this region.

Interestingly, the estimation of the FIR models carried out in this experiment sustains this assertion showing that these two systems could be distinguished based on their response patterns. The neural responses characterizing these circuits have different polarities: while the perisylvian circuit exhibited positive responses, the conflict-monitoring system showed negative responses. While we do not have a clear physiological explanation for these negative responses, they cannot be ignored. As has been previously argued, these deactivation patterns could be reflecting a functional relationship between these regions and the default mode network (Greicius et al., 2003; Greicius et al., 2009; Gusnard & Raichle, 2001; Koshino et al., 2014; Raichle, 2015; Raichle et al., 2001; Raichle & Snyder, 2007; Shulman et al., 1997; Uddin et al., 2009; Utevsky et al., 2014). This analysis also demonstrated that except for the temporal areas, the brain regions involved in agreement processing were more strongly recruited for ill-formed constructions than for grammatically correct sentences. This pattern fits well with previous work and suggests that dealing with grammatical violations implies additional processing costs in comparison with the integration of congruent information (Mancini et al., 2011a; Molinaro, Barber, et al., 2011; Molinaro, Vespignani, et al., 2008; Molinaro, Vespignani, et al., 2011). In addition, the methodological approach adopted here demonstrated that all these regions showed similar temporal dynamics with maximum differences around five seconds. However, critically, for the medial superior frontal gyrus, the pars triangularis within the IFG and the middle frontal gyrus, a second conspicuous peak was observed between 10 and 12 seconds. This pattern of responses concurs with a previous TMS study that demonstrated the involvement of the IFG during sentence comprehension in early (i.e., first fixation) and late (i.e., total reading times and regressive eye movements) processing measures (Acheson & Hagoort, 2013).

The similarities found between these three segregated nodes within the frontal lobe indicate that despite these two processing modules – i.e., the language-specific perisylvian system and the domain-general conflict monitoring system – have different roles, they operate hand in hand in order to properly interpret the agreement relation. Future research should be directed at characterizing the interaction between these two systems focusing on ^{1}the functional dynamics typifying each area within these networks and ^{2}the anatomical connections sustaining this interplay.

Disentangling the left-lateralized language-specific perisylvian circuit. Importantly, as the theoretical models of sentence processing proposed, within the language-specific left lateralized perisylvian circuit it is possible to distinguish regions with different roles (Bornkessel-Schlesewsky & Schlesewsky, 2013; Friederici, 2011, 2012; Friederici & Gierhan, 2013; Hagoort, 2005, 2013, 2014). Consistently, all these models proposed the left IFG as one of the central hubs of this network, which encompassed three different functional nodes – i.e., the pars opercularis, triangularis and orbitalis. While the left pars opercularis has been associated with a cost during the building of local syntactic structure, the left pars triangularis and orbitalis has been related with a processing cost triggered by the combination of semantic information (Carreiras et al., 2012; Goucha & Friederici, 2015; Hammer et al., 2007; Kuperberg, 2007; Kuperberg et al., 2003; Kuperberg, Sitnikova, et al., 2008; Nieuwland et al., 2012; Santi & Grodzinsky, 2012). In this particular case, the engagement of the IFG responds to the gender morpho-syntactic mismatch typifying the incongruent items [*el mesa/ the$_{\text{masc.}}$ table$_{\text{fem.}}$]. Here, the difference between incongruent and congruent constructions was circumscribed to **the pars triangularis and opercularis within the left IFG**. Interestingly, the methodological approach used here temporally distinguished between these two sub-regions: while in the pars opercularis a maximum difference was observed between three and five seconds, in the pars triangularis the difference between the mismatch and the match condition was evident until 12 seconds. The temporal distinction characterizing the pars opercularis and triangularis could not be explained by the gender type or the congruency pattern, since their brain responses across conditions were similar. Crucially, the differences in their temporal patterns could be indicating that the left IFG fulfill a variety of functions during agreement comprehension. As previous authors have proposed, this region seems to control the information flow between the other nodes of this language-specific network (Molinaro et al., 2015). The pars opercularis could be controlling the morpho-syntactic feature checking operations, whereas the pars triangularis could be controlling the lexico-semantic correspondence between the different sentence elements and the subsequent lexico-semantic integration processes.

In addition, as expected, differently from the IFG, temporal areas – i.e., encompassing **the anterior part of the MTG/STG and the superior and middle temporal poles** – showed higher activation for the congruent items relative to the incongruent ones. This finding is in accordance with the results reported in the previous chapter. Nonetheless, the main role this area play here seems to be different. In the previous experiment, the congruent items evoked higher responses in the posterior portion of the MTG/STG than the incongruent ones. This activity was associated with the access/retrieval of the morpho-syntactic and lexico/semantic information required for the building of a syntactic structure (Baggio & Hagoort, 2011; Hagoort, 2013; see Hagoort, 2014 for a discussion of this topic; and see also Hagoort & Indefrey, 2014). However, in the current experiment the temporal region resulting significant from the contrast Match vs. Mismatch included the anterior portion of the MTG/STG extended into the temporal pole. Different interpretations have been postulated concerning the role played by these anterior temporal areas. On the one hand, it has been argued that a ventral pathway, which connects the anterior part of the temporal cortex and the pars opercularis within the left IFG, sub-serves the building of local syntactic structures (Friederici, 2011, 2012). On the other hand, the response of this area has been also related with the integration of different types of conceptual information (Baron, S. G. et al., 2010; Bornkessel-Schlesewsky & Schlesewsky, 2013; Brennan et al., 2012; Brennan & Pylkkanen, 2012; Molinaro et al., 2015). However, these interpretations come from the sentence processing literature, where the response of this area is greater for syntactic or semantic violations rather than syntactically and/or semantically plausible constructions. As the results of the first two experiments [Experiment I and II] have demonstrated, when agreement is isolated from other sentential processes, the temporal areas exhibit higher responses for congruent than for incongruent constructions. This activation pattern points out that the function played by this area during agreement processing may not necessary correspond with the interpretations concerning sentence comprehension. During the processing of sentences, different mechanisms are boosted that may blur the mechanisms underlying the integration of local agreement information. In this case the anterior part of the MTG/STG could be reflecting the mapping between the formal and the conceptual information required to properly integrate the agreement relation. As previous fMRI evidence suggests, regarding the conceptual combinatorial processing, more critical than the neural response of this anterior temporal region per se, are the functional connections this area have with others heteromodal associative hubs (see Molinaro et al., 2015 for a link between the anterior MTG/STG and the angular gyrus). To characterize the functional connectivity pattern established between the different nodes of this network may be essential in assessing this hypothesis.

The role of the angular gyrus and adjacent areas during agreement processing. Critically, this is the first fMRI study directly exploring how the conceptual and the formal information embedded in the same linguistic representation is taken into account in order to interpret grammatical relations. Our data provides clear findings indicating that the recruitment of **the angular gyrus and adjacent areas** is crucial for the comprehension of linguistic material. In line with our predictions, the left angular gyrus extended into the left inferior parietal cortex showed higher congruency differential effects (i.e., Mismatch - Match) for conceptual gender (e.g., **abuelo*$_{masc.}$ *sabia*$_{fem.}$*/abuelo*$_{masc.}$ *sabio*$_{masc.}$ [grandfather wise]) as compared to formal gender (e.g., **faro*$_{masc.}$ *alta*$_{fem.}$*/faro*$_{masc.}$ *alto*$_{masc.}$ [lighthouse tall]). This empirical evidence goes in line with previous studies demonstrating the involvement of parietal areas during language processing (see Hagoort, 2013; 2014 for a recent theoretical proposal). However, combining these two dimensions – i.e., conceptual and formal features – within the same linguistic representation constitutes a new fMRI approach that enables strongest conclusions. Using this type of manipulation it is possible to identify the neural correlates of semantic processing without the confounding mechanisms triggered by the computation of meaningless constructions.

Interestingly, the angular gyrus has been linked not only with language-specific (e.g., single word processing; semantic processing and sentence/discourse comprehension), but also with domain-general functions (e.g., number processing, attention and spatial recognition, memory retrieval, conflict resolution, default mode network, episodic-memory and theory-of mind) (see Binder & Desai, 2011; Binder et al., 2009; Seghier, 2013; Seghier et al., 2010 for similar proposals). Taking into account the variety of cognitive functions the angular gyrus has been associated with, Seghier (2013) in a recent review postulated that this area constitutes *"a cross-modal integrative hub that gives sense and meaning to an event within a contextualized environment, based on prior expectations and knowledge, and toward an intended action"* (Seghier, 2013, p. 52). Likewise, Binder and Desai (2011) suggested that this parietal area is a heteromodal integrative hub responsible for the retrieval of conceptual representations of events, which include interlinked entities defined by their spatial and temporal configurations. The top-down and bottom-up connections existing between the angular gyrus and multiple fronto-temporal (e.g., the middle, superior and inferior frontal gyri, and the middle temporal gurys) and medial (e.g., the hippocampus, the caudate, and the precuneus) regions support these two proposals (see Seghier, 2013 for a review of this topic).

In consonance with these two accounts, the engagement of this left parietal cluster for the comprehension of grammatical relations points out an interfacing between a left-lateralized language-specific perisylvian circuit and a central hub of the highly heteromodal semantic associative system. The empirical evidence resulting from the current study indicates that the language system recruits this parietal area in order to access the concepts required for the proper interpretation of such grammatical relations. This hypothesis is underpinned by previous fMRI evidence, which demonstrated a functional coupling between the left angular gyrus and the anterior part of the left MTG/STG boosted by the comprehension of atypical but composable semantic combination (e.g., "*dry rain*") (Molinaro et al., 2015). These authors interpreted this coupling as a processing cost triggered by the building of a complex conceptual combination (see also Bemis & Pylkkänen, 2011, 2012a, 2012b; Hammer et al., 2007; Hammer et al., 2005). These findings fit nicely with previous experiments showing a functional dependency between dorsal and ventral fiber tracts and the comprehension of syntactic dependencies (for concomitant DTI results see Bonner et al., 2013; and see also Griffiths et al., 2012; Wilson et al., 2011). Further works should be directed to [1]isolate the neural region(s) through which these two systems communicate with each other and [2]identify which is the switch that controls this interfacing.

Interim conclusions. During the comprehension of phrases or sentences multiple neural mechanisms operate in a coordinated and agreed fashion. In line with most of the theoretical models of sentence processing, the present fMRI study demonstrated that the building of a syntactic structure recruits a left-lateralized perisylvian circuit typically associated with language-specific functions (Friederici, 2011, 2012; Friederici & Gierhan, 2013; Hagoort, 2005, 2013, 2014; Hagoort & Indefrey, 2014). However, our data suggest that concurrently, a domain-general conflict monitoring system bilaterally distributed is also engaged during this process. Nonetheless, these two systems play different roles; a clear interfacing between them was pointed out. Crucially, the main contribution of this study was the parietal involvement during the access and retrieval of conceptual information associated with the different grammatical elements. The interplay between these three functionally segregated systems during the computation of grammatical relations is a key piece of evidence for the better understanding of the neural dynamics supporting language comprehension.

In the context of agreement comprehension and even more specifically in the context of gender agreement processing, the outcomes of the current study are pivotal. According with our results, during the comprehension of nominal agreement relations the formal and conceptual information are taken into account. Nevertheless, more than a serial processing of these two types of information, our data indicate that the interaction between these dimensions is essential for the proper interpretation of grammatical relations. At a more general level, the current empirical evidence also impacts on the theoretical models of sentence comprehension questioning the functional semantic-syntactic distinction between the ventral and dorsal pathway(s) (for a different argument see Friederici, 2011, 2012). The processing of conceptual and formal information might involve a functional nexus between these neuro-anatomically different pathways (Griffiths et al., 2012; Wilson et al., 2011). It is essential for further investigations to address this question in order to integrate the current findings into new theoretical proposals.

Chapter 5.

Experiment III

Nominal and verbal agreement: Two sides of the same coin.

5.1 Overview

The previous two experiments evaluated the neuro-anatomical correlates sub-serving the establishment of nominal grammatical relations (i.e., determiner-nouns [Experiment I] and noun-adjectives [Experiment II]). However, as pointed out in the Introduction (Chapter 1, *Agreement*), an essential and still open question is how the brain process different types of grammatical configurations (e.g., determiner-noun and subject-verb). Does the brain use the same or different mechanisms for coding nominal and subject-verb agreement? Importantly, no research to date has investigated whether nominal and verbal agreement follow similar comprehension processes.

Regarding the electrophysiological correlates of nominal and verbal agreement, two previous studies investigated agreement processing separately in determiner-noun (Barber & Carreiras, 2005) and in subject-verb (Silva-Pereyra & Carreiras, 2007) configurations. Interestingly, these studies showed different effects for verbal and nominal agreement across experiments. On the one hand, Silva-Pereyra and Carreiras (2007) examined subject-verb agreement processing by comparing number mismatch and number match constructions. In accordance with the current electrophysiological literature on agreement processing, they reported a biphasic LAN/P600 effect with higher amplitude for number mismatch than for number match. On the other hand, Barber and Carreiras (2005) explored the processing of number agreement in determiner-noun pairs and found a LAN/N400 effect followed by a P3 effect. The early LAN effect was interpreted by these authors as reflecting the failure in the integration of the two words during the syntactic build-up of the noun-phrase structure, whereas they suggested a relationship between the N400-like effect and lexical integration processes associated to the word matching that participants have to carry out in order to perform the task. Critically, from a neuro-anatomical perspective, as mentioned above a few studies have investigated the effects of agreement on the BOLD signal (Carreiras et al., 2010; Hammer et al., 2007; Hernandez et al., 2004; Miceli et al., 2002; Nieuwland et al., 2012). In particular, Carreiras et al. (2010) investigated agreement in the processing of word pairs, either determiner-noun or noun-adjective Spanish items. They reported increased BOLD activity in the left premotor and left inferior frontal areas for the processing of number agreement violations as compared to the agreement baseline. On the other hand, Nieuwland et al. (2012) reported increase of activation in parietal and dorsolateral prefrontal regions using sentences in Basque with subject-verb number agreement violations. These findings were taken as evidence for the increased syntactic demands of the mismatch conditions compared to the grammatical control. Despite these ERP and fMRI findings, where different effects have been reported across experiments, it is difficult to reach a clear conclusion about whether verbal and nominal agreement operations are using the same or different processing mechanisms. Critically, no ERP or fMRI study has yet directly compared verbal and nominal agreement within-participants in the same experiment. In the current neuro-cognitive literature on language processing no hypothesis is formulated concerning a possible dissociation of nominal and verbal agreement in comprehension.

Thus, verbal and nominal agreement needs to be investigated using the same experimental procedure with the same participants. This is the aim of the present study, in which number violations will be created within both nominal and subject-verb agreement structures, to examine the neural substrates associated with their processing. Specifically, by comparing number matching patterns (e.g., determiner-noun: *el*$_{sg.}$ *anillo*$_{sg.}$ [the ring]; subject-verb: *ella*$_{sg.}$ *baila*$_{sg.}$ [she dances] and mismatching (e.g., determiner-noun: **los*$_{pl.}$ *anillo*$_{sg.}$ [the ring]; subject-verb: **ellas*$_{pl.}$ *baila*$_{sg.}$ [*they dances]), we hope to gain insight into feature-consistency and integration procedures as well as into the repair/reanalysis operations that finding a number anomaly triggers in both nominal and subject-verb agreement structures. It is important to highlight that the main goal of the present study was to investigate the brain regions involved in number agreement computation in two different constructions, and not to look at the processing differences between verb and noun processing per se. Since nouns and verbs differ in many dimensions, we did not contrast them directly[23] (for a review see Vigliocco et al., 2011). In the following, we proceed to detail our predictions emphasizing the distinction between different mechanisms supporting the establishment of an agreement relation.

As explained in the introductory section (Chapter1, *Linguistic Theoretical Framework of Agreement*), from a theoretical perspective the processing of a noun-phrase structure implies matching a noun with its real-world referent based on its morphological markers, without building any thematic representations. However, the analysis of a subject-verb structure implies not only the extraction of morpho-syntactic markers from the input, but also the projection of a complex representation in which the subject noun is associated to a specific role. On the one hand, if the two types of agreement operate with similar mechanisms, comprehending an instance of nominal or verbal agreement should not make any difference to the processor. In this case, the processing of the two types of agreement is expected to recruit overlapping neural networks related to feature checking, syntactic integration and interpretation, as well as conflict-monitoring operations. On the other hand, different checking operations might be shaped because of the different syntactic domains and features that the two types of agreement encompass. In addition, differences between the two patterns may also arise from the different interpretive outcomes that the syntactic integration of these two types of structures produces. In parallel to these language-specific operations, differences concerning the conflict-monitoring operations could also emerge. From a neuro-anatomical perspective, the differences between the two dependencies can emerge in qualitative and/or quantitative terms. In the former case, the difference should be reflected in the engagement of distinct neural networks that support the two types of agreement, while in the latter, greater or lesser neural responses within the same network would be found.

---

[23] It should be noticed that a direct comparison between a noun and a verb – e.g., *"anillo"* and *"baila"* – would have been inappropriate, since they are two inherently different lexical categories. As such, their analysis implies accessing different types of grammatical and referential information. While nouns refer to entities, verbs denote actions or states that can develop in specific time frames (tense information), progressively or punctually (aspect information), by means of agents or patients (thematic roles).

5.2 Materials and Methods

Participants. After the quality checking of the data, a total of 32 (19 females) undergraduate students, with ages ranging from 18 and 37 years, participated in the current study.

Stimuli and experimental procedure. The present experimental design manipulated number agreement (number match vs. number mismatch) and type of word pairs (determiner-noun pairs vs. subject-verb pairs) in a 2x2 factorial within-subject design. The stimuli consisted of 128 word pairs divided in four experimental conditions (in the proportion of 1:1:1:1): determiner-noun agreement pairs; determiner-number violation pairs; subject-verb agreement pairs and subject-verb violation pairs (see examples below). These word pairs were made up of a determiner article plus a noun (such as in (13a) and (13b) below), or a personal pronoun plus an inflected verb (such as in (14a) and (14b) below). All the nouns included in the determiner-noun word pairs were selected such that their corresponding plural form incorporates a morphological mark (in Spanish the canonical suffixes “-s” or “-es”). All four conditions contained 32 word pairs each. In every condition, half of the nouns or verbs were presented in their singular form, and the other half in their plural form. All nouns and verbs were of medium lexical frequency [nouns: mean = 38.37 per million, SD = 54.25; verbs: mean = 22.67 per million, SD = 61.65] and 4 to 9 letters long [nouns: mean = 5.69, SD = 0.91; verbs: mean = 6.41, SD = 1.65] according to the Spanish ESPaL database (Duchon et al., 2013). In addition to number agreement, in Spanish it is mandatory that determiners and nouns also agree in grammatical gender. To avoid possible gender effects, the grammatical gender agreement was strictly controlled: a) all nouns used are inanimate nouns; b) all the word pairs agree in gender; c) all nouns are morphologically marked for gender, that is, they end with the canonical suffixes in Spanish for gender (“–o” for masculine and “–a” for feminine). All the subject-verb word pairs used in the present study were constructed such that a third person plural subject is followed by a third person plural verb.

(13) Determiner-Noun word pairs

(a) Number Match: e.g., *El*$_{sg.}$ *anillo*$_{sg.}$ [The ring]

(b) Number Mismatch: e.g., **Los*$_{pl.}$ *anillo*$_{sg.}$ [The ring]

(14) Subject-Verb word pairs

(a) Number Match: e.g., *Ella*$_{sg.}$ *baila*$_{sg.}$ [She dances]

(b) Number Mismatch: e.g., **Ellas*$_{pl.}$ *baila*$_{sg.}$ [They dance]

Two lists of 128 experimental word pairs were generated depending on the agreement manipulation. Assignment of word pairs to the agreement conditions (*Number Match – Number Mismatch*) in each list was counterbalanced across participants. Thus, each pair occurred twice across subjects, once in the match condition and once in the mismatch condition, so that each participant only saw one form of each pair during the experiment (see Appendix 4 for the list of all the stimuli per condition).

In each trial, participants were visually presented with two words at the same time. As described in the materials, the pairs of words could be article-noun (e.g., *El anillo* [The ring]) or subject-verb word pairs (e.g., *Él*$_{sg.}$ *baila*$_{sg.}$ [He dances]), which could match or mismatch in number agreement (e.g., Match: *El*$_{sg.}$ *anillo*$_{sg.}$ [The ring] vs. *Él*$_{sg.}$ *baila*$_{sg.}$ *[He dances]*; Mismatch: **Los*$_{pl.}$ *anillo*$_{sg.}$ [*The ring] vs. **Ellos*$_{pl.}$ *baila*$_{sg.}$ [*They dances]). Participants were instructed to judge the grammaticality of each pair by pressing either one of two buttons (YES: grammatical; NO: ungrammatical). Specifically, each trial began with a cross “+” as a visual cue, presented for a variable time between a minimum of 2000 msec. and a maximum of 8000 msec. (mean = 6870 msec.; SD = 1840 msec.), followed by the two words for 300 msec., followed by a blank screen for 2000 msec. The inter-stimulus interval was varied in order to counteract expectation effects that might diminish or change participants’ strategies. In addition, varying these times also helped to ensure that brain activity was sampled at different points of the BOLD response. An event-related design was used in which a different randomization of trials was used for each participant.

Image Acquisition. Scanning was done on the same scanner than the two previous experiments. In all subjects 480 BOLD-contrast-weighted echoplanar images were taken in one run using the parameters described in Appendix 2C. After the functional run, a T1-weighted anatomical volume image was acquired from all participants following the parameters described in Experiment 1.

Functional Data Analysis. Functional data were analyzed using the same procedure described in Experiment 1. After that, at the subject level, statistical parametric maps were generated by modeling a univariate general linear model, using for each stimulus type a regressor obtained by convolving the canonical hemodynamic response function with delta functions at stimulus onsets, and also including the six motion-correction parameters as regressors. Following the same procedure used in the previous experimental chapters, robust regressions using weighted-least-squares were used to estimate the parameters of the GLM (Diedrichsen & Shadmehr, 2005). A pair-wise contrast comparing activity to each phrase type relative to the fixation baseline was then submitted into a second level design analysis to enable population inferences. A 2x2 Factorial design was performed with Agreement Pattern (*Number Match* vs. *Number Mismatch*) and Type of Word Pairs (*Determiner-noun pairs* vs. *Subject-verb pairs*) as factors, looking for the main effects and possible interactions. Those local maxima with a p-value corrected for multiple comparisons with family wise error (FWE: Nichols & Hayasaka, 2003) and/or false discovery rate (FDR: Genovese et al., 2002) and those local maxima that reach the FWE criteria at the cluster level were considered as significant and reported in the tables of results. Subsequently, in order to determine whether number agreement computation (tested by the contrast Mismatch vs. Match) engages a common neural circuitry for the two types of construction (*Determiner-Noun pairs* and *Subject-Verb pairs*), we tested the conjunction null hypothesis [both tails of the comparison *Mismatch vs. Match* for *Determiner-Noun pairs* & *Mismatch vs. Match* for *Subject-Verb pairs*] (Friston et al., 2005; Nichols et al., 2005). This test allows us to isolate those regions where both effects were significantly present and did not differ in magnitude (Results concerning this analysis are included in the Supplementary Material).

In order to disentangle whether differential effects (*Mismatch vs. Match*) between nominal and subject-verb agreement are related to language-specific or to general attentional mechanisms associated to increases of the task difficulty, two additional analyses were carried out. On the one hand, a series of correlation analyses between the behavioral measures (RT and error rates) and the BOLD responses corresponding to those regions that exhibited a significant interaction effect were conducted as an exploratory approach. This analysis allows us to explore whether the response of the critical neural regions is modulated by task difficulty. On the other hand, a series of causal mediation analyses[24] was performed in order to corroborate the previous correlation results in a more deterministic way. This analysis allows us to determine the causal relationship of the differential effects between nominal and subject-verb agreement at the neural level and the task difficulty effect arising from the behavioral results. This mediation analysis quantifies the extent to which the treatment [critical manipulation: *Mismatch vs. Match in Determiner-Noun pairs* and *Mismatch vs. Match in Subject-Verb pairs*] affects the outcome [interaction effect at the neural response level] through the mediator(s) [behavioural measures: RT and error rates] (Baron, R. M. & Kenny, 1986; Carreiras et al., 2014; Imai, Keele, & Tingley, 2010; Imai, Keele, & Yamamoto, 2010; MacKinnon, 2008; Tingley et al., 2013)

Two different statistical models were tested for each neural region independently: a) the mediator model, where the behavioral measures are influenced by the manipulation of the treatment, with this relationship mediating the causal effect between the treatment and the brain response; and b) the response model, where the behavioral measures and the critical manipulation act as predictors of the brain response (dependent variable). For each model we estimated the average causal mediation effect (a particular mechanism acting through the mediator of interest [Average Causal Mediation effect: ACME]) and the direct effect (which includes all other possible mechanisms [Average Direct Effect: ADE]). To improve the statistical power of these estimations, both measures (ACME and ADE) were expressed as a population average estimated through 1000 bootstrap random samples extracted from the data.

---

[24] The series of causal mediation analyses was estimated using a hierarchical multilevel regression model where all repeated measures will be the first hierarchical level and subjects the second one.

5.3 Results

<u>Behavioural results.</u> Mean reaction times (RT) and error rates for each condition are presented in Table 5.1, with the corresponding standard error between parentheses. The data was explored and cleaned following the procedure described in Experiment 1. 2x2 ANOVAs on mean response times and error rates were performed using Agreement Pattern (*Number Match* and *Number Mismatch*) and Type of Word Pair (*Determiner-noun pairs* and *Subject-verb pairs*) as factors.

Table 5.1. Percentage of error and mean decision times (in ms) for both agreement patterns (match and mismatch) in the two types of word pairs (determiner-noun and subject-verb) with standard error between parentheses.

	Mean reaction times		**Error rates**	
	Mismatch	**Match**	**Mismatch**	**Match**
Determiner-Noun	890.66 (34.61)	683.92 (26.25)	17.86 (1.81)	6.36 (1.05)
Subject-Verb	987.66 (36.81)	862.71 (31.74)	23.5 (1.55)	12.5 (1.19)

For RTs, a significant main effect of Type of Word Pair [F(1,31) = 119.70, p<.0001], was found indicating that reaction times were faster in the *Determiner-noun pairs* than in the *Subject-verb noun pairs*. The main effect of Agreement Pattern was also significant [F(1,31) = 102.70, p<.0001] suggesting that grammaticality judgment in the *Number Match* condition was faster than the *Number Mismatch*. Importantly, the interaction between these two factors was also significant [F(1,21) = 18.30, p<.0001]. However, the pairwise comparisons for the variable of interest (agreement) showed that *Number Match* was faster than *Number Mismatch* both in the determiner-noun pairs [t (31) = 10.28, p<.001], and in the verb-noun pairs [t (31) = 7.05, p<.001]. Regarding the error rate analysis, an analogous pattern was found. The 2x2 ANOVA showed a main effect of Type of Word Pair [F(1,31) = 29.69, p<.001], indicating that the percentage of errors was larger in the *Subject-verb pairs* than in the *Determiner-noun pairs*. The main effect of Agreement Pattern was also significant

[F(1,31)= 61.83, p<.001], indicating that the percentage of errors was larger in the *Number Mismatch* condition than in the *Number Match* condition. The interaction was not significant [F(1,31) = 0.46, p<.83].

FMRI data: All phrases vs. the baseline condition. To characterize the functional neuro-anatomical network that was recruited by the processing of different types of word pairs, independently of their grammatical pattern, we extracted the effect of all the stimuli used from the 2x2 Factorial design (Type of Word Pair: *Determiner-noun pairs* and *Subject-verb pairs*; Agreement Pattern: *Number Match* and *Number Mismatch*), comparing all the word pairs with the fixation point condition. The F-statistical parametric map resulting from the main effect is displayed in Figure 1, overlaid on the surface of the MNI single-subject T1 image.

This analysis reveals the significant response of a widespread fronto-parieto-temporal network bilaterally distributed (Figure 5.1A). This network includes brain regions such as the left pars opercularis and triangularis within the IFG, as well as the anterior and posterior part of the left middle temporal cortex, the left superior temporal sulcus, the superior parietal gyrus and the basal nuclei (the right pallidum, the right and left thalamus and the right and left putamen), previously related to language processing. Additionally, the left and right fusiform gyrus and the left and right inferior, middle and superior occipital cortex, associated to early stages of visual word perception, showed significant activation for all phrases compared to the baseline condition. Also, regions involved in the planning and execution of motor behavioral responses, such as the supplementary motor area and the precentral and postcentral cortex in both hemispheres exhibited a higher activation (see Table 5.2).

A similar bilateral network was found when we tested the effect of the *Determiner-noun pairs* and the *Subject-verb pairs* independently (Determiner-noun agreement pairs + Determiner-noun violation pairs vs. Fixation baseline; Subject-verb agreement pairs + Subject-verb violation pairs vs. Fixation baseline), suggesting that some of these neuro-anatomical regions are recruited independently of the type of construction involved (Figure 5.1B).

FMRI data: Grammaticality effect (Number Match vs. Number Mismatch condition). To characterize the neural correlates corresponding to commons procedures across the two configurations (*Subject-verb pairs* and *Determiner-noun pairs*) we extracted the main effect of Agreement Pattern (*Number Match* vs. *Number Mismatch*) from the 2x2 Factorial design. This effect allows us to dissociate between those processes evoked independently of the grammatical constructions (e.g., syntactic integration, feature checking, conflict-monitoring and reanalysis) from those dependent of the types of structures (e.g., semantic integration and/or conceptual processing). The significant effects included regions with higher responses for the *Number Mismatch* condition than the *Number Match* condition and regions that exhibited the opposite pattern, i.e. higher activation for *Number Match* than *Number Mismatch* condition.

On the one hand, significant activation increases emerged from the *Number Mismatch* > *Number Match* contrast, including regions such as the right and left insula, the left pars orbitalis, opercularis and triangularis within the IFG, the left precentral, the left supplementary motor area, and the left inferior parietal (see Table 5.3 and Figure 5.2 and 5.3 for details). On the other hand, the contrast *Number Match* > *Number Mismatch* produced higher brain activation in regions such as the angular gyrus, precuneus, middle temporal gyrus (MTG) and orbitofrontal cortex bilaterally and the left occipital and left superior frontal cortex (see Table 5.3 and Figure 5.2 and 5.3, see also Box 5.1 for the results of the conjunction null hypothesis).

FMRI data: Interaction between Type of Word Pairs and Agreement Pattern. Importantly, the main goal of the present study was to investigate the brain areas involved in number agreement computation in two different constructions (nominal and subject-verb agreement). Thus, with this aim we tested the interaction between the Type of Word Pairs (Determiner-noun and *Subject-verb pairs*) and the Agreement Pattern (*Number Mismatch* and *Number Match*). Interestingly, we found significant interaction effects in three different clusters (Figure 5.4 and Table 5.4). On the one hand, a significant differential effect emerging from the contrast mismatch vs. match in the left frontal lobule including voxels in the precentral cortex and voxels in the pars opercularis within the IFG was found only for determiner-noun pairs. No significant differential effect was found in this region for subject-verb pairs. On the other hand, the contrast match vs. mismatch showed significant response for determiner-noun pairs in the left temporal cortex (including voxels in the superior temporal and in the middle temporal cortex) and in the parietal lobule (including voxels in the right and left precuneus/cuneus). In contrast, no significant effects emerge from this contrast for subject-verb pairs.

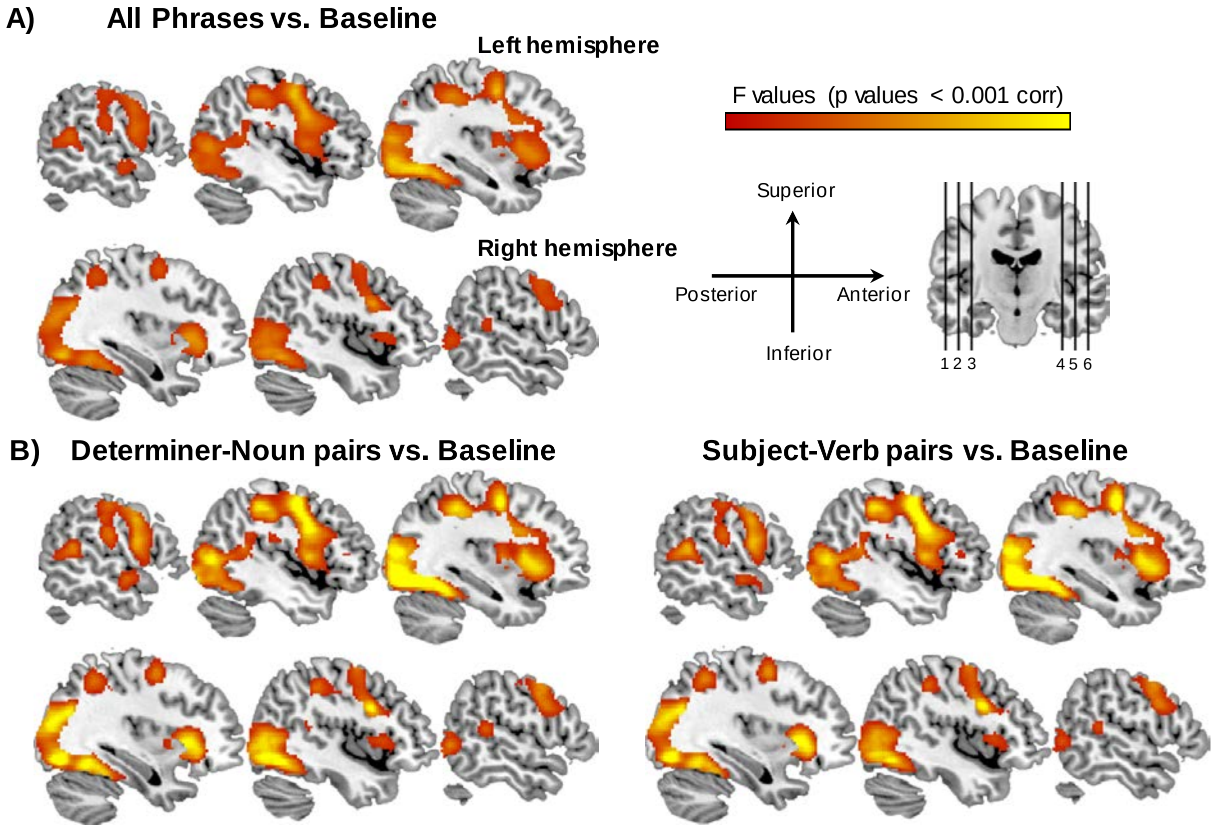


Figure 5.1. Significant activation clusters resulting from three different contrasts were projected on the MNI single-subject T1 image (sagittal slices). All clusters depicted at p<0.001 corrected for multiple comparisons. A) Contrast between each type of word pair including the two types of dependencies – Determiner-noun and Subject-verb pairs – and the two types of agreement patterns – Match and Mismatch – and the fixation baseline condition. B) The contrast between determiner-noun pairs (i.e., including both agreement patterns) and the fixation baseline condition was represented on the right side, whereas the contrast between subject-verb pairs (i.e., including both agreement patterns) and the fixation baseline condition was represented in the left side. 1: x = -56; 2: x = -46; 3: x = -36; 4: x = 34; 5: x = 44; 6: x = 54.

Table 5.2. Brain activation resulting from the comparison between all the critical items and the fixation baseline. This contrast includes both types of word pairs (Determiner-noun and Subject-verb) and both types of agreement patterns (Match and Mismatch).

Hemisphere	Region	x,y,z {mm}	Peak level	Cluster level
			F	No. Vox
Right	Occipital_Sup	26 -70 32	**56.89**	
	Occipital_Mid	27 -91 8	**52.42**	
	Calcarine	16 -66 10	**127.95**	30904
	Fusiform	35 -59 -13	**67.93**	
	Temporal_Inf	42 -73 -6	**70.39**	260
	Temporal_Sup	54 -38 14	**23.64**	
	SupraMarginal	46 -34 44	**27.12**	178
	Parietal_Sup	28 -55 51	**71.54**	
	Insula	32 20 4	**62.64**	853
	Putamen	32 14 -2	**39.03**	
	Pallidum	17 7 -1	**36.98**	
	Thalamus	19 -27 1	**28.97**	
	Frontal_Inf_Oper	44 8 28	**59.67**	1571
	Precentral	28 -4 52	**38.72**	
	Frontal_Mid	40 -4 58	**38.66**	
Left	Calcarine	-14 -72 6	**120.50**	107
	Occipital_Mid	-42 -76 36	**20.33**	
	Occipital_Sup	-20 -76 29	**89.84**	
	Occipital_Inf	-35 -80 -4	**101.12**	
	Lingual	-18 -62 -4	**44.57**	30904
	Fusiform	-35 -64 -12	**89.17**	
	Hippocampus	-21 -29 -3	**27.16**	
	Temporal_Mid	-56 -6 -10	**50.40**	
	Putamen	-28 14 -2	**29.10**	
	Thalamus	-10 -18 5	**55.06**	
	Temporal_Mid	-53 -45 13	**60.02**	
	Temporal_Sup	-58 -4 -8	**42.83**	
	Temporal_Pole_Sup	-54 12 -18	**36.85**	
	Cuneus	-10 -78 26	**43.72**	
	Parietal_Sup	-23 -59 50	**61.98**	
	Supp_Motor_Area	-6 10 48	**110.92**	
	Postcentral	-56 -18 24	**27.06**	
	Precentral	-40 -5 49	**84.12**	
	Frontal_Inf_Tri	-40 30 10	**30.94**	
	Frontal_Inf_Oper	-48 7 17	**76.54**	
	Insula	-38 -4 14	**25.25**	

Only those clusters with an effect corrected with FWE criterium were considered as significant. x,y,z {mm}= Coordinates in MNI space of local maxima. F = F scores. No.Vox. = Number of voxels significantly activated inside the cluster belonging to each local maximum. T-test values are reported in bold if they are significant at the peak level after FWE correction. All local maxima were reported as MNI coordinates (Evans et al., 1993).

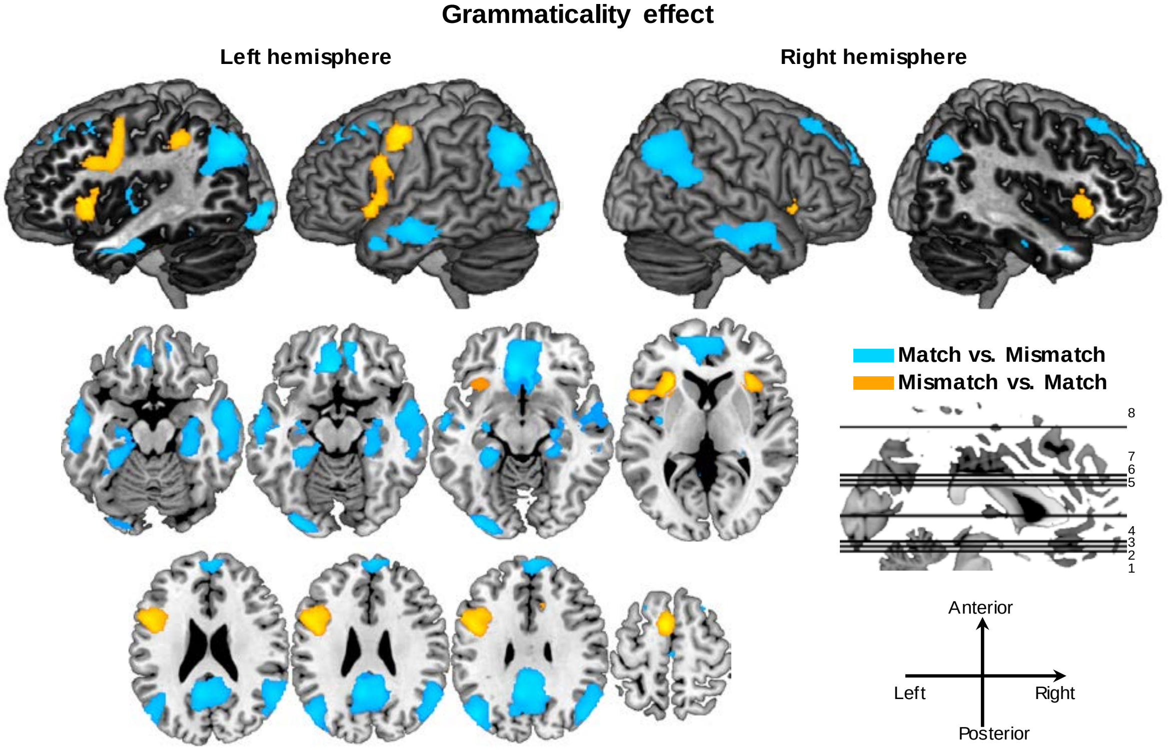


Figure 5.2. Statistical results emerging from the comparison between Mismatch and Match conditions (main effect of Agreement Pattern) were projected on the MNI single-subject T1 image (axial slices). All clusters depicted at p<0.001 corrected for multiple comparisons. Mismatch > Match is represented in yellow and Match > Mismatch is represented in blue.

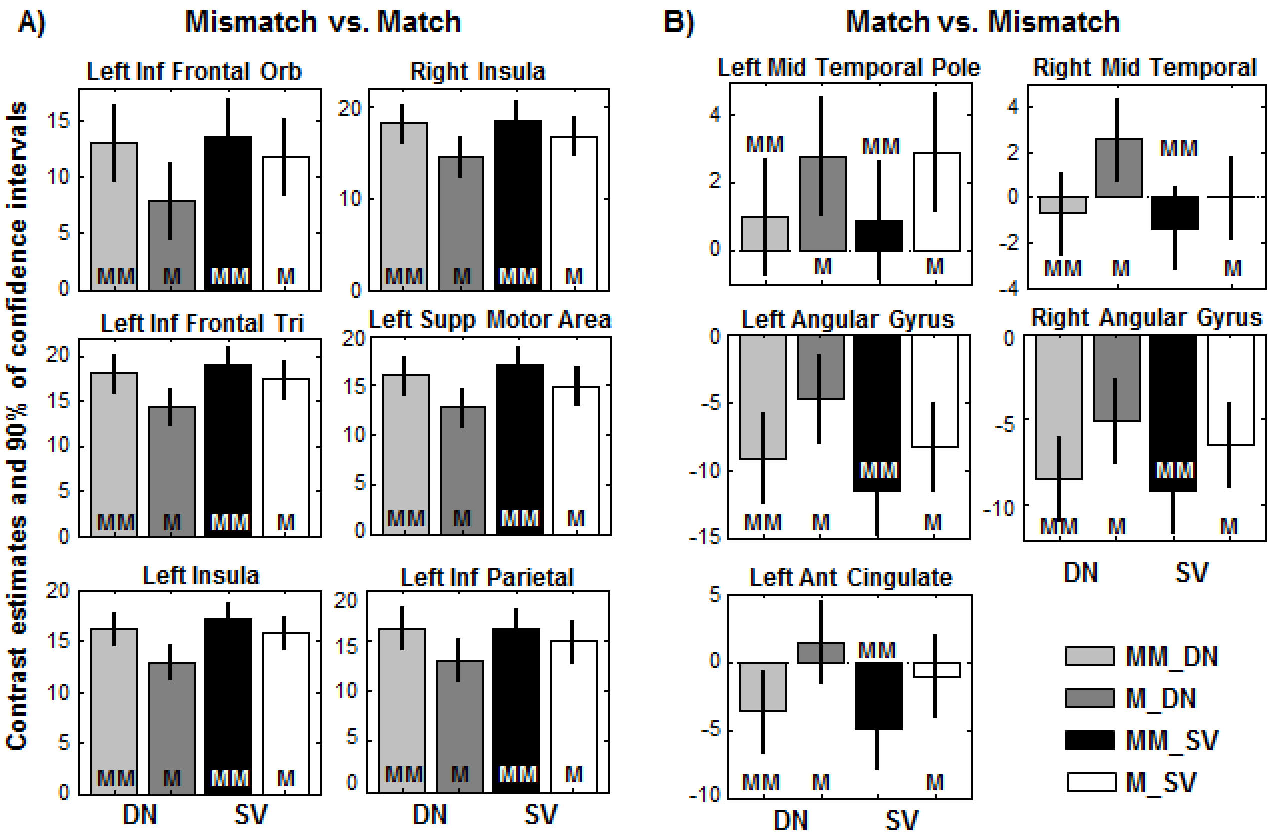


Figure 5.3. The bar graphs display the contrast estimates and 90% of confidence intervals at different maximum peaks representative of the significant activated clusters in the A) Mismatch > Match and B) Match > Mismatch contrasts. DN: Determiner-noun pairs; SV: Subject-verb pairs; M: Match; MM: Mismatch; Orb: Orbitalis; Tri: Triangularis; Mid: Middle; Inf: Inferior; Supp: Supplementary. 1: z = -17; 2: z = -14; 3: z = -11; 4: z = 5; 5: z = 24; 6: z = 27; 7: z = 30; 8: z = 60.

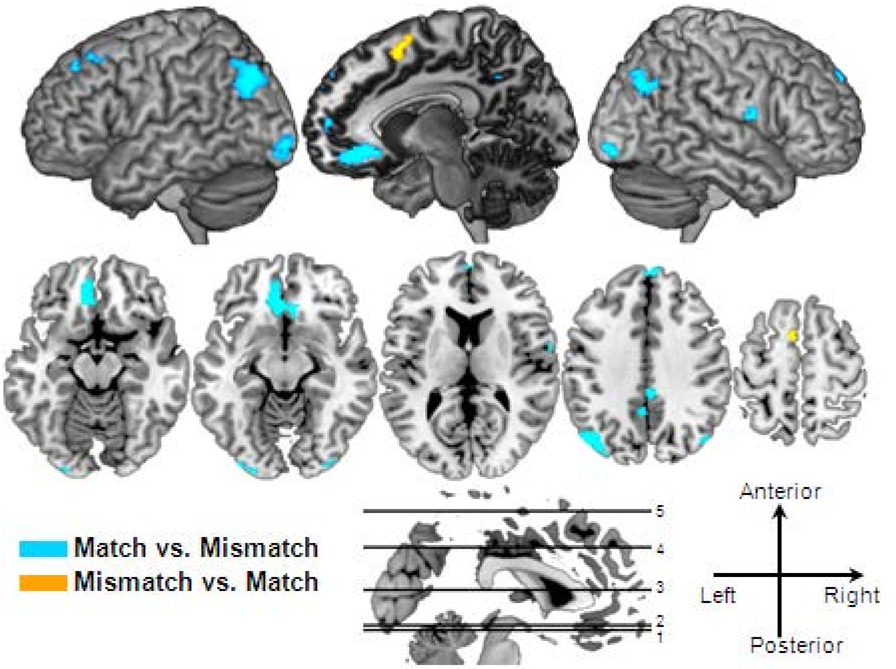
Table 5.3. Brain activation resulting from the main of Agreement Pattern (Mismatch > Match and Match < Mismatch) including both types of word pairs (Determiner-noun and Subject-verb).

Contrast	Region	x,y,z {mm}	Peak level	Cluster level
			T	No. Vox
Mismatch > Match	Insula_R	32 26 -2	**4.70**	338
	Putamen_R	28 20 4	3.37	
	Parietal_Inf_L	-36 -42 42	**4.11**	360
	Insula_L	-28 24 0	**5.42**	2172
	Frontal_Inf_Oper_L	-50 10 26	**4.48**	
	Frontal_Inf_Orb_L	-42 20 -4	4.07	
	Frontal_Inf_Tri_L	-40 14 28	3.93	
	Precentral_L	-46 -2 48	**4.83**	
	Supp_Motor_Area_L	-6 4 62	**5.16**	581
Match > Mismatch	Occipital_Inf_R	32 -92 -10	**5.24**	279
	Temporal_Mid_R	58 -12 -22	**4.85**	420
	Temporal_Pole_Mid_R	44 12 -30	3.94	
	Angular_R	46 -72 36	**4.73**	766
	Cingulum_Mid_R	2 -36 40	**5.78**	2473
	Precuneus_R	8 -52 38	**5.04**	
	Frontal_Med_Orb_R	6 28 -12	4.69	1355
	Cingulum_Ant_R	2 56 -4	3.86	
	Occipital_Mid_L	-26 -96 -4	**5.19**	218
	Lingual_L	-34 -90 -12	4.49	
	Precuneus_L	0 -52 36	**5.00**	
	Ant_Temporal_Mid_L	-60 -8 -16	**4.84**	183
	Ant_Temporal_Inf_L	-60 -20 -24	3.85	
	ParaHippocampal_L	-22 -18 -26	**5.03**	1227
	Angular_L	-44 -66 48	4.14	692
	Frontal_Sup_L	-24 38 46	**5.19**	363
	Frontal_Mid_L	-24 30 54	**4.71**	
	Rectus_L	-4 46 -18	4.26	1355
	Frontal_Med_Orb_L	-6 36 -12	**5.57**	
	Cingulum_Ant_L	-4 50 8	3.80	

Only those clusters with an effect corrected with FWE or FDR criteria were considered as significant and it was included in the table. x,y,z {mm}= Coordinates in MNI space of local maxima. T = T scores. No.Vox. = Number of voxels significantly activated inside the cluster belonging to each local maximum. T scores at the peak level are reported in bold if they are significant after FWE correction.

Box 5.1. Commonalities between nominal and verbal agreement processing.

Clusters resulting from the conjunction analysis



Statistical results derived from the conjunction analysis. Clusters identified as showing significant effects (i.e., p<0.001 corrected for multiple comparisons) were projected on the surface of the MNI single-subject T1 image. The two tails of this contrasts were explored independently (*Mismatch* > *Match* and *Match* > *Mismatch*). 1: z = -14; 2: z = -11; 3: z = 11; 4: z = 38; 5: z = 60.

Brain regions resulting from the conjunction null hypothesis (both tails of the contrast: Mismatch vs. Match & Mismatch vs. Match).

Contrast	Region	x,y,z {mm}	Peak level	Cluster level
			T	No. Vox
Mismatch > Match	Supp_Motor_Area_L	-8 12 52	3.12	24
Match > Mismatch	Occipital_Mid_L	-38 -76 40	3.63	78
	Occipital_Mid_L	-42 -76 36	3.52	
	Occipital_Mid_L	-26 -96 -4	3.49	57
	Occipital_Inf_L	-22 -98 -6	3.4	
	ParaHippocampal_L	-22 -18 -24	3.46	38
	Frontal_Sup_L	-24 38 46	3.38	45
	Rectus_L	-6 32 -14	3.62	57
	Frontal_Med_Orb_L	-4 28 -12	3.3	
	Frontal_Sup_Med_R	6 58 38	3.35	23
	Angular_R	48 -72 32	3.13	20
	Angular_R	52 -68 32	2.75	

Only those clusters with an effect corrected with FWE criteria were considered as significant and it was included in the table. x,y,z {mm}= Coordinates in MNI space of local maxima. T = T scores. No.Vox. = Number of voxels significantly activated inside the cluster belonging to each local maximum.

Table 5.4. Interaction between Type of Word Pairs (Determiner-Noun and Subject-Verb) and Agreement Pattern (Mismatch and Match).

Region	Interaction			Match vs. Mismatch in Determiner-Noun			Mismatch vs. Match in Determiner-Noun		
	x,y,z {mm}	T	No. Vox.	x,y,z {mm}	T	No. Vox.	x,y,z {mm}	T	No. Vox.
Frontal_Inf_Oper - Precentral (L)	-46 0 24	3.26	114				-48 6 30	**5.37**	114
Precuneus-Cuneus (L/R)	-8 -72 30	4.65	1409	14 -52 36	**5.69**	1373			
Temporal_Mid - Temporal_Sup (L)	-56 -6 -10	3.73	112	-58 -6 -14	**5.32**	112			

Only those clusters with a significant interaction effect ($p<0.001$ uncorrected) were resported. x,y,z {mm}= Coordinates in MNI space of local maxima. Vx = Number of voxels significantly activated inside the cluster belonging to each local maximum. T = T scores. T scores are reported in bold if they are significant at the peak level after FWE or FDR correction.

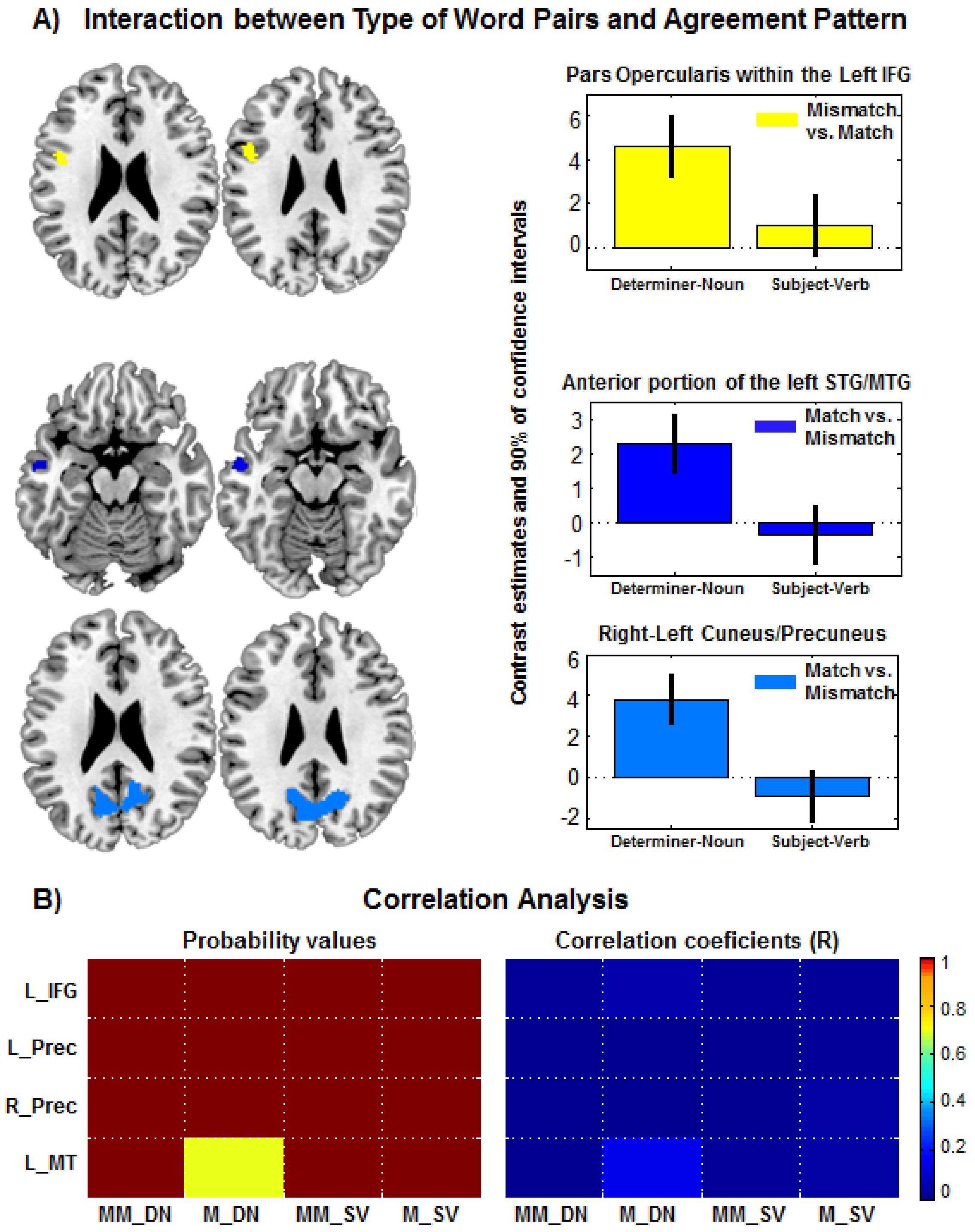


Figure 5.4. Significant clusters resulting from the interaction between the type of word pair and the type of agreement pattern were projected on the MNI single-subject T1 image. A)

The three significant clusters ($p<0.001$ corrected for multiple comparisons) were projected on the MNI single-subject T1 image (left side). The colours represent the tail of the interaction regarding the agreement pattern: Mismatch > Match (yellow) and Match > Mismatch (blue). The bar graphs (right side) display the contrast estimates and 90% of confidence intervals. B) Series of correlation analyses between the magnitudes of the neural response and the behavioural results for each condition. The left and the right panels represent the probability values and the correlation coefficients respectively. PS: Phrase structure; DN: Determiner-noun pairs; SV: Subject-verb pairs; M: Match; MM: Mismatch; L_IFG: Left inferior frontal gyrus; L_Prec: Left precuneus; R_Prec: Right precuneus; L_MTG: Left middle temporal gyrus.

In order to determine whether this interaction effect between the Type of Word Pair (Determiner-noun and *Subject-verb pairs*) and the Agreement Pattern (*Number Mismatch* and *Number Match*) are related to general attentional mechanisms associated to increases of the task difficulty for subject-verb agreement, we carried out two further analyses: 1) a series of correlation analyses and 2) a series of causal mediation analyses. The correlation analyses between the neural responses associated to each cluster exhibiting significant interaction effects and the corresponding behavioral effects were not significant ($p > 0.6$; $R^2 < 0.2$) either for RT and error rates (see Figure 5.4B).

In the case of the mediation analyses, both models (the mediator model and the response model) were tested for the three clusters (left inferior frontal, left temporal and precuneus-cuneus). These analyses allow us to identify the potential effect of the task difficulty over the causal pathway between the treatment [critical manipulation: *Mismatch vs. Match in Determiner-Noun pairs* and *Mismatch vs. Match in Subject-Verb pairs*] and the brain response [interaction effect at the neural response level]. The mediator model is represented by the semi-circle in the causal diagram (Box 5.2), where the causal effect of the treatment on the outcome is transmitted through an intermediate variable or a mediator [behavioral measures: RT or error rates]. The response model is represented by the triangle, where the behavioral measures and the critical manipulation act as predictors of the brain response. The effects of RT and error rates as mediator variables were estimated separately, represented by the black and the grey lines respectively. However, similar results emerged for the two analyses. The causal response effect between the treatment and the brain response outcome was significant for the three clusters. In contrast, no significant direct effect was found between the behavioral measures and the brain response outcome. Similarly, for the three clusters, the mediator model effects considering the RT as a mediator variable between treatment and neural response were not significant ($p > 0.05$). These results suggest that the interaction effect between the Type of Word Pair and the Agreement Pattern found at the neural level are not biased by the task difficulty.

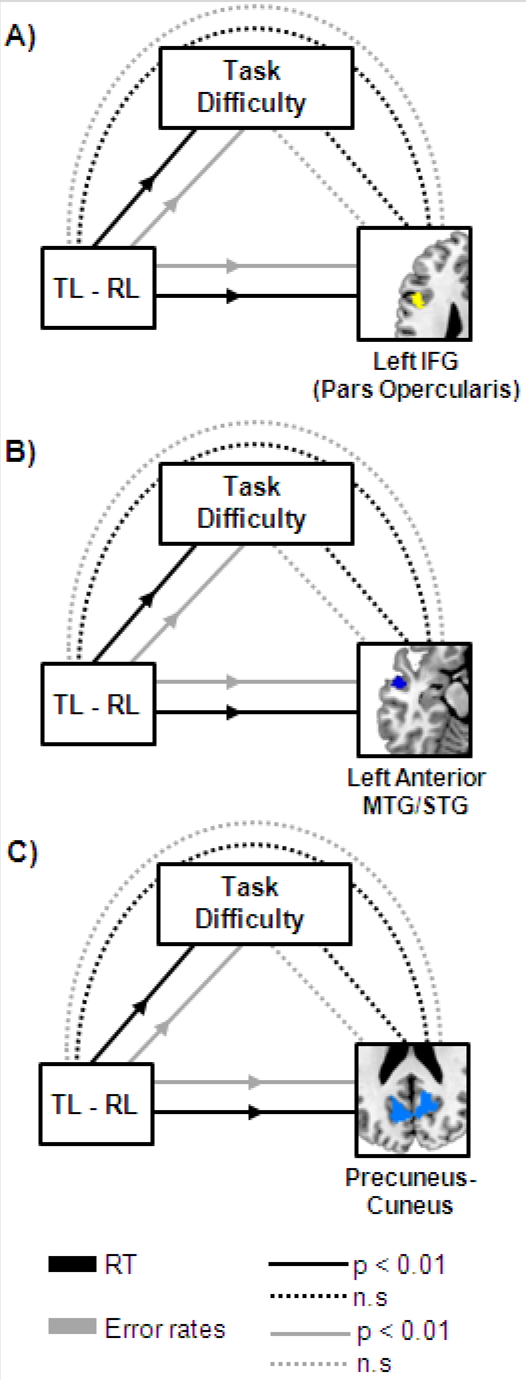
Box 5.2. Causal diagrams for the three regions exhibiting the interaction effects.

A) Causal diagram for the Pars Opercularis within the left inferior frontal gyrus.

B) Causal diagram for the anterior part of the left middle temporal gyrus.

C) Causal diagram for the precunues-cuneus.

For each region two causal models were tested (response model and mediator model). These models are represented in the same diagram: while the triangle represents the response model, the semi-circle represents the mediator model. Dotted lines represent those causal relations that not reach the predefined significance threshold and the solid arrows represent those with a p-value below 0.01 corrected for multiple comparisons. The grey color represents the estimations using the error rates as the mediator variable and the black color represents the estimations using the RT as the mediator variable.



5.4 Discussion

The main purpose of the current study was to investigate whether the neural substrates underlying number agreement processing in determiner-noun and subject-verb agreement differ as a function of the different syntactic domains and interpretive properties characterizing these two dependencies. The distinction between these two types of agreement patterns was measured using the differential response between correct grammatical and ungrammatical word pairs. It is important to stress that the experimental design and procedure adopted in this study, where the processing of nominal and verbal agreement configurations were included in the same experimental design, allowed us to characterize the neural network underlying number agreement operations. But more importantly, this procedure allowed us to distinguish between those common circuits that exhibited a similar pattern of activation across the two types of agreement construction (i.e., the main effect of Agreement Pattern and the conjunction analysis]) from those that showed a differential effect between them (i.e., the interaction between Agreement Pattern and Types of Word Pair).

Overall, the word pairs used in the current design produce the activation of a widespread left lateralized fronto-parieto-temporal network, similarly activated for both determiner-noun nominal and subject-verb agreement. In consonance with the previous two experiments (chapters 3 and 4), this fronto-parieto-temporal network included cortical and sub-cortical regions. This network includes cortical regions such as the left pars opercularis, triangularis and orbitalis within the IFG, as well as the anterior and posterior part of the left middle and superior temporal cortex [STG/MTG], the supramarginal cortex and the inferior and superior parietal gyrus, typically related to different stages of language processing. Interestingly, the word pairs used here elicited bilateral significant BOLD responses in sub-cortical regions, including areas such as the thalamus and the basal ganglia (putamen and pallidum). The comparison between these data and previous studies available in the agreement processing literature suggests that the presentation of nominal and subject-verb agreement word pairs elicits patterns of activation similar to those produced by the reading of these two types of agreement relations in larger sentential contexts (see Friederici, 2011 for a review; see also van Berkum et al., 1999).

Regarding the distinction between the neural regions that exhibited similar response patterns for both subject-verb agreement and determiner-noun concord, from those that showed different sensitivity for these two types of dependencies, a widespread fronto-parieto-temporal network emerges from the main effect of Agreement Pattern, independently of the Type of Word Pair[25]. This effect includes regions that exhibited higher activation for number mismatch than for number match and also regions that exhibited the opposite pattern, higher response for number match than for number mismatch. Interestingly, these significant neural responses capture the effects that were similarly present for both nominal and subject-verb agreement, and no effects were uniquely associated to only one of the two agreement relations (subject-verb and determiner-noun).

However, it is important to stress that although the processing of determiner-noun and subject-verb agreement drew upon largely overlapping neural circuits, some important differences were found. Significant interactions between the type of dependency and the agreement pattern emerged in a subset of those regions exhibiting the main effect: a) the left and right precuneus-cuneus, b) the left anterior part of the MTG-STG and c) the left pars opercularis within the IFG. These interactions were driven by different activation patterns between determiner-noun and subject-verb agreement both in the *match vs. mismatch* and in the *mismatch vs. match* contrasts. Critically, these interactions effects emerging at the neural level replicated the interaction effect found for the response times. In the following paragraphs we discuss how these main effects and interactions resulting from the current design fit with previous evidence concerning agreement processing, emphasizing the three

---

[25] In addition to the main effect we have estimated the conjunction analysis in order to establish those regions that equally responded to both types of constructions, nominal and subject-verb agreement. The conjunction null hypothesis was implemented in order to identify those regions significantly activated for two different contrasts (i.e., common regions), with no significant difference between the amplitude of the signal (Friston, 2005), testing in a very restrictive way the following alternatives: H0 = At least one effect present; H1= All effects present. This approach showed that whereas the left inferior and middle occipital cortex, the left parahippocampal gyrus, the left superior and superior medial frontal gyrus, the right medial orbitofrontal cortex and the right angular gyrus exhibited higher responses for number match than for number mismatch, only the left anterior and medial portion of SMA showed higher response for number mismatch than number match in both concord and subject-verb agreement.

different circuits where the interactions emerged (see Table 1S for an interim summary of the main results and a comparison across the experiments).

Table S1. Main Findings

	Behavioral results	**Neuro-anatomical results**	
		Grammaticality effects	**Effects related with the critical manipulation**
Experiment I (determiner-noun pairs)	**Main effect of Agreement Congruency**: Subjects classified determiner-noun pairs as grammatically correct more easily and accurately than incongruent pairs. This differentiation was evident for both transparent and opaque nouns. **Interaction effect**: Regarding RT, this effect was larger for opaque than for transparent nouns.	***Gender Mismatch* relative to *Gender Match***: the dorsal striatum, the middle and medial superior frontal gyrus, the medial orbito-frontal cortex, the pre- and post-central gyrus, as well as the anterior cingulate cortex. ***Gender Match* as compared to *Gender Mismatch*:** the pars opercularis and triangularis within the left IFG and the posterior part of the left MTG/STG.	Significant **interaction effects** between Gender Congruency and Gender-marking emerged in five left-lateralized clusters: ▪ Pars triangularis within the IFG ▪ Posterior part of the MTG/STG ▪ Hippocampus ▪ Angular Gyrus ▪ Supramarginal Gyrus
Experiment II	**Null effects** for RT and error rates.	***Gender Mismatch* relative to *Gender Match***: the pars triangularis, orbitalis and opercularis within the left IFG, the middle frontal gyrus, as well as the inferior parietal gyrus and the supramarginal and the angular gyri. ***Gender Match* as compared to *Gender Mismatch*:** the middle and medial superior frontal gyrus, the medial orbito-frontal cortex, the anterior cingulate cortex, as well as the anterior part of the left MTG/STG and the superior and middle temporal pole.	Significant **interaction effects** between Gender Congruency and Type of Gender emerged in two left-lateralized clusters: ▪ Inferior Parietal ▪ Angular Gyrus

Experiment III	**Main effect of Agreement Congruency**: Subjects classified word pairs as grammatically correct more easily and accurately than incongruent pairs. This Left angular gyrusdifferentiation was evident for both determiner-noun and subject-verb pairs. **Interaction effect**: Regarding RT, this effect was larger for determiner-noun pairs than for subject-verb pairs.	***Number Mismatch* relative to *Number Match***: the right and left insula, the pars orbitalis, opercularis and triangularis within the left IFG, the pre- and post-central gyrus, as well as the inferior parietal cortex. ***Number Match* as compared to *Number Mismatch**:* the middle and superior frontal gyrus, the anterior cingulate cortex, the medial orbito-frontal cortex, as well as the anterior part of the MTG/ITG.	Significant **interaction effects** between Number Congruency and Type of Word Pair emerged in three left-lateralized clusters: ▪ Left pars opercularis within the IFG ▪ Left anterior part of the MTG/STG ▪ Left and right precuneus/Cuneus
Experiment IV			
Experiment V			

Conflict-monitoring system. Firstly, a bilateral widespread network results from the contrast *Number Match > Number Mismatch,* including regions such as the anterior and middle cingulate cortex, the precuneus-cuneus, the dorsal part of the middle frontal gyrus and the angular gyrus. It is not surprising that different kinds of agreement dependency share this pattern of response. The increases in the activation of the dorsal part of the middle frontal gyrus often covaries with significant increases in the de-activation patterns of the anterior cingulate cortex (the hub of the conflict monitoring system, Carter & van Veen, 2007; Taylor et al., 2007) and the angular gyrus (the sub-region associated with the default mode network, (see Seghier et al., 2012 for a revision of this topic). The coupling between these regions probably reflects the engagement of conflict monitoring mechanisms and the subsequent re-analysis and repair processes triggered by the grammatical error detection, a common process taking place for both types of dependencies. As we extensively explained in Chapter 3, the involvement of this monitoring system in the processing of mismatches[26] is consistent with previous evidence (Bambini et al., 2011; Kerns et al., 2004; Kuperberg et al., 2003; Kuperberg, Sitnikova, et al., 2008; Lauro et al., 2008; Ni et al., 2000; Novick et al., 2005; van de Meerendonk et al., 2011; van de Meerendonk et al., 2009; van de Meerendonk et al., 2010; Ye & Zhou, 2009) and may subserve the generation of the P600 effect typically reported for this type of manipulations (Aron & Poldrack, 2006; Du et al., 2013; Mancini et al., 2011a, 2011b; Molinaro, Barber, et al., 2011; Olichney et al., 2010; Silva-Pereyra & Carreiras, 2007). This amodal monitoring system, probably working in parallel to the language-specific machinery, seems to be enhanced whenever an inconsistency is detected, independently of its nature, in order to prevent behavioral mistakes.

As mentioned above, in spite of these commonalities between determiner-noun and subject-verb number agreement processing, some important differences were also found in a particular node of this network. Specifically, a significant interaction between type of dependency and grammaticality emerged in the bilateral precuneus-cuneus. The differential

---

[26] These regions exhibited negative responses patterns (de-activation) compared to the fixation baseline condition, with greater de-activation for mismatching than matching constructions. Note that in the anterior cingulate cortex, one of the core regions of this monitoring system, no significant responses were found associated with the match conditions in both nominal and subject-verb agreement.

effect [difference between match and mismatch] found here at the neural level was higher for determiner-noun pairs than for subject-verb pairs. Importantly, the differential effect in this node for subject-verb dependencies did not reach the statistical threshold. Interestingly, the differential effect at the behavioral level was also higher for determiner-noun pairs than for subject-verb pairs, which could suggest a direct link between the interaction found in this parietal region and the behavioral results. However, when causal mediation analyses were performed to determine whether these interaction effects[27] were driven by the task related mechanisms, no significant relation was found between treatments and predictors.

In sum, the current set of data shows that general conflict-monitoring processes are at work in the computation of grammatical relations such as nominal and subject-verb agreement. However, in contrast with our hypothesis, they show that in spite of their general nature, such fundamental processes appear to be modulated by the type of grammatical relation, at least for the two agreement patterns considered in our experiment: determiner-noun concord and subject-verb agreement. This modulation could be related to general task-related mechanisms affecting the two types of dependencies in different ways. Recently, Zhang, S. and Li (2012) explored how the precuneus resting state connectivity pattern could explain the functional heterogeneity of this region. Using k-means algorithm, these authors corroborated the existence of three different functional sub-regions: dorsal-anterior, dorsal-posterior and ventral. Interestingly, the ventral sub-region, which contains the significant activation cluster found in the current study, showed positive connectivity with other regions resulting from the *Match* vs. *Mismatch* contrast, the orbito-frontal cortex, the rectus, the anterior, middle and posterior cingulate cortex and the angular gyrus, as well as some nuclei of the basal ganglia and the middle frontal gyrus. These authors extensively discuss the engagement of this ventral sub-region as part as the default mode network and its involvement in task related mechanisms. However, its specific role is still unknown. Further studies should aim to functionally characterize each node within this amodal network, establishing how this network interacts with language specific mechanisms.

---

[27] The mediation analyses were performed for the three clusters where the interaction effect emerged between the type of dependency and the agreement pattern, but no significant mediation effects were found.

Anterior part of the left middle temporal gyrus. In addition to this monitoring system, we found increase of activation in the anterior portions of the left MTG-STG extended to the middle and superior temporal pole, for number match in both agreement dependencies. The posterior portion of this region and the adjacent areas corresponding to the posterior part of the left MTG-STG exhibited similar responses for the four conditions included in the present design (the 2 *Agreement Pattern* and the 2 *Types of Word Pairs*). Critically, in line with our hypothesis, in addition to the main effect presented in the anterior part of the left MTG-STG, we also found a significant interaction effect between the type of dependency (determiner-noun concord and subject-verb agreement) and the type of agreement pattern (match and mismatch) in the same region. This interaction was restricted to the anterior portion of the left MTG-STG, whereas no significant interaction was found in the middle and superior temporal pole. This interaction was driven by different activation patterns between nominal and subject-verb agreement in the *Match* > *Mismatch* contrast: while the differential activation for subject-verb pairs in the *Match* > *Mismatch* contrast did not reach the statistical threshold, this differential activation was very strong in the determiner-noun pair.

Summarizing the response pattern in the left temporal area, a posterior to anterior functional gradient emerged from our results: a) the posterior portion of the left MTG-STG did not (Hagoort, 2003a) distinguish between determiner-noun and subject-verb dependencies or even between incongruent and congruent trials; b) the anterior part of the left MTG-STG distinguished between determiner-noun and subject-verb dependencies, showing significant differential [differences between *Match* and *Mismatch* conditions] response only for determiner-noun pairs and c) the left middle and superior temporal pole exhibited greater responses for congruent than incongruent trials independently of the type of dependency. This pattern of activation in the left temporal cortex is in line with previous evidence showing that the involvement of this region seems to be extended to different domains of language processing (Baldo et al., 2012; Binder et al., 2011; Visser et al., 2012; Visser & Lambon Ralph, 2011; Wei et al., 2012). Previous evidence supports a posterior- to-anterior functional gradient within this anatomical region, proposing a distinction between syntactic and semantic processes (Friederici, 2011, 2012; Pallier et al., 2011).

However, as detailed in the Introduction, the specific role of each functional sub-region is still under dispute (see Friederici, 2011 for a revision of this topic). The inclusion of both nominal and subject-verb agreement in the same experimental design has allowed us to gain valuable insights into this debate. The processing of these two different types of dependencies implies the detection of local relations among constituents to construct syntactic structures (i.e., syntactic building processing). This process implies the retrieval of lexical and morpho-syntactic information from the elements forming both types of dependencies. Despite the difference in the nature of these two types of information, our results point to the posterior part of the MTG-STG as the major candidate to mediate these common operations, as no differential response emerged in this region from the mismatch vs. match contrast. This idea is consistent with previous results (Acheson & Hagoort, 2013; Baggio & Hagoort, 2011; Hagoort, 2003a) and corroborates the claim advanced by Hagoort (2003a) in the MUC model of sentence processing about the critical role of the left posterior temporal cortex during the storage and retrieval of lexico-syntactic information.

Subsequently, this lexical and morpho-syntactic information is sent to the anterior part of the MTG-STG, where plausible syntactic units are formed by means of a looping operation that takes incoming material and merges it with previously analyzed stimuli incrementally. Importantly, this recursive operation equally applies to subject-verb and determiner-noun patterns, but different outcomes are generated depending on the grammaticality of the patterns (see Figure 3, middle panel). While the building of noun-verb pairs produces a similar response whether the two constituents match in number or not, the construction of a determiner-noun relation does not, with the mismatching pair generating a significant reduction in the response pattern of this region, leading to the observed interaction between Type of Word Pairs and Agreement Pattern. A possible explanation for this difference between the two types of agreement resides in the nature of these two relations. As pointed out in the Introduction, given the essentially syntactic nature of determiner-noun relations, the reading of a number mismatch in such a configuration can block subsequent analysis steps, preventing this pair from receiving an interpretation. In contrast, the reading of a number mismatch within a subject-verb configuration yields an equivalent activation pattern compared to a matching pair, suggesting that a dependency can be successfully built regardless of the mismatch.

The engagement of this anterior temporal region in the building of the syntactic structure underlying a linguistic input is consistent with previous ERP and neuro-anatomical findings. In their ERP study, Barber and Carreiras (2005) investigated the processing of determiner-noun agreement patterns both in isolated word pairs and in sentential contexts and showed that the electrophysiological response to a number violation could be modulated by the presence (or absence) of a richer linguistic context. Specifically, when embedded in a sentential context, determiner-noun number anomalies engendered the classical biphasic LAN/P600 pattern. In contrast, when presented in isolation, determiner-noun number anomalies generated a composite LAN/N400/P600 pattern. While LAN effects can be attributed to the detection of a number mismatch between the two elements, regardless of the linguistic context in which they are presented, the presence of N400 effects for isolated presentation only was associated by the authors to difficulties in integrating the lexical and conceptual features of the words. It is therefore possible that the anterior portion of the MTG-STG contributes to the generation of the N400 effect associated with the processing of number anomalies between determiner and noun in isolated word pairs, although this hypothesis requires further evidence (see Lau et al., 2008 for a revision of the N400 generators). Moreover, Brennan et al. (2012) recently demonstrated anterior temporal lobe involvement (including portions of the MTG and STG) in syntactic structure building. These authors reported a positive correlation between the anterior temporal response and the amount of syntactic nodes needed to integrate each word into the input being processed during the passive listening of a story fragment (see Methods in Brennan et al., 2012).

After this syntactic building process, the system seems to recognize that while the grammatical word pairs for both types of dependencies can be further mapped to a congruent semantic representation, the number violation included in the mismatch conditions blocks such mapping process. These processes seem to be working in both nominal and subject-verb agreement. In the case of a noun-phrase structure this process implies matching a noun with its real-world referent, without building any thematic representation, whereas the processing of a subject-verb structure implies the projection of a complex representation in which the subject noun is associated to a specific role in the event being described. Despite this difference, the two dependencies did not differ in terms of differential activation found in the left middle and superior temporal pole, suggesting an equivalent processing disruption.

It is worth noticing that the posterior to anterior functional gradient within the left temporal cortex that we report here points to the involvement of this region in multiple domains of linguistic processing. More specifically, our results suggest that it is not possible to distinguish between a syntactic and a semantic specialization of this region, since the patterns of activation found in this area can be related to several processes, including retrieval of morpho-syntactic and lexical information from the input, as well as structure building and form-to-meaning mapping mechanisms. Evidence consistent with this multi-functional hypothesis has been recently reported by (see the Methods section in Brennan et al., 2012; and Pallier et al., 2011) , who observed a functional distinction within the temporal lobe during sentence processing. Specifically, while posterior temporal areas demonstrated similar correlation patterns between normal prose and jabberwocky sentences, the temporal pole evidenced sensitivity only to complete (or nearly complete) sentences in normal prose stimuli but not in jabberwocky ones. The authors therefore took these data as suggestive of the key role that the temporal pole may be playing in linking form to meaning during sentence processing (see also Brennan et al., 2012). Moreover, Turken and Dronkers (2011) using anatomical and functional connectivity, demonstrated that these different regions within the temporal lobe are part of an interconnected network which also comprises frontal and parietal areas (see also Griffiths et al., 2012). More recently, Molinaro et al. (2013), compared magneto-encephalographic responses associated with determiner-noun matching and mismatching patterns, including both gender and number agreement violations. These authors found a left temporal response between 200 and 400 ms with some functional differences emerging at different time intervals. While posterior temporal regions were activated around 220 ms, the response of the left temporal pole (the more anterior part of the left temporal cortex) was elicited around 400 ms after the stimulus onset (Molinaro et al., 2013). Further studies combining the high temporal resolution of the magneto-encephalographic recording and the high spatial resolution of the fMRI techniques would be the keystone to corroborate this theory and reconcile the contradictory evidence about the role of the temporal regions during phrase and sentence comprehension.

Left inferior frontal gyrus. A left lateralized fronto-parietal network emerges from the contrast *Number Mismatch > Number Match* independently of the type of dependency. This network includes regions such as the LIFG [pars triangularis, orbitalis and opercularis], the left insula and the left inferior parietal cortex. However, in spite of this main effect, we also found a significant interaction between the type of dependency (determiner-noun concord and subject-verb agreement) and the type of agreement pattern (match and mismatch) in the pars opercularis within the LIFG including the frontal operculum, a critical node of this network.

Regarding the main effect, there are two different explanations for this common activation. First, from a language-specific perspective, the large differential activation in the LIFG resulting from the *Mismatch vs. Match* contrast for both nominal and subject-verb agreement is consistent with evidence that points to the critical role of this region in the processing of different language-relevant information. For instance, while the pars opercularis, within the IFG appears to underlie syntactic processes, the pars triangularis and orbitalis seem to be involved in the processing of semantic-related information (see Friederici, 2011 for a revision of this topic; 2012). More specifically, activation of the left pars opercularis and the frontal operculum have been consistently reported in the presence of phrase structure violations and have therefore been linked to different stages of syntactic processing such as phrase structure building (Friederici, 2012; Grodzinsky & Friederici, 2006) and/or syntactic complexity processing (see Grodzinsky, 2000 for a syntactic movement manipulation).

Second, from a more domain-general perspective, it may be that the left inferior frontal response reflects the involvement of cognitive control functions (see Novick et al., 2005 for a discussion about the role of the LIFG in cognitive control), probably engaged when the system is confronted with conflicting cues such as the ones we are considering here (i.e., determiner-noun and subject-verb number agreement violations). In line with this hypothesis, the inferior frontal cortex, including the anterior insula, has been related to cognitive mechanisms shared by different types of tasks, language-specific or not, such as response inhibition, task switching and attentional interference control (Aron et al., 2003; Aron & Poldrack, 2006; 2004; Levy, B. J. & Wagner, 2011; Michael et al., 2006; see also Wager & Barrett, 2004; Wager et al., 2007; 2005). In this respect, the coupling found here between the left inferior frontal and inferior parietal regions may also be considered as a key piece of evidence sustaining this idea. The modulation of the parietal cortex activation by attention mechanisms has been previously demonstrated (see Corbetta & Shulman, 2002 for a review about the role of the parietal regions as part as the attentional network; and also see Ravizza et al., 2004).

Based on this second hypothesis, it is plausible to expect a parallelism between the predominant activation of this left fronto-parietal network for the mismatch condition and the behavioral results. Interestingly, the behavioral data showed that the mismatch conditions, for both nominal and subject-verb agreement, were more difficult to detect compared to their correct counterpart. However, following this perspective we would also expect a distinction between nominal and subject-verb agreement in some of these regions, based on the interaction found at the behavioral level. In addition to the main effect of agreement pattern found for the RT and the error rates, our results show that readers are more accurate and need less time to evaluate the well-formedness of a concord dependency, compared to a relation that is built on a more complex syntactic structure that encompasses different levels of analysis, such as subject-verb agreement. A closer look at the RT pattern shows that the processing penalty generated by the evaluation of a determiner-noun number mismatch (relative to its match counterpart) is significantly greater than the cost generated by the evaluation of a subject-verb number anomaly (207 ms vs. 125 ms, respectively). As the interaction in the pars opercularis within the LIFG reflects, the impossibility of constructing a reliable phrase structure in the concord violation pairs could block subsequent interpretative steps, making the evaluation of the ungrammaticality of the pattern difficult and leading to a greater difference between mismatch and match for determiner-noun pairs than for subject-verb agreement[28].

In line with this idea, Molinaro et al. (2013) distinguished between two different stages related to the processing of number agreement relations: an earlier stage starting around 220 ms involving left anterior temporal regions, and a later stage starting around 300 ms involving the pars opercularis within the inferior frontal cortex. These authors suggested that the left temporal activity would reflect initial compositional operations, whereas the subsequent left inferior frontal response would be involved in more general and high-level mechanism related with task resolution. This interpretation is also compatible with a recent proposal by Bornkessel-Schlesewsky & Schlesewsky (2013), according to which, activation in these left inferior frontal areas would reflect the involvement of more general top-down processes that link linguistic processing to behavior, such as in the evaluation of the grammaticality of a sentence.

It is feasible to find a merger between the involvement of the pars opercularis/frontal operculum, within the LIFG, during the processing of local structural dependencies (Friederici et al., 2006); and its role coordinating syntactic operations in a more controlled mode (see Bornkessel-Schlesewsky & Schlesewsky, 2013 for an in-depth discussion; and see also Friederici, 2011). Recent evidence has demonstrated that within the LIFG two functional sub-regions coexist (Fedorenko, Nieto-Castanon, et al., 2012; Fedorenko et al., 2013), one specifically engaged in language processing (e.g., sentence processing) and another that is recruited by different domain-general mechanisms (e.g., arithmetic, spatial and verbal working memory and cognitive control). This evidence could reconcile the two contradictory points of view about the role of the LIFG, suggesting that this region could be the junction between a language specific system and an amodal control monitoring system.

---

[28] The difference between concord and subject-verb agreement pairs that we found in this study, and the interpretation that we give to it, seem to be supported also by language acquisition data showing that Spanish speaking children tend to learn determiner-noun pairs such as “el anillo” as single items, that is including the determiner in the lexical representation of the noun (Demuth, 2007). Under this account, a number violation such as “*los anillo*” would not be considered entirely syntactic, but also lexical in nature. This would account for the greater differential activation found for concord pairs in left inferior frontal and temporo-parietal areas. While we found this alternative interpretation appealing and relevant for the purposes of our study, we believe that a broader discussion of this issue would be beyond the scope of the current study.

Interim conclusions. In sum, the data discussed here show that two different but closely related systems seem to be working in parallel during the processing of nominal and subject-verb agreement: a) a bilateral fronto-parietal monitoring system not language specific and b) a left fronto-temporal system that seems to be specifically related to different aspects of phrase and sentence processing (see Figure 4). Consistently with existing neuro-cognitive models of sentence comprehension (Bornkessel-Schlesewsky & Schlesewsky, 2013; Friederici, 2011, 2012; Hagoort, 2005, 2013, 2014; Hagoort & Indefrey, 2014), the experimental evidence reported in the current study pointed out the crucial role of the left frontal and temporal regions in the establishment of relations among words. Critically, however, the comparison between verbal and nominal agreement allowed us to isolate neural substrates supporting the operations involved in agreement comprehension, which have not been described in previous models. Our data show that the processing of verbal and nominal agreement relies on common mechanisms, as shown by the overlapping brain activation networks. However, at the same time, brain activation in some critical areas is modulated by the specific type of agreement. These differential strengths of activation may be accounted for by some specific linguistic differences between them. The major difference between these two dependencies was found in the anterior portion of the left MTG-STG, which we relate to syntactic-combinatorial building mechanisms apparently controlled by the pars opercularis within the LIFG. In contrast, lexical and morpho-syntactic information, represented in the posterior portion of the left MTG-STG, seems to feed into this syntactic building machinery, with no difference between subject-verb and nominal agreement. The subsequent form-to-meaning mapping processes take place in the most anterior part of the left temporal cortex, corresponding with the middle and superior temporal pole. In contrast to the proposal by Bornkessel-Schlesewsky & Schlesewsky (2013), we do not find the involvement of parietal regions in the processing of these two types of relations (but see Results section in Chapter 4 and 7). Further investigation is needed to shed light onto the functional role of parietal regions in sentence comprehension.

Overall, the current findings demonstrate that the coupling between the frontal and temporal regions typically supporting language processing is flexible enough to show sensitivity to the fine-grained combinatorial mechanisms that underlie nominal and subject-verb agreement. Crucially, this property represents an aspect of language processing that needs to be taken into account in the elaboration of a comprehensive neuro-cognitive framework. So far, none of the current neuro-cognitive models can account for the current set of results; determiner noun and subject-verb agreement recruit the same brain circuits, but with some functional specificities depending on the type of dependency involved.

Chapter 6.

Experiment IV

“Who does what”: Left anterior temporal involvement for verbal agreement processing.

Chapters 3 and 4 examined the neural substrates of nominal agreement, trying to disentangle the contribution of formal and conceptual factors during the establishment of local grammatical relations. These two chapters provided significant insights into this topic, pointing out the critical contribution of different frontal, temporal and parietal regions during agreement comprehension. In addition, Chapter 5 provided empirical evidence for the brain’s sensitivity to the type of dependency involved in an agreement relation, and highlighted the similarities and differences between subject-verb and determiner-noun dependencies.

The next two chapters will focus on the study of subject-verb agreement relations. As mentioned above, subject-verb agreement plays a crucial role in the multifaceted process of language comprehension because it indicates “who does what” in the sentence. Critically, doing this requires careful unpacking of the linguistic input so that information about participants and their role in discourse is extracted from morpho-syntactic cues (Mancini et al., 2013a, 2013b). For this reason, in Chapter 6 and 7 we will investigate the subject-verb agreement phenomenon in a more complex sentence context. Specifically, in the current chapter (Chapter 6) we will [1]evaluate whether two different morpho-syntactic features such as person and number differ as a function of its interpretive properties and more importantly we will [2]establish where this difference, if it is indeed found, is mapped in the brain. In this study we will directly contrast grammatical sentences with sentences containing subject-verb person and number agreement mismatches.

6.1 Overview

As has already been pointed out throughout this thesis, the dissociation between form and meaning (cf. Hagoort, 2005) has taken center stage in the neuro-cognitive literature on sentence comprehension. However, the neuro-cognitive mechanisms through which form and meaning are linked during agreement processing have received far less attention. The vast majority of studies exploring this phenomenon have treated form-to-meaning mapping as an issue essentially limited to case and thematic role assignment (Bornkessel & Schlesewsky, 2006). This has led to potentially neglect and obscure finer-grained interpretive mechanisms that can be of great relevance for the characterization of agreement processing mechanisms in the brain. Critically, here we will investigate agreement between subject and verb by comparing person and number anomalies, a paradigm that has proved to be effective to highlight behavioral and electrophysiological differences in the elaboration of different aspects of agreement interpretation (Mancini et al., 2011a; Mancini et al., 2014). But why will we explore this phenomenon through the comparison between different types of morpho-syntactic features? Feature-specific mechanisms for the extraction and the mapping of the morpho-syntactic information onto higher-level semantic-discourse representations are not considered in the neuro-cognitive models of sentence processing described above (see Chapter 1, *Neuro-cognitive models of sentence processing*), despite the relevance of such mechanisms for an in-depth functional characterization of the language network (but see Carreiras et al., 2010; Molinaro et al., 2013 for a comparison between number and gender). Moreover, which neural mechanisms each unit supports is still an open question, since across models substantial differences are found concerning the brain regions recruited during agreement processing, as reviewed below. Crucially, in this study, we seek to fill this gap by uncovering the neuro-anatomical substrates involved in the construction of person and number representations.

Different theoretical linguistic frameworks suggest that form-to-meaning mapping should not be regarded as a monolithic operation, but as a composite process through which the structural relation identified in the input and the information extracted from a single morpheme in the verb (e.g., *"–amos"*, in *celebramos* [we celebrate]) is interfaced separately with *cardinality* and *discourse role* representations (see Chapter 1, *Agreement features*). Theoretical analyses lend support to this view and describe the qualitatively different types of form-to-meaning mapping that underlies person and number interpretation. In particular, the intrinsically different information conveyed by the two features (person and number) determines their autonomous representation in the hierarchical syntactic tree, which in turn determines qualitatively distinct connections with higher-level representations where spatial, temporal and participant coordinates are encoded (Bianchi, 2006; Mancini et al., 2013a, 2013b; Sigurdsson, 2004). Because of its direct link to discourse, person is claimed to occupy a higher node in syntactic structure compared to number (Bianchi, 2006; Mancini et al., 2013a, 2013b; Shlonsky, 1989; Sigurdsson, 2004). This link has clear interpretive relevance, as it makes it possible to associate each morphological realization of person (1st, 2nd or 3rd) with a specific participant (speaker, addressee, non-participant), leading to the assignment of a discourse role. In contrast, no such linking to discourse is required for number: the number information extracted from verb is mapped onto the cardinality representation invoked by the subject argument (Chomsky, 1995, 2000), independently from the discourse role of this argument (Mancini et al., 2013a, 2013b; Mancini et al., 2014).

In line with this hypothesis, recent experimental studies have showed that the same formal relation – subject-verb agreement – can yield distinct behavioral and electrophysiological responses as a function of the feature involved (see Molinaro, Barber, et al., 2011 for a review). A self-paced reading study in Italian (Mancini et al., 2014) evidenced significantly higher reading times for person violations compared to number violations, a finding that can be accounted for by taking into account the different structural and interpretive properties that characterize the two features. Nonetheless, despite these differences, person and number have something in common: during the processing of an agreement relation, the parser checks the consistency of subject and verb morpho-syntactic values. Thus, the two types of agreement undergo similar feature-checking mechanisms. This hypothesis is confirmed by an ERP study in Spanish (Mancini et al., 2011a), which reported both similar and different electrophysiological patterns for person and number-anomalous sentences. In both cases, a similar positive deflection was found about 600 milliseconds post-stimulus onset (P600) when comparing anomalous sentences with their grammatical counterpart. However, the early components exhibited qualitative differences between the two types of anomalies: while person violations gave rise to N400 effects, number agreement anomalies elicited a LAN effect. Importantly, the authors pointed out that the negative effect elicited by person anomalies could be the result of a superimposition of LAN and N400 effects, as suggested by the failure to find a difference between the two violations in frontal scalp areas in the 300-500 ms window, and by the similar latency and onset of the two topographically different negativities. While the similar left-anterior negative effect would evidence the presence of shared feature-checking mechanisms, the different posterior negative effect can be taken to reflect the different mapping procedures that the interpretation of the two features requires, i.e. the different higher-order representations to which morpho-syntactic values are mapped.

From a language architecture perspective, the findings described above seem to point to a language processing system that a) functionally dissociates checking and interpretation; and b) employs feature-based mapping procedures to assign an interpretation to the agreement dependency (see Bianchi, 2006; Sigurdsson, 2004, 2009). A testing ground for this hypothesis is to investigate whether person and number agreement recruit different and/or overlapping neural regions, as a result of the similar checking and different mapping mechanisms they undergo during processing. To test this goal in the current fMRI experiment person and number processing will be directly contrasted using a grammaticality judgment task. By contrasting correct agreement with both person and number violations, we aim to identify the neural network involved in the building and interpretation of agreement dependencies. The results derived from the previous experimental chapters point to cortical areas that are part of the language network, such as the LIFG and the MTG, as primarily involved in the agreement comprehension processes. Within this network, the finding of differential responses for person and number violations would provide evidence for the presence of feature-specific mechanisms at work in the building and interpretation of a sentential relation, in line with theoretical analyses that posit distinct structural and interpretive requirements for person and number features (Bianchi, 2006; Mancini et al., 2013a, 2013b; Sigurdsson, 2004, 2009). Based on this, one could expect to find a dissociation 1) in areas that are thought to support the extraction of morpho-syntactic information to build syntactic structure (Hagoort, 2005; Pallier et al., 2011) and 2) in areas supporting the mapping between morpho-syntactic and semantic-discourse information, whereby person is linked to discourse roles and number to cardinality representations.

In the former case, we expect a difference between person and number to emerge in quantitative terms, because of the additional syntactic structure to be projected at the discourse level to represent person information. The projection of this additional node for person could arguably generate greater cognitive costs compared to number, and so greater activation in the posterior portion of the MTG/STS (Hagoort, 2005; Lau et al., 2008; Pallier et al., 2011). As for mapping mechanisms, a qualitative difference could arise between person and number. While the interpretation of person requires discourse roles to be assigned, the interpretation of number does not. Hence, differential patterns of activation could be expected in areas that have been associated with the computation of the propositional meaning of a sentence, such as the aMTG/STG (Bornkessel-Schlesewsky & Schlesewsky, 2013; Lau et al., 2013; Lau et al., 2008) and the pars triangularis/orbitalis of the IFG (Friederici, 2011).

The contrast between the two violations and correct sentences will permit the identification of the neural substrates involved in the checking of feature consistency between subject and verb. Based on the ERP results reported by Mancini et al. (2011a), the reading of anomalous subject-verb relations (regardless of the feature manipulated) could engage areas associated with the detection of morpho-syntactic mismatches. As the previous chapters suggest, the left middle frontal gyrus could be a potential candidate for the feature-checking operations. If person and number agreement share similar feature-checking mechanisms, the superimposition of the *Person Agreement Violations* > *Standard Agreement* and the *Number Agreement Violation* > *Standard Agreement* contrasts should evidence common response patterns in this frontal area.

Similarly, the attentive mechanisms involved in the monitoring of the match between the expected and the perceived linguistic event in both person and number violations should lead to the recruitment of conflict-monitoring areas, including the dorso-lateral pre-frontal cortex and the anterior cingulate cortex. Previous work on the processing of agreement and other morpho-syntactic dependencies has consistently demonstrated the involvement of this network as a result of a (task-driven) mismatch detection process (and see also Kuperberg et al., 2003; Kuperberg, Sitnikova, et al., 2008; Newman et al., 2003; Ni et al., 2000; Nieuwland et al., 2012; van de Meerendonk et al., 2009 for a review).

6.2 Materials and Methods

Participants. A total of twenty one healthy volunteers (nine females and twelve males), with ages ranging from 17 to 35 years (mean = 22.62, standard deviation = 4.43), gave written informed consent to participate in this study.

Stimuli and experimental procedure. The experimental material consisted of 120 sentences divided into three experimental conditions (in the proportion of 1:1:1), as illustrated in (15), (16) and (17) below. All sentences contained a lexical subject followed by a past tense verb (the critical word), which was always followed by at least two words. The *Standard Agreement* condition presented a plural subject, while the *Number Agreement Violation* and the *Person Agreement Violation* conditions both contained a singular subject. The *Number Agreement Violation* condition was followed by a plural verb, while the *Person Agreement Violation* condition was followed by second person singular verb. However, the length of the critical word was balanced across the three experimental conditions: *Standard Agreement*: mean length = 9.66, SD = 2.5; *Person Agreement Violation*: mean = 9.38, SD = 2.34; *Number Agreement Violation*: mean = 9.66, SD = 2.34. Planned statistical comparisons showed no differences across conditions. In order to maintain the same number of acceptable and unacceptable sentences across the whole set of materials and avoid expectations concerning the morphological form of the verb, 120 filler sentences with a similar sentence structure, but including different types of feature syntactic mismatches, were added to the experimental sentences so that half of the sentences were grammatically correct and the other half incorrect. In addition, half of the sentences had plural subjects and the other half singular subjects. The experimental material was randomly assigned to three different lists according to a Latin Square design, so that each subject could see only one version of the same sentence.

(15) *Person Agreement Violation*

*[29]El turista llevaste un sombrero muy grande.
The tourist wore a very big hat.
The tourists$_{3.sg}$ wore$_{2.sg}$ a hat very big.

(16) *Number Agreement Violation*

*El turista llevaron un sombrero muy grande.
The tourist wore a very big hat.
The tourists$_{3.sg}$ wore$_{3.pl}$ a hat very big.

(17) *Standard Agreement*

Los turistas llevaron un sombrero muy grande.
The tourist wore a very big hat.
The tourists$_{3.pl}$ wore$_{3.pl}$ a hat very big.

Participants were tested individually in a silent room. They were seated in front of a computer monitor, on which sentences were visually presented word by word. Words were displayed in white letters on a dark background. Each word was presented for 500 ms, followed by a 300 ms blank screen. Sentence order was randomized and, after each sentence, participants were asked to evaluate its acceptability by pressing the relative YES/NO button on a response pad.

Image acquisition. Experiment was performed on the same scanner and coil used in the previous experiments. Two functional event-related scan consisted of 625 echoplanar images were acquired using a T2*-weighted gradient-echo pulse sequence with the

---

[29] *The asterisk indicates a grammatical violation

parameters detailed in Appendix 2D. In the structural session, a MPRAGE T1-weighted structural image was acquired with the parameters described in Experiment I.

Functional data analysis. Data processing and statistical analysis per subject were performed following the same procedure used in Experiment 1. A pair-wise contrast comparing activity to each phrase type relative to every other phrase type was performed. Resulting contrast images were then entered into a second level design analysis to enable population inferences. Additionally, contrast images for each of the three experimental conditions (*Person Agreement Violations, Number Agreement Violations* and *Standard Agreement*) compared to the fixation baseline were submitted into a second level One Way ANOVA. This analysis allows us to determine whether differences between experimental conditions were due to activation or deactivation with respect to the fixation baseline condition. Population-level inferences were tested using a threshold of $p < 0.001$ uncorrected with a voxel extent higher than 100 such that only those peaks or clusters with a p-value corrected for multiple comparisons with family wise error (FWE; Nichols & Hayasaka, 2003) and/or false discovery rate (FDR; Genovese et al., 2002) were consider as significant. All local maxima were reported in the results tables as MNI coordinates (Evans et al., 1993).

6.3 Results

Behavioural results. Percentage of correct response (Hits) and mean reaction times (RT) for *Standard Agreement*, *Number Agreement Violation* and *Person Agreement Violation* are presented in Table 6.1, with the corresponding standard error between parentheses. One way ANOVA with the accuracy of the three conditions (*Standard Agreement*, *Number Agreement Violation* and *Person Agreement Violation*) as factor was performed. For all experimental conditions percentage of correct responses was above 90 % and the ANOVA showed no significant difference among the three conditions ($F(1, 20) = 0.14$, $p = 0.98$, $\varepsilon = 0.\ 83$), indicating that the participants properly judged the sentences as acceptable or not independently of its grammaticality.

Additionally, to detect possible difference between the times of processing required for each type of sentences an additional one way ANOVA on mean response times was performed using the conditions (*Standard Agreement*, *Number Agreement Violation* and *Person Agreement Violation*) as factor. This analysis showed a significant main effect of condition (F (1, 20) = 6.78, $p < 0.01$, ε = 0.71). To disentangle this effect planned comparisons were performed to compare the means. This analysis revealed that the detection of *Person Agreement Violation* (t (20) = -2.60, $p < 0.01$) and *Number Agreement Violation* (t (20) = -2.86, $p < 0.01$) was faster (lower RT) than the detection of grammatically acceptable sentences, reflecting the additional time required for the syntactic-semantic integration processes triggered by grammatical sentences relative to the grammatical error detection processes evoked by ill-formed constructions. There were no significant differences between the two types of syntactic feature violations (t (20) = 0.75, p = 0.46).

Table 6.1. Percentage of correct response and mean decision times (in ms) for the three types of constructions with standard error between parenthesis.

	RT	**Hits**
Standard Agreement	629.32 (38.06)	90.37 (1.80)
Number Agreement Violation	558.49 (34.25)	91.13 (2.31)
Person Agreement Violation	568.03 (35.38)	90.00 (2.68)

All Sentences versus the fixation baseline. To characterize the functional neuro-anatomical network that was recruited by the processing of sentences independently of the experimental manipulation we compared all sentences with the fixation baseline condition. The statistical parametric map resulting from this contrast is displayed on the surface of the MNI single-subject T1 image. All sentences versus the fixation baseline revealed significant activation of a widespread fronto-parieto-temporal network bilaterally distributed, but with a strongly left lateralization (see Table 6.2 and Figure 6.1). This network includes brain areas associated to different stages of sentence processing such as the left pars opercularis and triangularis within the inferior frontal gyrus, the anterior and posterior part of the left middle temporal cortex, the left superior temporal pole, the left and right fusiform gyrus, the left and right inferior and middle occipital cortex, as well as the supplementary motor area and the precentral and postcentral cortex in both hemispheres (see Table 6.2 for a detailed list of the regions resulting from this contrast).

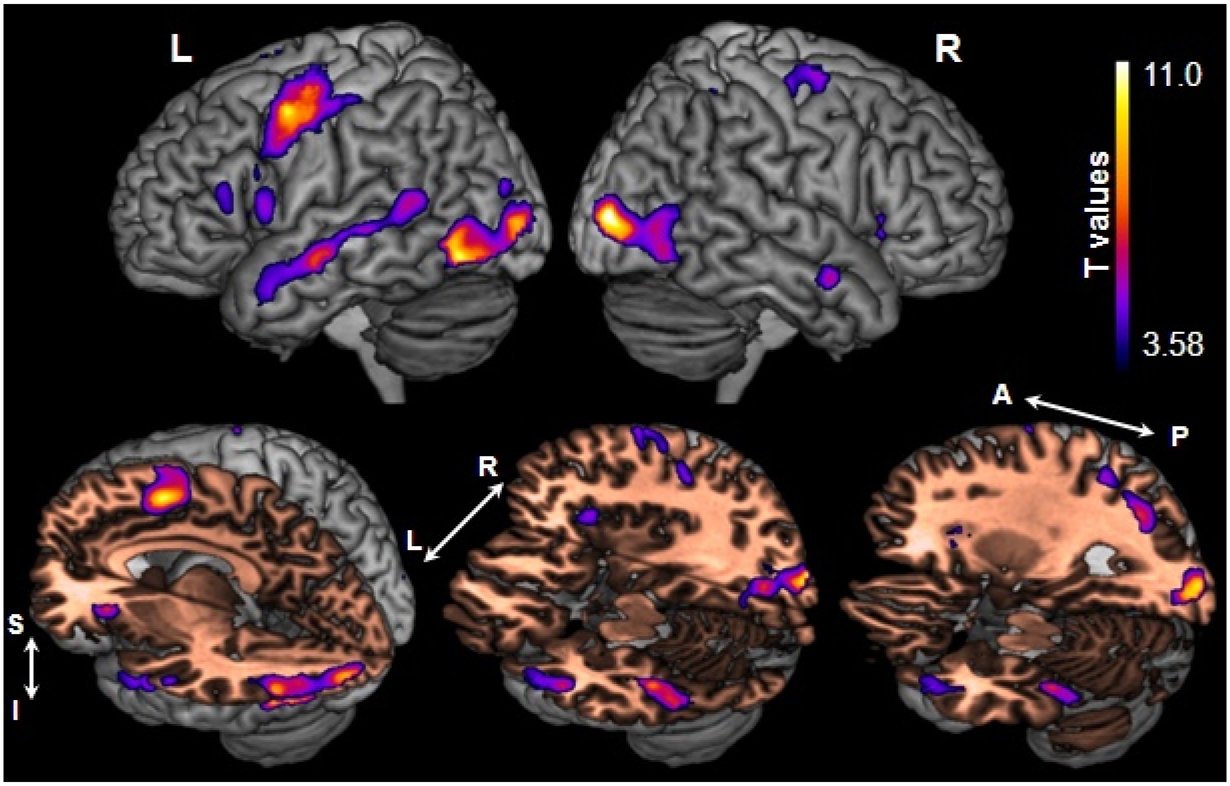


Figure 6.1. Statistical parametric map resulting from the contrast All Sentences (*Person Agreement Violation + Number Agreement Violation + Standard Agreement*) vs. Fixation are overlaid on the surface of the MNI single-subject T1 image. The lower part of the figure shows a more detailed anatomical localization of the maximum peaks of activation using the sagittal and axial sections of the MNI single-subject T1 image. L: left; R: right; A: Anterior; P: Posterior; I: Inferior; S: Superior.

Table 6.2. Significant activation clusters resulting from the contrast All Sentences versus the fixation baseline.

Hemisphere	**Region**	**All Sentences > Fixation**		
		x,y,z {mm}	**Z**	**Vx**
Left	Inferior Frontal Gyrus (BA45 - Tri)	-46 28 16	4,06	196
	Insula (BA47)	-30 26 0	**5,25**	227
	Precentral (BA6)	-50 2 48	**6,04**	2272
	Postcentral (BA40)	-54 -6 46	**5,41**	2272
	Supplementary Motor Area (BA32/6)	-4 12 50	**6,2**	1339
	Anterior Middle Temporal (BA21)	-56 -10 -12	**5,37**	3156
	Inferior Occipital (BA37)	-44 -66 -10	**6,01**	3156
	Middle Occipital (BA37)	-28 -90 2	**5,82**	3156
Right	Insula (BA47)	34 24 2	**4,64**	223
	Precentral (BA6)	38 -6 64	**4,5**	483
	Postcentral (BA3)	42 -26 46	**4,67**	483
	Inf Parietal (BA40)	30 -46 52	4,4	363
	Middle Temporal (BA21)	42 -70 2	**4,98**	1284
	Inferior Occipital (BA18)	28 -86 -2	**5,83**	1284
	Middle Occipital (BA18)	36 -90 6	**6,73**	1284
	Superior Occipital (BA19)	28 -62 36	**5,06**	363

x,y,z {mm} = Coordinates of the local maxima. Z = Z scores. Vx = Number of voxels significantly activated inside the cluster belonging to each local maximum. Z scores and Vx are reported in bold if they are significant at the peak level after FWE or FDR correction (p<.05), if indicated underline are significant at p<.001 uncorrected. All others are significant at the cluster level after FWE or FDR correction (p<.05). Tri: Pars Triangularis. BA: Brodmann Area.

Dissociation between ungrammatical and grammatical sentences. To highlight the neural regions involved in the analysis of subject-verb agreement dependencies the *Standard Agreement* > [*Person Agreement Violation* + *Number Agreement Violation*] contrast was carried out. The resulting statistic parametric map included regions with higher responses for grammatically correct sentences than for ungrammatical constructions, revealing a significant increase of activation in left temporal and frontal regions. The frontal activation patch comprised two inferior frontal regions (pars triangularis and pars orbitalis) and the precentral cortex, while temporal areas included the anterior and posterior part of the left middle temporal gyrus (see Table 6.3 and Figure 6.2 [in purple]). In addition, significant increases of activation for the ungrammatical relative to grammatical constructions were observed in the middle frontal gyrus, the middle cingulate cortex and the precuneus. All these neural regions showed a similar activation pattern in both cerebral hemispheres. In addition, we also found significant increases of activation in the supramarginal, the inferior parietal and the middle temporal gyrus exclusively in the right hemisphere (see Table 6.4 and Fig. 6.2).

Table 6.3. Brain activation resulting from the comparison between grammatical and ungrammatical constructions.

Hemisphere	**Region**	**Standard Agreement > Violations**		
		x,y,z {mm}	**Z**	**Vx**
Left	Inferior Frontal Gyrus (BA45 - Tri)	-56 24 14	**5,63**	2785
	Inferior Frontal Gyrus (BA47/38 - Orb)	-48 34 -6	**4,61**	2785
	Superior Frontal Gyrus (BA9)	-8 50 44	**4,66**	456
	Middle Temporal Pole (BA38)	-46 16 -28	**5.12**	971
	Superior Temporal Pole (BA38)	-46 16 -21	3,37	971
	Anterior Middle Temporal Gyrus (BA20)	-56 -10 -16	**4,67**	971
	Posterior Middle Temporal Gyrus (BA22)	-58 -38 4	**5,1**	1155
	Posterior Middle Temporal Gyrus (BA21)	-52 -54 12	**4,78**	1155

x,y,z {mm} = Coordinates of local maxima. Z = Z scores. Vx = Number of voxels significantly activated inside the cluster belonging to each local maximum. The regions reported are significant at the cluster level after FWE or FDR correction (p<.05). Z scores and Vx are reported in bold if they are significant at the peak level after FWE or FDR correction (p<.05). Tri: Pars Triangularis; Orb: Pars Orbitalis; BA: Brodmann Area.

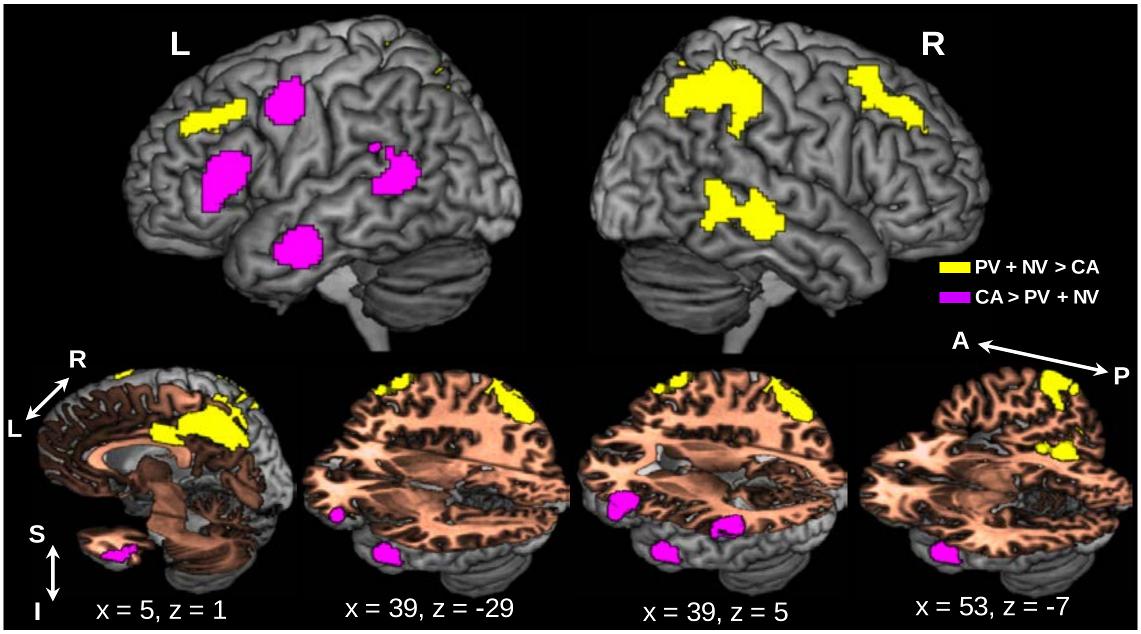


Figure 6.2. Statistical parametric map resulting from the contrasts Anomalous Sentences (*Person Agreement* Violation + Number Agreement Violation) vs. Standard Agreement are overlaid on the surface of the MNI single-subject T1 image. The right tale of the t-test was represented in yellow, while the left tale (*Standard Agreement* vs. Anomalous Sentences) was represented in violet. The lower part of the figure shows a more detailed anatomical localization of the maximum peaks of activation using the sagittal and axial sections of the MNI single-subject T1 image. L: left; R: right; A: Anterior; P: Posterior; I: Inferior; S: Superior.

Table 6.4. Brain activation resulting from the comparison between ungrammatical and grammatical constructions.

Hemisp.	Region	Violations > Standard Agreement			Person Agreement Violation > Standard Agreement			Number Agreement Violation > Standard Agreement		
		x,y,z {mm}	Z	Vx	x,y,z {mm}	Z	Vx	x,y,z {mm}	Z	Vx
Left	Middle Frontal Gyrus (BA45)				-40 46 22	4.26	459	-40 32 36	3.21	626
	Middle Frontal Gyrus (BA46)	-32 44 34	4.24	190	-32 46 34	4.68	459	-32 44 34	3.97	626
	Middle Frontal Gyrus (BA44)	-40 22 40	3.56	190	-44 22 36	4.33	459			
	Middle Frontal Gyrus (BA10)				-34 54 6	4.02	109			
	Middle Cingulate (BA23)							-2 -16 32	3.49	164
	Inferior Parietal (BA40)				-42 -46 58	4.31	238	-48 -48 56	2.8	118
	Superior Parietal (BA40)							-36 -54 58	3.19	118
	Paracentral				10 -32 52	4.43	1195			
	Postcentral (BA40)							-42 -44 62	3.23	118
	Precuneus (BA7)	-4 -62 58	**5.38**	2261	-6 -66 50	**5.14**	1195	-10 -62 44	4.62	2770
Right	Middle Frontal Gyrus (BA46)							40 52 8	3.2	232
	Middle Frontal Gyrus (BA45)							36 46 18	4.2	232
	Middle Frontal Gyrus (BA48)							32 18 56	3.37	325
	Middle Frontal Gyrus (BA8)	28 18 58	3.71	290				24 16 52	3.07	325
	Middle Frontal Gyrus (BA9)	32 38 40	4.42	290				30 38 40	3.98	243
	Medial Superior Frontal Gyrus (BA32)				2 34 34	**4.89**	408			
	Anterior Cingulate (BA11)				6 40 26	4.36	408			
	Middle Cingulate	6 -36 52	**5.07**	2261	8 -22 38	4.06	396			
	Supplementary Motor Area (BA8)							14 14 60	4.18	325
	Inferior Parietal (BA40)	42 -56 52	**5.3**	873	56 -42 50	4.25	438	48 -44 52	3.95	689
	Supramarginal Gyrus (BA40)	56 -34 46	4.42	873	58 -36 44	4.19	438	52 -32 42	4.33	689
	Middle Cingulate (BA23)							2 -12 40	3.41	164
	Precuneus (BA5)	8 -58 58	**5.4**	2261				8 -60 56	4.69	2770
	Middle Temporal (BA21)	54 -44 -6	4.58	458				68 -24 -12	3.82	468
	Caudate (BA11)							14 18 -8	3.75	112

x,y,z {mm} = Coordinates of local maxima. Z = Z scores. Vx = Number of voxels significantly activated inside the cluster belonging to each local maximum. The regions reported are significant at the cluster level after FWE or FDR correction (p<.05). Z scores and Vx are reported in bold if they are significant at the peak level after FWE or FDR correction (p<.05). Hemisp. = Hemisphere. BA: Brodmann Area.

Interestingly, when contrasting each type of anomalous sentences (*Person Agreement Violation* and *Number Agreement Violation*) with grammatical constructions (*Standard Agreement*) a similar fronto-parieto-temporal network was found for both contrasts (see Table 6.4 and Figure 6.3). In particular, the superimposition of the significant neural activations of these contrasts (*Person Agreement Violation* versus *Standard Agreement* and *Number Agreement Violation* versus *Standard Agreement*) demonstrated that the activation of the right and left middle frontal gyrus, the right and left inferior parietal region, the right and left middle cingulate cortex, the right and left precuneus, the right supramarginal and the right middle temporal gyrus are common to both types of violations. Figure 6.3 shows this comparison, where the common response for both contrasts is represented in yellow, the specific response for *Person Agreement Violation* is represented in red and the response for *Number Agreement Violation* is represented in green. Note that the response patterns of these regions with respect to the fixation are different: while the left anterior cingulate cortex, the right middle temporal and the right middle frontal gyrus exhibited negative response (de-activation) compared to the fixation baseline condition, with greater de-activation for matching than mismatching constructions, the rest of the regions exhibited positive response respect to the fixation with higher amplitude for anomalous sentences (see the bar graph in the left-hand side of the Figure 6.3 B).

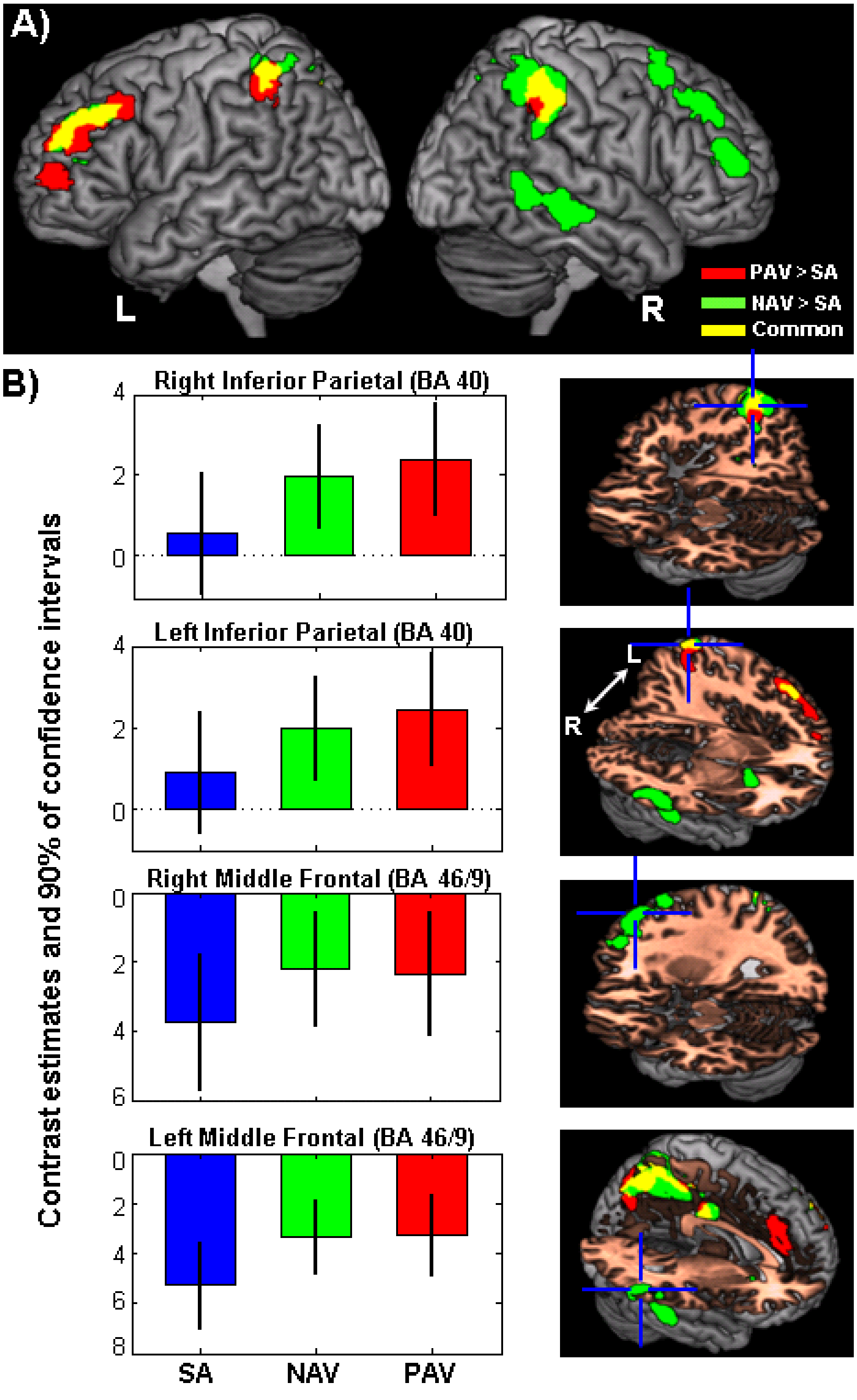

A)
L
R
PAV > SA
NAV > SA
Common
B)
Contrast estimates and 90% of confidence intervals
Right Inferior Parietal (BA 40)
4
2
0
Left Inferior Parietal (BA 40)
4
2
0
L
R
Right Middle Frontal (BA 46/9)
0
2
4
6
Left Middle Frontal (BA 46/9)
0
2
4
6
8
SA
NAV
PAV

Figure 6.3. Superimposition of the significant activation clusters resulting from the contrasts *Person Agreement Violation* **vs.** *Standard Agreement* and *Number Agreement Violation vs. Standard Agreement*. Statistical parametric maps were projected on the surface of the MNI single-subject T1 image. Yellow voxels represent significant activated voxels in both contrasts. Bar graph in (B) displays the contrast estimates and 90% of confidence intervals for the three experimental conditions compared to the fixation baseline (SA: Standard Agreement; NAV: Number Agreement Violation; PAV: Person Agreement Violation) at different maximum peaks, representative of the significant activated clusters. The three experimental conditions are represented in (B) with different colours (Standard Agreement in blue; Number Agreement Violation in green; Person Agreement Violations in red). The right-hand side of (B) show a more detailed anatomical localization of the maximum peaks of activation using the sagittal and axial sections of the MNI single-subject T1 image. L: left; R: right.

Distinguishing between Person and Number Agreement Violations. *Person Agreement Violation* relative to *Number Agreement Violation* evoked significant ($p<0.001$ corrected for multiple comparisons) increases of activation in the anterior and posterior part of the left middle temporal gyrus (see Table 6.5 and Figure 6.4). However, as can be observed in Figure 6.4, the response pattern of these two regions with respect to the baseline differs: while the anterior part of the middle temporal gyrus is sensitive only to *Person Agreement Violation*, the posterior portion is sensitive to both *Person Agreement Violation* and *Number Agreement Violation,* although with higher amplitude for *Person Agreement Violation*. In addition, this contrast also revealed significant ($p<0.001$ uncorrected) responses in the pars triangularis and orbitalis within the left IFG, with neural responses being more conspicuous for *Person Agreement Violation* than for *Number Agreement Violation* (see Table 6.5 and Figure 6.4). Importantly, non-significant response was found from the other tail of this contrast (i.e., *Number Agreement Violation* > *Person Agreement Violation*).

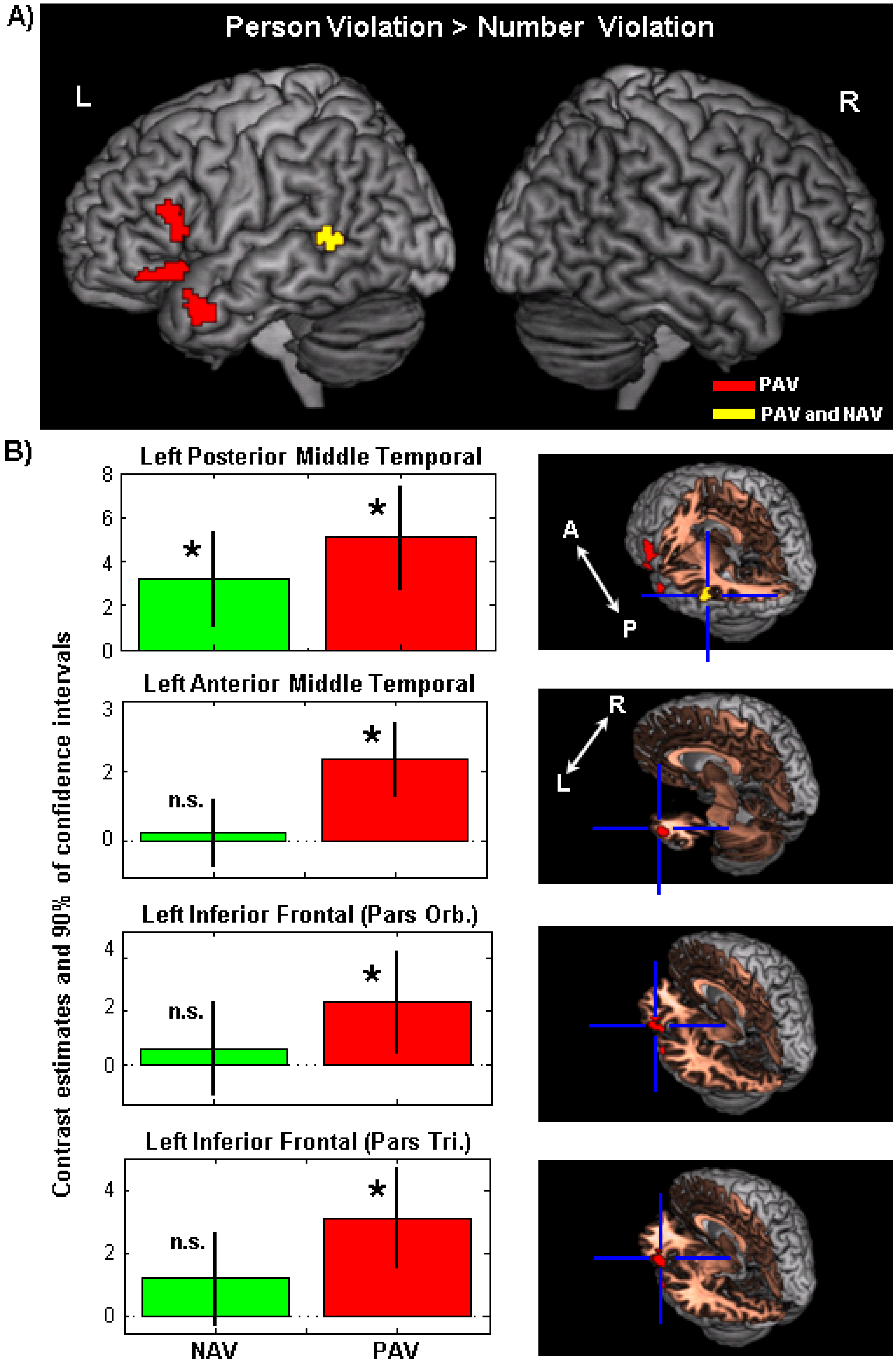

A)
Person Violation > Number Violation
L
R
PAV
PAV and NAV
B)
Left Posterior Middle Temporal
Left Anterior Middle Temporal
Left Inferior Frontal (Pars Orb.)
Left Inferior Frontal (Pars Tri.)
Contrast estimates and 90% of confidence intervals
n.s.
*
NAV
PAV
A
P
R
L
8
6
4
2
0
3
2
0
4
2
0
4
2
0

Figure 6.4. Significant activation clusters resulting from the contrast *Person Agreement Violation* vs. *Number Agreement Violation* are represented in red. Statistical parametric map was overlaid on the surface (A) of the MNI single-subject T1 image. Bar graph in (B) displays the contrast estimates and 90% of confidence intervals for the two anomalous sentences compared to the fixation baseline (NAV: Number Agreement Violation; PAV: Person Agreement Violations) at the two significant activated clusters. The two experimental conditions are represented in (B) with different colours (Number Agreement Violation in green; Person Agreement Violations in red). The right-hand side of (B) show a more detailed anatomical localization of the maximum peaks of activation using the sagittal and axial sections of the MNI single-subject T1 image. The asterisks in the upper part of the bars indicate that the comparison between each condition and the fixation baseline was statistically significant. L: left; R: right; n.s.: non-significant t-test.

Table 6.5. Brain activation resulting from the comparison between Person Agreement Violations and Number Agreement Violations.

Hemisphere	**Region**	**Person Agreement Violation > Number Agreement Violation**		
		x,y,z {mm}	**Z**	**Vx**
Left	Inferior Frontal Gyrus (BA45 - Tri)	-58 20 16	3.31	192
	Inferior Frontal Gyrus (BA47/38 - Orb)	-48 22 -10	3.65	161
	Superior Temporal Pole (BA38)	-46 16 -20	3,41	89
	Middle Temporal Pole (BA38)	-50 12 -24	3.85	89
	Anterior Middle Temporal (BA21)	-52 6 -26	4,09	89
	Posterior Middle Temporal (BA20/21/22)	-56 -46 6	3,72	62

x,y,z {mm} = Coordinates in MNI space of local maxima. Z = Z scores. Vx = Number of voxels significantly activated inside the cluster belonging to each local maximum. Z scores and Vx are reported in bold if they are significant at the peak level after FWE or FDR correction (p<.05), if indicated underline are significant at p<.001 uncorrected. All others are significant at the cluster level after FWE or FDR correction (p<.05). Tri: Pars Triangularis; Orb: Pars Orbitalis; BA: Brodmann Area.

6.4 Discussion

The goal of the current study was to [1]evaluate whether two different morpho-syntactic features such as person and number differ as a function of its interpretive properties and more importantly [2]investigate where is this difference, if it is indeed found, mapped in the brain. As comprehension mechanisms can be best highlighted when the system is forced to deal with mistakes (Mancini et al., 2011a; Wagers et al., 2009; Wagers & Phillips, 2009), we manipulated subject-verb agreement relations so that the establishment of discourse roles and cardinality representations could be disrupted, by creating person and number agreement violations. In consonance with the previous experimental chapters, the comparison between correct and incorrect agreement dependencies gave us the possibility to disentangle neural substrates associated with the building and interpretation of congruent relations from those associated with the analysis of ungrammatical agreement. Specifically, the comprehension of grammatical sentences (*Standard Agreement* > *Agreement Violations* contrast) recruited a network that included the aMTG, the pMTG and the LIFG, while sensitivity to ungrammatical sentences (*Agreement Violations* > *Standard Agreement*) emerged in a widespread bilateral fronto-parietal network.

The direct contrast between *Person Agreement Violation* and *Number Agreement Violation* permitted the uncovering of finer-grained mechanisms related with the establishment of agreement relations. A clear dissociation between person and number violations emerged in the pMTG and in the aMTG, as well as in the pars orbitalis and triangularis of the LIFG, although with a less strict threshold (see Figure 6.4). A closer inspection reveals that the regions where the Person-Number dissociation is found belong to the fronto-temporal network recruited by the comprehension of correct agreement, suggesting that the areas, arguably involved in the building and interpretation of sentential relations, operate in a feature-specific fashion. In contrast, the failure to find a dissociation between person and number violations in areas sensitive to the processing of ungrammatical constructions, such as middle frontal and parietal regions, together with the common responses evidenced by the contrast between the two violations and correct agreement (*Person/Number Agreement Violations* > *Standard Agreement*), seems to imply that consistency checking and conflict monitoring mechanisms operate in a feature-insensitive manner.

Critically, this pattern of results (see Table 1S for an updated interim summary of the main results and a comparison across the experiments) enables us to associate the main components of sentence processing – structure building, checking and interpretation – to specific neuro-anatomical regions, and to outline a more precise map of linguistic functions in the brain, as discussed below in detail.

Table S1. Main Findings

	Behavioral results	Neuro-anatomical results	
		Grammaticality effects	Effects related with the critical manipulation
Experiment I (determiner-noun pairs)	**Main effect of Agreement Congruency**: Subjects classified determiner-noun pairs as grammatically correct more easily and accurately than incongruent pairs. This differentiation was evident for both transparent and opaque nouns. **Interaction effect**: Regarding RT, this effect was larger for opaque than for transparent nouns.	***Gender Mismatch* relative to *Gender Match***: the dorsal striatum, the middle and medial superior frontal gyrus, the medial orbito-frontal cortex, the pre- and post-central gyrus, as well as the anterior cingulate cortex. ***Gender Match* as compared to *Gender Mismatch****:* the pars opercularis and triangularis within the left IFG and the posterior part of the left MTG/STG.	Significant **interaction effects** between Gender Congruency and Gender-marking emerged in five left-lateralized clusters: ▪ Pars triangularis within the IFG ▪ Posterior part of the MTG/STG ▪ Hippocampus ▪ Angular Gyrus ▪ Supramarginal Gyrus
Experiment II	**Null effects** for RT and error rates.	***Gender Mismatch* relative to *Gender Match***: the pars triangularis, orbitalis and opercularis within the left IFG, the middle frontal gyrus, as well as the inferior parietal gyrus and the supramarginal and the angular gyri. ***Gender Match* as compared to *Gender Mismatch****:* the middle and medial superior frontal gyrus, the medial orbito-frontal cortex, the anterior cingulate cortex, as well as the anterior part of the left MTG/STG and the superior and middle temporal pole.	Significant **interaction effects** between Gender Congruency and Type of Gender emerged in two left-lateralized clusters: ▪ Inferior Parietal ▪ Angular Gyrus

Experiment III	**Main effect of Agreement Congruency**: Subjects classified word pairs as grammatically correct more easily and accurately than incongruent pairs. This Left angular gyrusdifferentiation was evident for both determiner-noun and subject-verb pairs. **Interaction effect**: Regarding RT, this effect was larger for determiner-noun pairs than for subject-verb pairs.	***Number Mismatch* relative to *Number Match***: the right and left insula, the pars orbitalis, opercularis and triangularis within the left IFG, the pre- and post-central gyrus, as well as the inferior parietal cortex. ***Number Match* as compared to *Number Mismatch****:* the middle and superior frontal gyrus, the anterior cingulate cortex, the medial orbito-frontal cortex, as well as the anterior part of the MTG/ITG.	Significant **interaction effects** between Number Congruency and Type of Word Pair emerged in three left-lateralized clusters: ▪ Left pars opercularis within the IFG ▪ Left anterior part of the MTG/STG ▪ Left and right precuneus/Cuneus
Experiment IV	**Main effect of Agreement Congruency**: Subjects classified word pairs as grammatically incorrect more easily and accurately than congruent items. This differentiation was evident for both person and number agreement violations.	***Ungrammatical* relative to Grammatical sentences**: the medial superior frontal gyrus, the middle frontal gyrus, the postcentral gyrus, the middle cingulate cortex, as well as the inferior and superior parietal cortices. ***Grammatical* relative to Ungrammatical sentences***:* the pars orbitalis and triangularis within the left IFG, the superior frontal gyrus, as well as the posterior and anterior portions of the left MTG/STG and the superior temporal pole.	Significant **differences** between *Number* and *Person Agreement Violation* emerged in four left-lateralized clusters: ▪ Left pars orbitalis within the IFG ▪ Left pars triangularis within the IFG ▪ Left anterior part of the MTG/STG ▪ Left posterior part of the MTG/STG
Experiment V			

Structure building: the role of the pMTG. A significant involvement of the pMTG was found for the *Standard Agreement > Agreement Violations* contrast, suggesting the sensitivity of this area to well-formed agreement configurations. However, pMTG involvement was not limited to correct-agreement sentences: when contrasting the two incorrect conditions (*Person > Number Agreement Violation* contrast), *Person Agreement Violation* condition was found to generate a greater response in this area than *Number Agreement Violation*, suggesting differential sensitivity to the type of information manipulated in verbal morphology. As reviewed above, functional interpretations on the involvement of the pMTG in language processing range from proposals advancing its role in the extraction of morphological information to build syntactic structure (Pallier et al., 2011) or in the retrieval of syntactic frames from semantic memory (Hagoort, 2005), to views emphasizing the centrality of this region in mechanisms at the syntax-semantics interface, such as the analysis of verb-argument relations (Bornkessel-Schlesewsky & Schlesewsky, 2013; Bornkessel et al., 2005; Friederici, 2011). The current set of data allows us to distinguish between the two proposals.

While the activation for correct verbs that is found in the pMTG could be equally accounted for under proposals that claim a role of this region in lexical access processes, (Hagoort, 2003a, 2005, 2013), as well as under positions that argue for pMTG involvement in the analyses of verb-argument relations (Bornkessel-Schlesewsky & Schlesewsky, 2013; Friederici, 2011, 2012), the same cannot be said for the differential activation profile evidenced by the *Person > Number Agreement Violation* contrast. The verb-argument relation hypothesis would predict activation for person, but not for number agreement anomalies in the pMTG: while the interpretation of person agreement implies the mapping of morpho-syntactic information onto specific roles (i.e. discourse roles), no role assignment is involved for the interpretation of number agreement. In other words, the activation patterns that emerge from the comparison between the two violations disconfirm the verb-argument hypothesis.

A better frame for the discussion of these data is provided by studies and models that assume pMTG involvement in the extraction of information from the input to build syntactic structure (Hagoort, 2005; Hickock & Poeppel, 2007; Lau et al., 2008; Libertus & Needham, 2010; Molinaro et al., 2015; Pallier et al., 2011). In this respect, the quantitative dissociation found between person and number would result from their different underlying structural representations (Bianchi, 2006; Lu et al., 2011; Mancini et al., 2011a; Sigurdsson, 2009). While the extraction of person information from verbal morphology implies projecting nodes at the morpho-syntactic and discourse level, the extraction of number information does not, leading to differential processing costs. The information extracted from the input in the pMTG could be made available to further regions in the network, thanks to ventral and dorsal connections to anterior portions of the temporal cortex and left frontal areas (Bornkessel-Schlesewsky & Schlesewsky, 2013; Dronkers et al., 2004; Griffiths et al., 2012; Hagoort, 2013; Molinaro et al., 2015; Papoutsi et al., 2011; Saur et al., 2008; Wilson et al., 2012), where subsequent analysis steps could be carried out, as described below.

Assignment of interpretively relevant roles: the role of the aMTG. In line with our predictions and in accordance with the previous experimental chapters, the comparison between *Standard Agreement* and *Agreement Violations* revealed the activation of a large portion of the aMTG for agreeing verbs. Moreover, the comparison between person and number violations revealed a remarkable asymmetry between the two features, with the former producing a significant increase of activation in this area, but not the latter. As reviewed above, activity in this region has been associated with the building of local syntactic structure, thanks to the ventral pathway connecting the anterior portion of the temporal cortex and the frontal operculum (Friederici, 2011, 2012). Another interpretation attributes the aMTG a critical role in the integration of different types of information to derive the propositional meaning of a sentence (Bornkessel-Schlesewsky & Schlesewsky, 2013), a claim that connects with a larger literature on the role of this region in semantic memory and conceptual combination (cf. Baron, S. G. et al., 2010; Molinaro et al., 2015; Patterson et al., 2007). Crucially, the current set of data allows us to distinguish between these two proposals. Clearly, the finding of different patterns of activation for grammatical and ungrammatical sentences in this region does not argue in favor of the local syntactic structure building hypothesis: in this case one would have expected the three contrasts to give rise to equivalent responses in this area, since the three types of sentences are characterized by the same local syntactic structure (regardless of morpho-syntactic consistency). On the contrary, aMTG increased activation that we report for the *Standard Agreement* > *Agreement Violations* contrast is in line with previous data on agreement processing by Kuperberg et al. (Kuperberg et al., 2003; Kuperberg, Sitnikova, et al., 2008), who have reported aMTG involvement in the processing of grammatical sentences (see also the Results section in Chapter 3, 4 and 5), and more in general with claims advancing the role of this region in the elaboration of higher-level information (Bornkessel-Schlesewsky & Schlesewsky, 2013; Lau et al., 2008; Molinaro et al., 2015; Pallier et al., 2011). Under this assumption, the finding of a significant response in this area for person, but not for number anomalies, give us an important insight into the type of mechanisms supported by this area. Specifically, our data point to a critical role of aMTG in the assignment of interpretively relevant roles, which, in our case, correspond to discourse roles. While identifying and assigning a discourse role to the subject argument is crucial for the derivation of the overarching meaning of the sentence, the identification of whether this argument refers to a single entity or a multitude of entities is not, hence the qualitatively different response for the two violations. Critically, such an interpretation meshes well with results obtained in the ERP study by Mancini et al. (2011a), who reported an N400 effect for *Person Agreement Violation* relative to *Standard Agreement*. Indeed, it is possible that the anterior portion of the left middle temporal gyrus is involved in the generation of this negative component (cf. Lau et al., 2013; Lau et al., 2008), although further investigation is certainly needed to validate this hypothesis.

Evaluation of subject-verb morpho-syntactic fit: interplay between domain-general and domain-specific processes in frontal areas. In frontal areas, the analysis of grammatical (relative to agreement violations) and ungrammatical sentences (relative to their correct counterpart) revealed an interesting clear-cut dissociation between regions selectively involved in the analysis of congruent sentences, as opposed to regions sensitive to the presence of agreement inconsistencies. A significant response for grammatical sentences (relative to ungrammatical ones) was present in LIFG areas, including the pars triangularis and orbitalis (see Figure. 6.2), in line with results from the previous agreement processing studies that report a significant response of this area to grammatical agreement (Kuperberg et al., 2003; Kuperberg, Sitnikova, et al., 2008; see also Results section in Chapter 1 for similar results). Current neuro-cognitive models advance contrasting hypotheses on the role played by frontal areas in sentence comprehension, ranging from domain-specific to domain-general functions (Bornkessel-Schlesewsky & Schlesewsky, 2013; Friederici, 2011, 2012; Friederici & Gierhan, 2013; Grodzinsky & Friederici, 2006; Hagoort, 2003a, 2005, 2013; Lau et al., 2008; Novick et al., 2005; Thompson-Schill et al., 2005).

Importantly, a clearer understanding of the sentence-level processes supported by these two regions can be gained from the comparison between person and number violations. Although with a less strict threshold, the two anomalies differ in the pars orbitalis and triangularis of the LIFG, where *Person Agreement Violation* gave rise to a greater response compared to *Number Agreement Violation*, thus mirroring the activation profile found in the aMTG and the pMTG. It is possible that activity in the anterior portion of the LIFG thus reflects a constant and incremental evaluation of the semantic-discourse fit of the elements being processed, that is the matching between subject and verb in terms of morpho-syntactic values, to evaluate whether the two elements can be integrated in a meaningful conceptual representation. Such a response profile is compatible with views proposing that more anterior regions of the LIFG are involved in the analysis of meaning at the sentence level (Friederici, 2011, 2012; Friederici & Gierhan, 2013; Hagoort, 2005; and Vigneau et al., 2006 for an extensive review). In this respect, the greater response that we find for person could be attributed to the greater relevance for propositional meaning that this feature has, because of the interpretively relevant roles that it assigns. Crucially, this interpretation suggests a tight functional connection existing between the aMTG and inferior frontal regions, which appears to be corroborated neuro-anatomically by the presence of a ventral pathway connecting anterior temporal to inferior frontal regions (cf. Friederici, 2011). Critically, a recent study has demonstrated the presence of a significant coupling between anterior temporal regions and IFG during semantic processing (Molinaro et al., 2015).

A different scenario is found in the left middle frontal gyrus, which was found to respond more to incorrect agreement stimuli (regardless of the feature manipulated). These data appear in line with those reported in the previous experimental chapters (see Discussion section of Chapter 3) and more in general with studies manipulating the morpho-syntactic fit between sentence parts [e.g., gender mismatch between pronouns and antecedents in Dutch (Folia et al., 2009); finiteness violations in English (Kuperberg et al., 2003; Kuperberg, Sitnikova, et al., 2008); verb-object violations in Basque (Nieuwland et al., 2012)]. A number of studies point to a critical role of the middle frontal gyrus in domain-general verbal working memory mechanisms (Katsuki & Constantinidis, 2012a, 2012b; Rogalsky & Hickok, 2011). In the context of the current experiment, middle frontal areas could support working memory mechanisms aimed at comparing incoming verbal information with previously analyzed information, such as the one contained in the subject argument (see Discussion in Chapter 7 for a similar argument). Importantly, these memory mechanisms could be tightly involved in morpho-syntactic consistency checking operations that are assumed to take place during agreement processing. This interpretation appears to be in line with the ERP data reported by Mancini et al. (2011a), in which a common left-anterior negative effect was found for the two violations, suggesting the presence of a common feature checking operation for the two types of agreement. Critically, studies investigating the processing of mismatches in domains other than language syntax, such as music syntax, have localized the source of early negative effects in middle frontal gyrus (Maess et al., 2001) and have thus proposed that this region supports general mechanisms involved in checking consistency across the stimuli (see Koelsch, 2005; Koelsch et al., 2005; Koelsch et al., 2004 for a discussion on the interaction between musical and linguistic processing).

A further remark concerns the dissociation that emerges in the frontal lobe between inferior frontal areas – selectively activated by the processing of correct dependencies – and middle frontal regions, which show sensitivity to the presence of a mismatch between subject and verb. This division has been already discussed in the extant neuro-cognitive literature, especially in relation to the debate concerning the domain-general vs. language-specific function of frontal areas. One relevant position maintains that LIFG role is neither strictly domain-general nor strictly language-specific (Fedorenko, Duncan, et al., 2012). Indeed, handling of both types of processing is ensured by the presence of functionally complementary sub-regions: while LIFG is specifically engaged in linguistic processing, its surrounding areas appear to be broadly engaged in a variety of tasks across different domains. The current set of data is compatible with this proposal and contributes to characterizing the nature of the mechanisms that each sub-region supports. In particular, this dissociation could reflect the interplay between language-specific mechanisms that incrementally integrate linguistic information coming from temporal areas, and domain-general processes that ensure the detection of possible mismatches between the perceived and the expected input.

Conflict monitoring system triggered during agreement processing. There is yet another aspect of the set of data showed here that deserves to be discussed, namely the activation profile emerged in bilateral fronto-parietal areas, including the anterior and middle cingulated cortex, the inferior parietal cortex and the precuneus. As we extensively discussed in the previous chapters, activity in these areas has been consistently associated with task-related conflict-monitoring operations aimed at monitoring the match between the expected and the perceived stimulus (Botvinick et al., 2004; Ye & Zhou, 2009). These could precisely be the mechanisms that led to the involvement of these regions in our experiment, during which participants were required to evaluate sentence grammaticality. Importantly, this finding is consistent with further sentence processing studies that required the evaluation of the morpho-syntactic fit in a variety of dependencies (Folia et al., 2009; Kuperberg et al., 2003; Kuperberg, Sitnikova, et al., 2008; Nieuwland et al., 2012). Further corroboration for this interpretation comes from the fact that both person and number agreement violations elicit a P600 (cf. Mancini et al., 2011a), an effect that has been linked to conflict-monitoring mechanisms (see van de Meerendonk et al., 2011; van de Meerendonk et al., 2009 for a discussion) and whose sources have been related to the anterior cingulate cortex (Du et al., 2013; Olichney et al., 2010).

Interim conclusions. In sum, two main findings result from this study. Firstly, we had hypothesized that the on-line building of agreement comprehension relied on the application of mechanisms that distinctly mapped morpho-syntactic information onto discourse and cardinality representations, and that this dissociation could be reflected at a neural level. The current results confirmed our hypothesis and showed that the comprehension of an agreement dependency hinges on composite, feature-sensitive mechanisms of extraction and mapping in which the nodes of the agreement network are differentially involved. Secondly, the observation of the neural response to person and number agreement violations allowed us to associate the main components of agreement processing to their neuro-anatomical seats, thus adding up to current views on the neuro-cognition of language. On the one side, we have been able to localize processes related to the extraction of the representation underlying agreement features in the posterior portion of the middle temporal cortex, where differential sensitivity to the type of information manipulated in verbal morphology is found. This is of great relevance, as it gives us the opportunity to disentangle the processing of person and number from a perspective that could not be approached with either electrophysiological or behavioral techniques. On the other side, we pinpointed the neural substrates supporting the assignment of interpretively relevant roles in the anterior portion of the left middle temporal gyrus. In particular, this takes on great relevance both for the neuro-cognitive and theoretical study of agreement and sentence processing, suggesting the need i) to widen the range of interpretively relevant features and dependencies, to which person agreement is to be added (besides case and thematic roles), and ii) to design models that accommodate feature-based mapping procedures. Moreover, we could envisage the role of inferior and middle frontal areas in sentence processing by appealing to a tight interplay between language-specific and domain-general functions, which crucially evaluate and regulate subject-verb integration at the morpho-syntactic and semantic-discourse level. Lastly, we identified a center in fronto-parietal areas that regulates attentive mechanisms in order to monitor conflicts between the expected and the perceived input. Critically, future work will have to test the possibility to extend the assumptions made above to further features, syntactic contexts and different types of sentential relations.

Chapter 7.

Experiment V

Where agreement merges with disagreement: fMRI evidence of subject-verb integration.

7.1 Overview

The previous experiment (Chapter 6) investigated the neuro-cognitive mechanisms of subject-verb agreement comprehension by comparing ungrammatical sentences which present agreement feature mismatches with correct sentences, such as in (18) and (19) below. Despite the huge amount of studies using this approach to explore different aspects of sentence processing, it critically confounds the neurophysiological routines involved in agreement comprehension with the ones triggered by the detection of syntactically ill-formed constructions.

(18) *El pintor trajiste los cuadros a la galería <u>*Person Mismatch*</u>
*The painter$_{3.sg}$ brought$_{2.sg}$ the paintings to the gallery

(19) Los pintores trajeron los cuadros a la galería <u>*Standard Agreement*</u>
The painters$_{3.pl}$ brought$_{3.pl}$ the paintings to the gallery

Critically, a new perspective in understanding these mechanisms is possible if we take advantage of "legal" agreement mismatches (i.e., agreement mismatches that are nevertheless *grammatically correct*) that are available in some languages. One such case is Unagreement in Spanish, an agreement pattern characterized by the presence of a morpho-syntactic person mismatch between the subject and the verb (Höhn, 2012; Mancini et al., 2013b; Mancini et al., 2011b). In (20) below, despite the fact that a third person plural subject is followed by a first person plural verb, a well-formed grammatical Spanish sentence is generated. This morpho-syntactic mismatch is overcome by assigning to the 3rd person subject argument a 1st person plural interpretation (from "*The painters*" to "*We painters*"). From the point of view of the discourse representation of the sentence, this person shift for the subject implies a covert integration operation through which the speaker underlying the 1st person plural verb is included in the group of individuals referred to by the subject argument (from "*they*" to "*they + myself*"). In contrast, no such integration operation can be performed in (18), where the non-participant status of the subject form ("*he*/*she*") is incompatible with the addressee role invoked by the 2nd person verb ("*you*").

(20) Los pintores trajimos los cuadros a la galería *<u>Unagreement</u>*
The painters$_{3.pl}$ brought$_{1.pl}$ the paintings to the gallery

The uniqueness of the Unagreement pattern in (20) resides in the fact that it shares properties with both Standard Agreement (i.e., grammaticality) and Person Mismatch (i.e., morpho-syntactic mismatch), but at the same time it differs from both (as illustrated in Table 7.1). On the one hand, Unagreement shares a subject-verb morpho-syntactic mismatch with person violations but differs from them because it can be successfully integrated. Thus, both person violations and Unagreement should trigger processing difficulties in the evaluation of the morpho-syntactic consistency of subject and verb, independently of the grammaticality of the utterance. On the other hand, Unagreement shares grammaticality with Standard Agreement, but unlike this, it requires additional semantic-discourse analyses to overcome the morpho-syntactic incongruity and to perform the person shift (from "they" to "they + myself", a process referred to as "person anchoring" by Mancini et al., 2013b). From the perspective of sentence processing, the "grammatical mismatch" status of Unagreement offers therefore the opportunity to isolate the neural mechanisms supporting successful semantic integration that characterize correct sentences, from those underlying the evaluation of the morpho-syntactic subject-verb consistency. Importantly, these two processing steps cannot be disentangled using traditional contrasts between correct and agreement-anomalous sentences because of the impossibility of integrating two utterly mismatching values into a common and meaningful semantic representation. Therefore, in the current experimental chapter we have improved on the methodological limitations mentioned above, using an event-related design in which the experimental manipulation always concerns a simple local subject-verb agreement configuration (e.g., “_Los pintores trajeron/Los pintores trajimos/*El pintor trajiste_”). This type of manipulation therefore permits a cleaner observation of agreement processing, without the potential contamination from other confounds. In addition, we take advantage of the “intermediate” status of Unagreement between Standard Agreement and person violation.

Table 7.1. Increased processing (+) sensitive to the different linguistic properties of the subject-verb agreement constructions for each experimental condition.

Process	Def. Agreem.	Unagreem.	Person Mism.
Grammatical Error Detection	−	−	+
Morphosyntactic Mismatch Detection	−	+	+
Semantic-Discourse Integration	+	++	−

Taken into account the advantage of this type of grammatical construction, Mancini et al. (2011b) used Unagreement sentences and compared them to default agreement and ill-formed patterns (see examples 1, 2 and 3). These authors found an N400 component for both the Unagreement and the person mismatch conditions compared to default agreement. However, while the negativity elicited by the Unagreement extended between 350 and 750 ms mainly in the left posterior electrodes, the person mismatch elicited a widely distributed and larger negative effect between 350 and 500 ms that was evident also in bilateral frontal and posterior scalp regions. Mancini et al. (2011b) also reported that in contrast to Unagreement, person violations generated a P600 effect widely distributed over the scalp.

As for the N400 effect, the differences found in the timing and the topographic distribution of the Unagreement and person mismatch effects could reflect a functional dissociation between the two conditions after around 350 ms. Mancini et al (2011b) consider that the N400 could be associated in both conditions with the violation of the expectation about the morpho-syntactic verb feature, triggering semantic-pragmatic difficulties in the composition of the speech act participant representation. Nonetheless, these authors note that while in the case of person mismatch the speech participants underlying subject and verb cannot be integrated into one unitary discourse representation, integration clearly occurs in Unagreement. Here, the first person plural interpretation results from including a speaker within the group referred to by “The painters”. This functional dissociation possibly implies the engagement of different neural generators (underlying the topographically and temporally dissociable N400 effects) that are respectively recruited by the reading of grammatical (Unagreement) and ungrammatical (person violations) mismatches (Mancini et al., 2011b). From a neuro-anatomical perspective, Lau et al. (2008) indicate the anterior temporal cortex and the angular gyrus as crucial areas for the integration of incoming information into contextual and syntactic representations (see Bemis and Pylkkanen, 2012 for experimental evidence). Thus, these two neuro-anatomical regions are plausible candidates responsible for the successful integration that takes place in Unagreement sentences. On the other hand, the subsequent positive effect for person mismatch has been attributed to re-analysis operations taking place when ungrammatical information is being processed (Barber and Carreiras, 2005; Bornkessel and Schlesewsky, 2006; Friederici, 2012), while the absence of the P600 effect for Unagreement was taken to indicate that no reanalysis operation was triggered, since the sentence is grammatical. Thus, Unagreement and default agreement sentences undergo the same processes in this later phase.

However, the proposed early (starting ~350 ms) dissociation between the neurophysiological processes elicited by person violations and Unagreement is not completely supported by the ERP data. In fact, the main difference between the negative effects elicited by those two conditions (compared to default agreement) is reflected in the amplitude of the 300-500 ms effect (larger for person violations compared to Unagreement;

see amplitude-topography interaction for ERPs discussed by McCarthy and Wood, 1985). Thus, it could be argued that the same initial process is at work for both Unagreement and person violations (involving the same neural network) and that this process is more taxed by encountering person violations. Unfortunately, electroencephalographic measures suffer from low spatial resolution at the brain level, thus limiting possible inferences about the extent of the brain networks underlying a specific scalp-measured effect. However, defining whether different or similar neurophysiological processes are initially elicited by person violations and Unagreement is crucial, since the early stages of processing are the ones reflecting core agreement computations[30] (Molinaro et al., 2013).

The present study capitalizes on the Mancini et al. (2011b) design, to finely detail the neural networks involved in different aspects of subject-verb agreement comprehension using the high spatial resolution of fMRI. This experimental paradigm attempts to isolate the neural substrates involved in agreement computation, with a special focus on both the evaluation of morpho-syntactic feature consistency and semantic integration complexity. In light of the fMRI and ERP data discussed in the previous experimental chapters, we expect a dissociation between the neural networks involved in the processing of correct grammatical sentences and the networks involved in the processing of anomalous sentences with a person mismatch. Based on the previous experiment (Chapter 6), we predict that grammatical sentences (Standard Agreement and Unagreement) in comparison to anomalous constructions should lead to increased activity within an extended left fronto-temporal network, including the anterior and posterior middle temporal gyrus and the inferior and middle frontal gyri (Kuperberg et al., 2003; Kuperberg, Sitnikova, et al., 2008). For the processing of grammatically anomalous constructions with a person violation, relative to grammatical ones (Standard Agreement and Unagreement), we expect predominant activation of the anterior cingulate cortex and parietal areas, brain regions previously related

---

[3] In natural language (when each word is perceived/read every ~350 ms), comprehension of Unagreement constructions is not as penalized as Person Mismatch comprehension (see Mancini et al., under review). This means that native Spanish speakers automatically acknowledge the grammaticality of Unagreement constructions before 500 ms post-stimulus onset. As a consequence, this suggests that differential processes would be at work in the 300-500 ms time interval.

to conflict-monitoring operations (Kolk et al., 2003; Kuperberg, Sitnikova, et al., 2008; van de Meerendonk et al., 2011; Vissers et al., 2006).

More importantly, the present experimental design allows fine-grained discrimination of brain regions that are critically involved in core agreement processing. In fact, we should be able to report some region(s) associated to subject-verb morpho-syntactic mismatch detection showing increased activation for both Unagreement and Person Mismatch, irrespective of sentence grammaticality. Previous findings point to the pars opercularis (within the left inferior frontal gyrus) and the anterior part of the left superior temporal gyrus as possible candidates for the processing of syntactic mismatches (Friederici, 2011; Hagoort, 2005).

Moreover, as indicated above, the successful integration of different speech roles in Unagreement sentences (speaker and non-participants) should involve the activation of areas related to semantic integration processes, reflecting the increased semantic-discourse complexity of these constructions compared to Standard Agreement. In this sense, the angular gyrus and the anterior middle temporal gyrus could be plausible candidates, and increased activation for the Unagreement compared to the other two conditions would confirm this. Among these two candidates, the angular gyrus could critically serve complex semantic integration operations (Bemis & Pylkkänen, 2012a) (see also the Discussion section of Chapter 4). This would be supported by the neuro-anatomical localization of this region in the parietal cortex and its anatomical connectivity with different subsystems, including parietal (e.g., precuneus), temporal (e.g., inferior, middle and posterior temporal regions) and frontal networks (e.g., inferior frontal gyrus at the level of areas BA44 and BA45) (Catani et al., 2012; Catani & Mesulam, 2008; Catani & Thiebaut de Schotten, 2008; Thiebaut de Schotten et al., 2012). Recent meta-analyses have indeed emphasized the crucial role of the angular gyrus in the processing of different types of semantic complexity. Binder et al. (2009) proposed that this brain structure "occupies a position at the top of a processing hierarchy underlying concept retrieval and conceptual integration, thus suggesting that the angular gyrus mediates fluent conceptual combination, such as sentence comprehension, discourse, problem solving, and planning" (Binder et al., 2009, page 2776).

7.2 Materials and Methods

Participants. Twenty-five healthy subjects participated as paid volunteers in the study. After the quality checking of the data, a total of twenty-one participants (nine females), with ages ranging from 17 to 35 years (mean = 22.62, standard deviation = 4.43), were used to estimate the group effects.

Stimuli and experimental design. Each subject participated in a single session consisting of two pseudo-randomized repetitions of an event-related design functional scan. Each scan consisted in a serial presentation of sentences grammatically acceptable or ungrammatical. Sentences were visually presented word by word and after each sentence a cue was shown instructing the participant to make a grammaticality judgment by pressing one of two different buttons (a go/go paradigm) (Fig. 7.1). Words were displayed in white letters on a black background. Each word was presented for 300 ms, followed by a 500 ms blank screen. In order to optimize the design statistical efficiency, a fixation point ("+") between successive sentences were presented in different ("jittered") durations across trials (1.87, 3.56, 4.96 seconds, in the proportion of 57:28:15) (Dale, 1999).

The stimulation set consisted of 120 sentences which included three different conditions (in the proportion of 1:1:1): *Standard Agreement*, *Unagreement* and *Person Mismatch* (see Figure 7.1 A). All sentences contained a lexical subject followed by a past tense verb (the critical word), which was always followed by at least two words. The two grammatical conditions included a plural subject, i.e. the *Standard Agreement* and the *Unagreement*, whereas the ungrammatical condition (*Person Mismatch)* contained a singular subject. In the *Standard Agreement* condition the third person plural subject is followed by a third person plural verb, while in the *Unagreement* condition the third person plural subject could be followed by both a first and a second person plural verb. Meanwhile, the *Person Mismatch* condition contained a third person singular subject followed by a second singular verb. The choice of past tense verbal forms was mainly motivated by the need to keep the length of the critical word balanced across conditions (*Standard Agreement*: mean length = 9.66, SD = 2.5; *Unagreement*: mean length = 9.39, SD = 2.34;

Person Mismatch: mean length = 9.38, SD = 2.34), which could not be done with other verb tenses.

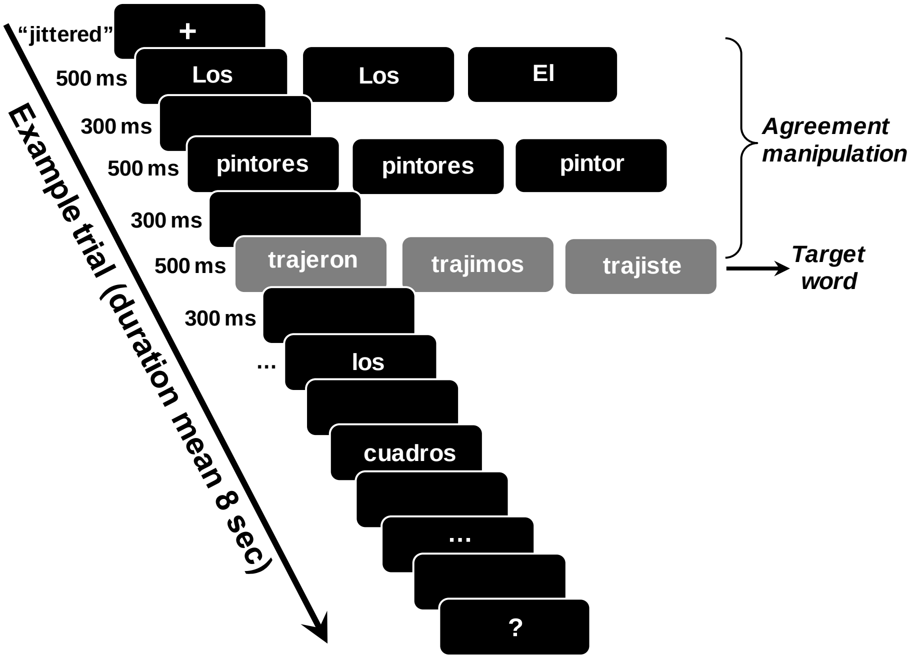


Figure 7.1. Schematic representation of an experimental trial.

In order to balance the proportion of acceptable/unacceptable sentences and avoid expectations concerning the morphological form of the verb, 120 filler sentences with a similar sentence structure were added to the material. Ungrammatical sentences contained both person and number mismatches between subject and verb. Importantly, since unacceptable experimental sentences (*Person Mismatch* condition) always involved a third person singular subject followed by a second person singular verb, incorrect fillers comprised both a third person singular subject followed by a third person plural verb (40 sentences, e.g., "**El pintor*$_{3.sg}$ *trajeron*$_{3.pl}$ *un cuadro…*"), and a third person plural subject followed by a third person singular verb (40 sentences, e.g., "**Los pintores*$_{3.pl}$ *trajo*$_{3.sg}$ *un cuadro…*"). Forty additional correct fillers of the type *"El pintor*$_{3.sg}$ *trajo*$_{3.sg}$ *un cuadro…"* were also added to balance the overall number of correct and incorrect sentences. This was in order to avoid expectations concerning the morphological form of the verb, especially for the ungrammatical sentences (for a similar design see Mancini et al., 2011b).

Despite the fact that the *Unagreement* pattern represents a marked agreement construction compared to the full agreement counterpart, its frequency of use is very high, above all in spoken Spanish. Due to the lack of an adequate corpus of spoken Spanish from which to draw the frequency of this pattern, previous studies of our lab assessed the acceptability of this type of construction (Mancini et al., 2011b; Pérez et al., 2012). They tested a group of native speakers of Spanish using a naturalness judgment task. The task was to read all of the sentences in the three experimental conditions (i.e., Unagreement, Standard Agreement and Person Agreement Violation) and judge how natural each of them sounded on the basis of a 1-to-7 point scale. These participants reported awareness only of the *Person Mismatch* manipulations; while they rated *Unagreement* and *Standard Agreement* sentences as being equally natural.

Image acquisition and functional data analysis. The acquisition of the functional and the structural images and also the pre-processing of the data were carried out following the same procedure used in Experiment IV (Chapter 6). Statistical parametric maps were generated by modeling univariate general linear model, using for each stimulus type a regressor obtained by convolving the canonical hemodynamic response function with delta functions at stimulus onsets[31], and also including the six motion-correction parameters as regressors. The GLM were estimated using a robust regression (see previous experimental chapters for similar procedures). A pair-wise contrast comparing activity to each phrase type relative to every other phrase type was performed (*Unagreement > Standard Agreement, Person Mismatch > Standard Agreement, Standard Agreement > Person Mismatch, Unagreement > Person Mismatch and Person Mismatch > Unagreement*). Resulting contrast images were then entered into a second level design analysis to enable population inferences. Additionally, contrast images for each of the three conditions compared to the fixation baseline were submitted into a second level One Way ANOVA (*Standard Agreement*, *Unagreement* and *Person Mismatch*). This analysis would allow us to determine

---

[31] The stimuli onsets include six different components. The first one corresponded to the onset of each sentence trial and was modelled as a single regressor, independently of the experimental conditions. The next four corresponded to each experimental condition (Full Agreement, Unagreement, Person Mismatch and Fillers) and lasted from the onset of the critical verb. In the last component the response time was included, lasting from the onset of the response mark.

whether differences between experimental conditions were due to activation or deactivation with respect to the fixation baseline condition. Population-level inferences were tested using the SPM8 random effects model that estimated the second level t statistic at each voxel. Those peaks or clusters with a p-value corrected for multiple comparisons with family wise error (FWE; Nichols & Hayasaka, 2003) and/or false discovery rate (FDR; Genovese et al., 2002) were reported in the tables of results. All local maxima were reported as MNI coordinates (Evans et al., 1993).

7.3 Results

Behavioral results. Percentage of correct response and mean reaction times (RT) for *Standard Agreement*, *Unagreement* and *Person Mismatch* are presented in Table 7.2, with the corresponding standard error between parentheses. Percentage of correct responses was above 85 % for all experimental conditions, indicating that the participants judged the sentences corresponding to the *Standard Agreement* and *Unagreement* conditions as grammatically acceptable in contrast to the *Person Mismatch* sentences that were judged as grammatically unacceptable.

Table 7.2. Percentage of correct response and mean decision times (in ms) for the three types of sentences with standard error between parentheses.

	RT	Hits
Standard Agreement	629.32 (38.06)	90.37 (1.80)
Unagreement	664.28 (39.29)	87.50 (1.60)
Person Agreement Violation	568.03 (34.53)	90.00 (2.68)

One way ANOVAs on mean response times and accuracy were performed using the conditions (*Standard Agreement*, *Unagreement* and *Person Mismatch*) as factor. This analysis showed no significant difference in accuracy among the three conditions. However, for RTs, a significant main effect of condition was found ($F (2, 40) = 9.11$, $p < 0.001$, $\varepsilon =$

0.99). In consonant with the previous experiment (Chapter 6), planned comparisons demonstrated that the detection of *Person Mismatch* was faster (lower RT) than the detection of grammatically acceptable sentences, including *Standard Agreement* (t (20) = 2.60, p < 0.05) and *Unagreement* (t (20) = 4.48, p < 0.001) conditions. This result is consistent with previous ones (Kuperberg et al., 2003; Mancini et al., 2011a, 2011b; Nevins et al., 2007; Nieuwland et al., 2012) and may reflect the additional time required for the syntactic-semantic integration processes triggered by grammatical sentences relative to the grammatical error detection processes evoked by ill-formed constructions (see Molinaro et al., 2013 for a discussion of this behavioral pattern of results). It is important to note that although Unagreement processing entails more processing difficulties in constructing sentence meaning than the Standard Agreement pattern, the time required to judge the grammaticality of these two conditions was not statistically different (t (20) = 1.50 , p > 0.05).

All Sentences versus Fixation. To characterize the functional neuro-anatomical network that was recruited by the processing of sentences, independently of the experimental manipulation, we performed a One-Way ANOVA comparing each sentence type with the fixation point condition. The statistical parametric map resulting from the main effect is displayed in Figure 7.2, overlaid on the surface of the MNI single-subject T1 image (for more details see Box 7.1 that shows the comparison between each sentence type and the fixation baseline condition) and reveals the significant response of a widespread fronto-parieto-temporal network bilaterally distributed but with a strong left lateralization (Figure 7.2). This network includes brain regions such as the left pars opercularis, triangularis and orbitalis within the inferior frontal gyrus, as well as the anterior and posterior part of the left middle temporal cortex, the left superior temporal sulcus, the supramarginal cortex, the inferior parietal gyrus and the angular gyrus, typically related to different stages of language processing. Additionally, the left and right fusiform gyrus and the left and right inferior and middle occipital cortex, associated to early stages of visual word perception, showed significant activation for all sentences compared to the baseline condition. Also, regions involved in the planning and execution of motor behavioral responses, such as the supplementary motor area and the precentral and postcentral cortex in both hemispheres exhibited a higher response pattern in this comparison.

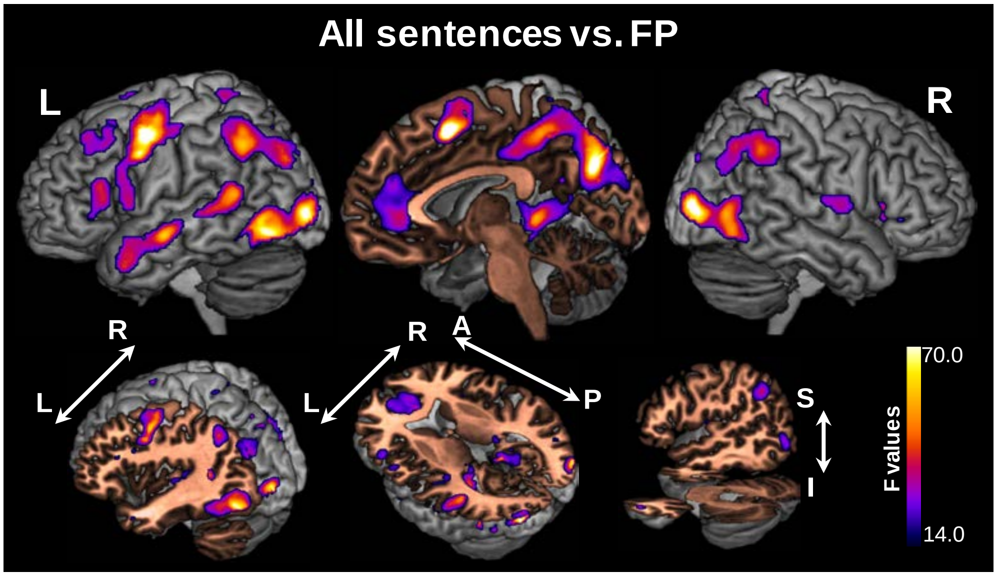
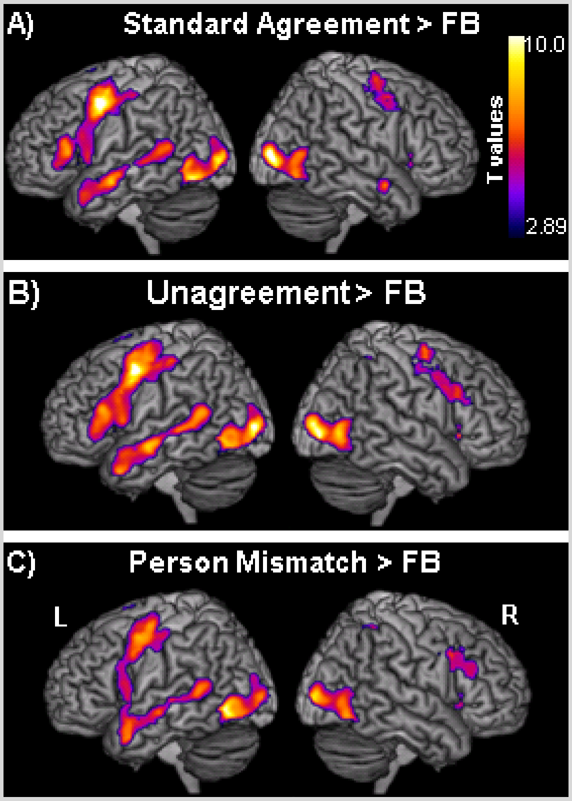


Figure 7.2. Significant activation clusters resulting from the contrast *All sentences vs. Fixation baseline* were projected on the surface of the MNI single-subject T1 image. All clusters depicted at p<0.05 corrected for multiple comparisons. L: left; R: right; A: Anterior; P: Posterior; I: Inferior; S: Superior; FB: Fixation baseline.

Box 7.1. Significant activation clusters resulting from the contrast *Default Agreement vs. Fixation baseline* (A), *Unagreement vs. Fixation baseline* (B) and *Person Mismatch vs. Fixation baseline* (C). Statistical parametric maps were projected on the surface of the MNI single-subject T1 image. All clusters depicted at $p<0.05$ corrected for multiple comparisons. L: left; R: right; FB: Fixation baseline.

Note that similar results emerge from the three types of sentences independently of their grammaticality.



Person Mismatch versus Grammatical Sentences. To dissociate the neural correlates corresponding to morpho-syntactic mismatch detection and conflict-monitoring from those related to the integration of meaningful information, we compared the response pattern between *Person Mismatch* and the grammatical sentences (*Standard Agreement* and *Unagreement*). A significant increase of activation for the *Person Mismatch* relative to the *Standard Agreement* condition was observed in a bilateral fronto-parietal network (see Table 7.3 and Figure 7.3). This network included the middle frontal gyrus, the anterior and middle cingulate cortices, the inferior parietal cortex and the cuneus/precuneus. All these neural regions showed a similar activation pattern in both cerebral hemispheres. In addition, we found a significant increase of activation for the supramarginal gyrus exclusively in the right hemisphere. Furthermore, significant difference in the response pattern of the rectus within the ventro-medial orbitofrontal cortex was found, although this region exhibited deactivation when the three types of sentences were compared to the fixation baseline condition. In the same way, the recruitment of a similar pattern of activation was found when comparing *Person Mismatch* and *Unagreement* (see Table 7.3).

<u>*Grammatical Sentences versus Person Mismatch.*</u> The *Standard Agreement* relative to *Person Mismatch* condition showed a significant increase of activation with a left hemisphere lateralization, including temporal and frontal regions (see Table 7.3 and Figure 7.4 A). The frontal activation patch comprised inferior frontal regions (pars triangularis and pars orbitalis) and the precentral/postcentral cortex. The increase of activation in the temporal areas recruited by *Standard Agreement* included the superior temporal gyrus, anterior and posterior part of the middle temporal gyrus and the inferior temporal gyrus, as well as the fusiform area and the lingual cortex.

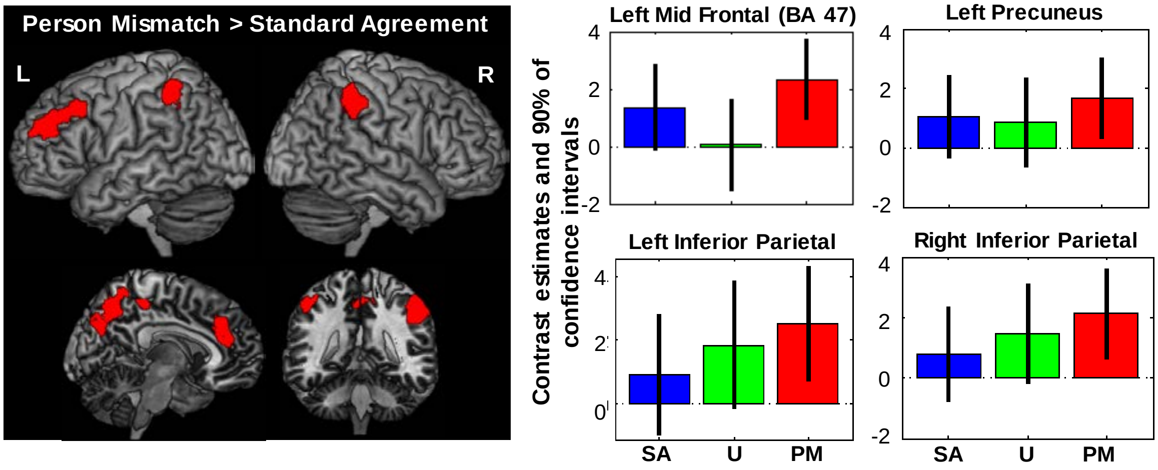


Figure 7.3. Significant activation clusters resulting from the contrast *Person Mismatch* vs. *Standard Agreement* are represented in red. Statistical maps were overlaid on the surface (left panel) of the MNI single-subject T1 image. The bar graph in the right panel displays the contrast estimates and 90% of confidence intervals for the three experimental conditions compared to the fixation baseline (SA: Standard Agreement; U: Unagreement; PM: Person Mismatch) at different maximum peaks representative of the significant activated clusters. The three experimental conditions are represented in the right panel with different colors (Standard Agreement in blue; Unagreement in green; Person Mismatch in red). L: left hemisphere; R: right hemisphere.

Table 7.3. Brain activation for each critical pair-wise comparison.

Region	Person Mismatch > Standard Agreement			Standard Agreement > Person Mismatch			Unagreement > Person Mismatch			Unagreement > Standard Agreement			Person Mismatch > Unagreement		
	x,y,z {mm}	Z	Vx	x,y,z {mm}	Z	Vx	x,y,z {mm}	Z	Vx	x,y,z {mm}	Z	Vx	x,y,z {mm}	Z	Vx
L Inf Frontal Tri (BA45)				-52 28 10	3.55	128	**-46 30 4**	**4.77**	**1353**						
L Inf Frontal Tri (BA48)							-46 16 30	4.01	1353						
L Inf Frontal Orb (BA47)							-49 30 -4	3.12	1353						
L Rectus				**-8 26 -14**	**4.91**	**426**	-4 46 -18	4.31	281						
L Med Frontal Orb				**-4 50 -12**	**4.77**	**426**									
L Sup Med Frontal	**-2 34 34**	**4.89**	**406**				**-10 54 32**	**4.82**	**330**						
L Mid Frontal (BA44)	-44 22 36	4.33	459							-42 18 40	3.78	173			
L Mid Frontal (BA45)	-40 46 22	4.26	459												
L Mid Frontal (BA46)	-32 46 34	4.68	459										-30 56 22	**4.77**	**602**
L Ant Cingulate													-4 36 8	4.04	583
L Inf Parietal	-42 -46 58	4.31	225												
L Postcentral				-60 2 20	3.94	125									
L Precentral (BA6)				-54 0 26	2.87	125	-34 2 58	3.22	107						
L Precentral (BA9)							-34 10 44	3.1	107						
L Precuneus	**-6 -66 50**	**5.14**	**1171**												
L Angular										-40 -56 28	3.51	74			
L Sup Temporal				-44 -36 20	3.4	283									
L Mid Temporal P							-42 14 -32	4.36	415						
L Ant Mid Temporal				-62 -4 -20	4.76	221	-58 -12 -18	3.97	415						
L Post Mid Temporal				-44 -48 14	4.21	283	-54 -50 14	3.8	259						
L Inf Temporal				-56 -4 -26	3.7	221									
L Lingual				-14 -82 -8	4.26	272									
L Fusiform				-32 -74 -10	3.74	272									
R Rectus							4 26 -18	3.96	281						
R Sup Frontal										**12 32 38**	**5.07**	**89**			
R Mid Frontal (BA45)													40 42 6	3.86	622
R Paracentral Lobule	10 -32 52	4.43	1171												
R Ant Cingulate	6 40 26	4.36	406										6 42 2	4.46	583
R Inf Parietal	56 -42 50	4.25	434												
R Supramarginal	58 -36 44	4.19	434										58 -32 48	4.75	754
R Mid Cingulate													10 -26 38	4.61	1614
R Precuneus													6 -54 66	4.27	1614

x,y,z {mm} = Coordinates in MNI space of local maxima. Z = Z scores. Vx = Number of voxels significantly activated inside the cluster belonging to each local maximum. Z scores and Vx are reported in bold if they are significant at the peak level after FWE or FDR correction (p<.05), if indicated by underline they are significant at p<.001 uncorrected. All others are significant at the cluster level after FWE or FDR correction (p<.05). Inf: Inferior; Tri: Triangularis; Orb: Orbitalis; Med: Medial ; Sup: Superior; Mid: Middle; Ant: Anterior; L: Left; R: Right.

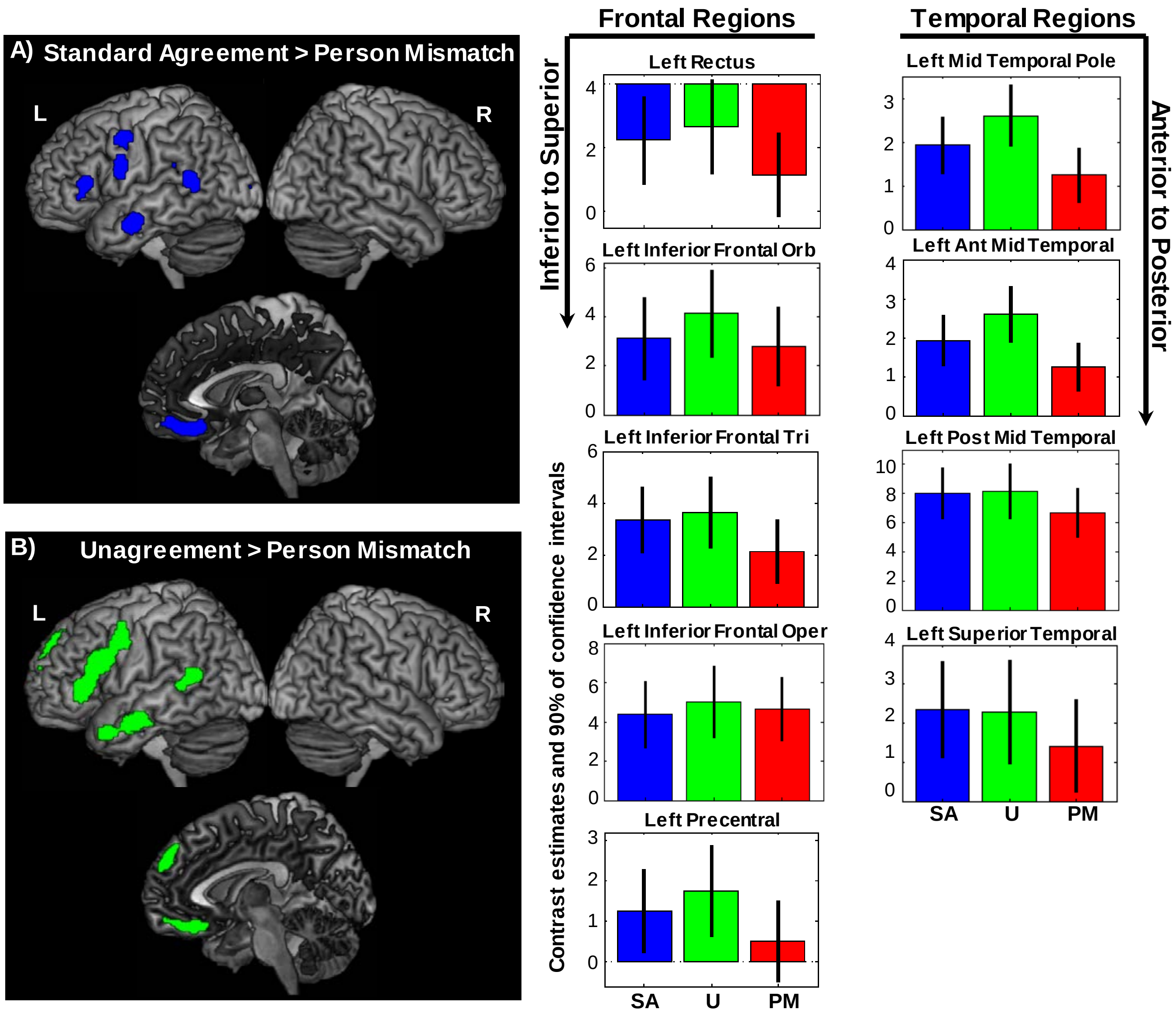


Figure 7.4. Significant activation clusters resulting from the contrast *Standard Agreement vs. Person Mismatch* (A) and *Unagreement vs. Person Mismatch* (B). Statistical maps were projected on the surface (A) of the MNI single-subject T1 image. The bar graph in (B) displays the contrast estimates and 90% of confidence intervals for the three experimental conditions compared to the fixation baseline (SA: Standard Agreement; U: Unagreement; PM: Person Mismatch) at different maximum peaks representative of the significant activated clusters. The three experimental conditions are represented with different colors (Standard Agreement in blue; Unagreement in green; Person Mismatch in red). L: left; R: right; Mid: middle; Ant: anterior; Post: posterior.

Similarly to the *Standard Agreement* versus *Person Mismatch* contrast presented above, when comparing *Unagreement* and *Person Mismatch* (see Table 7.3 and Fig. 7.4 B), the activation of a similar fronto-temporal network was found, highlighting that the processing of grammatical sentences, whether fully agreeing or “unagreeing”, involves akin neural substrates. This was confirmed by the comparison between the pattern of activation evoked by *Unagreement* and *Standard Agreement* with the fixation point, from which the engagement of analogous neural substrates emerged. Box 7.1 (A and B) summarize this result. Note that the activation pattern evoked by *Unagreement* and *Standard Agreement* was restricted to the left hemisphere, contrary to the activation pattern elicited by *Person Mismatch* that comprised regions in both hemispheres. Interestingly, if we observe the activation pattern of the *Unagreement* and *Full Agreement* sentences compared to the *Person Mismatch* (bar graph in the right side of Figure 7.4) we can note differences between *Unagreement* and Standard *Agreement* in the pars orbitalis and the most anterior part of the middle temporal cortex. These regions appear to be more activated by the Unagreement sentences.

<u>*Unagreement versus Standard Agreement.*</u> The *Unagreement* response compared to *Standard Agreement* evoked significant increases of activation in the left angular gyrus, the left middle frontal and the right superior frontal cortex (see Table 7.3 and Figure 7.5 A). Within this network it is possible to detect the regions involved in morpho-syntactic mismatch detection and also regions recruited by the increased semantic complexity of the Unagreement construction. To disentangle between these different qualitative processes, we superimposed this response (*Unagreement* versus *Standard Agreement*) on the *Person Mismatch* versus *Standard Agreement* contrast (Figure 7.5 B, where the common response is represented in yellow). The posterior part of the left middle frontal gyrus is commonly activated by both *Unagreement* and *Person Mismatch*, suggesting that this region is involved in morpho-syntactic mismatch detection (see Table 7.1).

On the other hand, the left angular gyrus is specifically activated by the *Unagreement* sentences (represented in green in Figure 7.5 B). The mean of the contrast estimates between subjects for each condition (*Standard Agreement*, *Unagreement* and

Person Mismatch) in both regions (the left angular gyrus and the left middle frontal cortex) are shown on the right side of the Figure 7.5. The engagement of the angular gyrus in subject-verb agreement comprehension is a relatively novel finding (see the Discussion section of the current chapter and also the Discussion section of the Chapter 4). When we explored the single-subject activation response of this region we observed a large variability in the activation pattern across participants.

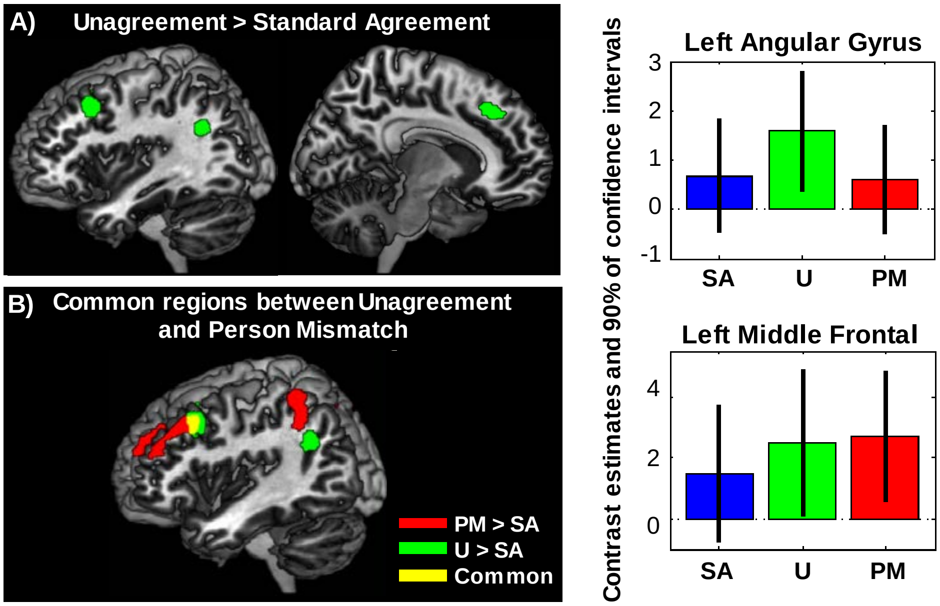


Figure 7.5. A) Significant activation clusters resulting from the contrast *Unagreement vs. Standard Agreement.* B) Superimposition of the significant activation clusters resulting from the contrasts *Person Mismatch* vs. *Standard Agreement* and *Unagreement vs. Standard Agreement*. Statistical maps were projected on the surface of the MNI single-subject T1 image. Yellow voxels represent significant activated voxels in both contrasts. The bar graph in the right side of the image displays the contrast estimates (*Unagreement vs. Standard Agreement*) and 90% of confidence intervals for the three experimental conditions compared to the fixation baseline (SA: Standard Agreement; U: Unagreement; PM: Person Mismatch) at different maximum peaks, representative of the significant activated clusters. The three experimental conditions are represented in the bar graph with different colors (Standard Agreement in blue; Unagreement in green; Person Mismatch in red). Mid: middle. Note that only Unagreement condition statistically differs from the fixation baseline condition.

In an attempt to clarify this finding and explore the behavioral consequence of this activation variability, we estimated the correlation between the signal change in this region and the corresponding reaction time and percentage of accuracy per condition (*Standard Agreement*, *Unagreement* and *Person Mismatch*). Remarkably, a significant correlation was obtained between the activation pattern of the left angular gyrus and the performance scores of the *Unagreement* grammaticality judgment (see Fig. 6.6). Participants with greater activation in left angular gyrus showed faster reaction time ($\beta = -0.0003$ [$t(19) = -2.17$, $p < 0.05$], $R^2 = 0.20$, adjusted $R^2 = 0.16$, $F(1, 19) = 4.69$, $p < 0.05$) and higher percentage of accuracy ($\beta = 0.011$ [$t(19) = 2.82$, $p < 0.01$], $R^2 = 0.30$, adjusted $R^2 = 0.26$, $F(1, 19) = 7.96$, $p < 0.01$). The recruitment of this region thus seems critical for the successful integration of the Unagreement pattern: the activation pattern of the left angular gyrus does not show any relation with the behavioral measures associated to the other two conditions.

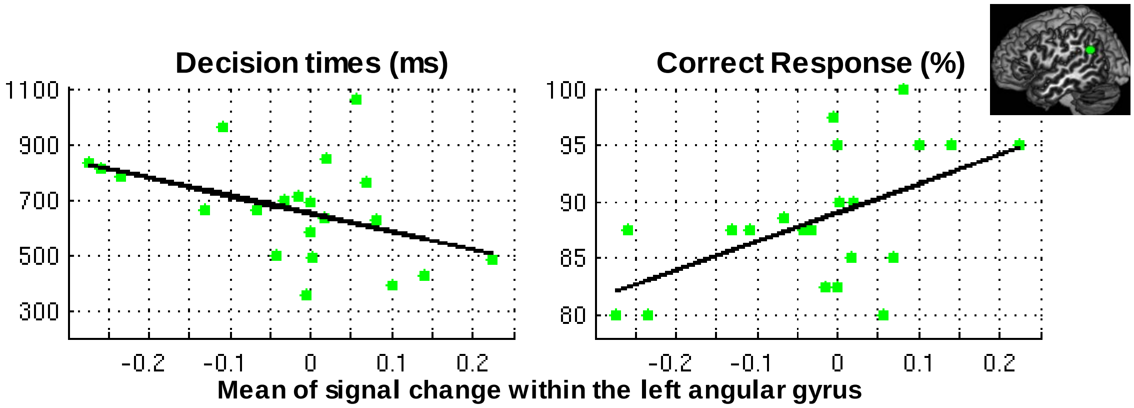


Figure 7.6. Correlation analysis between the behavioral measures (decision times and percentage of correct responses) and the signal change of the left angular gyrus.

7.4 Discussion

The main goal of the present study was to dissociate the neuro-anatomical substrates of the different processing steps involved in subject-verb agreement comprehension in Spanish by taking advantage of the Unagreement construction. First of all, in line with our predictions, we isolated the brain network involved in subject-verb morpho-syntactic integration from the ones related to conflict-monitoring triggered by the detection of agreement grammatical errors. On the one hand, all sentences types (Unagreement, Standard Agreement and Person Mismatch relative to baseline) evoked increase of activation in a left lateralized fronto-temporal network, with higher activation for grammatical than anomalous sentences (grammatical sentences relative to Person Mismatch). This network includes the inferior frontal gyrus, the precentral/postcentral cortex, the superior temporal cortex, anterior and posterior part of the middle temporal gyrus and the inferior temporal gyrus, as well as the fusiform area and the lingual cortex. On the other hand, an additional bilateral fronto-parietal network was recruited exclusively by the Person Mismatch condition (Person Mismatch relative to baseline; Person Mismatch relative to grammatical sentences), including the anterior part of the middle frontal gyrus, the rectus, the anterior and middle cingulate cortices, the inferior parietal cortex and the cuneus/precuneus.

The engagement of this bilateral fronto-parietal network associated to anomalous sentences has been previously reported, not only in the context of subject-verb agreement computation (Kuperberg et al., 2003; Kuperberg, Sitnikova, et al., 2008; Ni et al., 2000), but also related to the processing of other aspects of language perception (Bambini et al., 2011; Kerns et al., 2004; Lauro et al., 2008; Novick et al., 2005; van de Meerendonk et al., 2011; van de Meerendonk et al., 2009; van de Meerendonk et al., 2010; Ye & Zhou, 2009). As we previously discussed, the response of this network may reflect the engagement of the conflict monitoring system, probably triggered by the grammatical subject-verb agreement error (for instance, "The painter$_{3.sg}$ brought$_{2.sg}$") (for alternative viewpoints see the Discussion Section of Kuperberg, Sitnikova, et al., 2008). The involvement of this monitoring system in the processing of the Person Mismatch condition is consistent with Mancini et al. (2011b). Their ERP results demonstrated a clear distinction in the electrophysiological responses associated to ungrammatical and grammatical sentences: only Person Mismatch evoked the P600 component.

As indicated above, the three conditions (Standard Agreement, Unagreement and Person Mismatch) recruit a left lateralized fronto-temporal network irrespective of their grammaticality. However, some regions within this network exhibited a different sensitivity to grammatical than anomalous sentences (see Figure 7.4). In fact, while the pars opercularis and the pars orbitalis within the inferior frontal gyrus respond similarly to both grammatical and ungrammatical sentences, the pars triangularis and the precentral/postcentral cortex dissociate between grammatical and ungrammatical conditions, with Standard Agreement and Unagreement generating greater activation compared to Person Mismatch. A similar dissociation was found in the temporal regions. In fact, while the anterior and posterior part of the middle temporal gyrus and the inferior temporal cortex exhibited a greater response for grammatical sentences than ungrammatical ones, in the superior temporal cortex a similar increased response was found for the three conditions, irrespective of the grammaticality of the sentence.

As we previously pointed out, this left fronto-temporal network has been the focus of attention of the sentence comprehension research community during the last decade (see Bornkessel-Schlesewsky & Schlesewsky, 2013; Friederici, 2011 for two recent and divergence points of view). Different theoretical frameworks have hypothesized about the specific role played by each node of this network during sentence processing (see Chapter 1 for an extensive discussion about this topic). Taking the current data in isolation, we cannot elucidate which of these proposals fits better with our data. For instance, the activation of the left inferior frontal gyrus for all the sentence types independently of grammaticality is compatible with the most recent model of sentence comprehension proposed by Bornkessel-Schlesewsky and Schlesewsky (2013). This perspective suggests that the functional role of the frontal regions (including the inferior frontal gyrus) is not specifically related to language per se, but serves to integrate different linguistic information with behavior, due to its role in cognitive control mechanisms (in an experimental context this would be reflected in the task responses). This idea is highly appealing and consistent with previous evidence (for an extensive revision of this topic see Bornkessel-Schlesewsky & Schlesewsky, 2013). However, the higher activation level of the pars triangularis exhibited by grammatical sentences (Standard Agreement and Unagreement) as compared to ungrammatical ones (Person Mismatch) fits well with the model proposed by Friederici and colleagues (Friederici, 2011, 2012; Friederici & Gierhan, 2013), suggesting that this inferior frontal sub-region is part of a (larger) semantic network (see Newhart et al., 2012 for a double dissociation between working memory/cognitive control mechanisms and sentence processing in the inferior frontal gyrus).

However, crucially, the experimental design used here can shed light on the neural correlates of two different processing stages underlying agreement computation: a) the evaluation of subject-verb morpho-syntactic consistency recruits the posterior part of the left middle frontal gyrus and b) discourse-semantic integration processes critically rely on the involvement of the left angular gyrus as part of the more domain-general semantic network. In the following paragraphs we will detail these two major points (see Table S1 for an updated summary of the results and a comparison across the experiments).

Table S1. Main Findings

	Behavioral results	Neuro-anatomical results	
		Grammaticality effects	Effects related with the critical manipulation
Experiment I (determiner-noun pairs)	**Main effect of Agreement Congruency**: Subjects classified determiner-noun pairs as grammatically correct more easily and accurately than incongruent pairs. This differentiation was evident for both transparent and opaque nouns. **Interaction effect**: Regarding RT, this effect was larger for opaque than for transparent nouns.	***Gender Mismatch* relative to *Gender Match***: the dorsal striatum, the middle and medial superior frontal gyrus, the medial orbito-frontal cortex, the pre- and post-central gyrus, as well as the anterior cingulate cortex. ***Gender Match* as compared to *Gender Mismatch***: the pars opercularis and triangularis within the left IFG and the posterior part of the left MTG/STG.	Significant **interaction effects** between Gender Congruency and Gender-marking emerged in five left-lateralized clusters: ▪ Pars triangularis within the IFG ▪ Posterior part of the MTG/STG ▪ Hippocampus ▪ Angular Gyrus ▪ Supramarginal Gyrus
Experiment II	**Null effects** for RT and error rates.	***Gender Mismatch* relative to *Gender Match***: the pars triangularis, orbitalis and opercularis within the left IFG, the middle frontal gyrus, as well as the inferior parietal gyrus and the supramarginal and the angular gyri. ***Gender Match* as compared to *Gender Mismatch***: the middle and medial superior frontal gyrus, the medial orbito-frontal cortex, the anterior cingulate cortex, as well as the anterior part of the left MTG/STG and the superior and middle temporal pole.	Significant **interaction effects** between Gender Congruency and Type of Gender emerged in two left-lateralized clusters: ▪ Inferior Parietal ▪ Angular Gyrus

Experiment III	**Main effect of Agreement Congruency**: Subjects classified word pairs as grammatically correct more easily and accurately than incongruent pairs. This Left angular gyrusdifferentiation was evident for both determiner-noun and subject-verb pairs. **Interaction effect**: Regarding RT, this effect was larger for determiner-noun pairs than for subject-verb pairs.	***Number Mismatch* relative to *Number Match***: the right and left insula, the pars orbitalis, opercularis and triangularis within the left IFG, the pre- and post-central gyrus, as well as the inferior parietal cortex. ***Number Match* as compared to *Number Mismatch****:* the middle and superior frontal gyrus, the anterior cingulate cortex, the medial orbito-frontal cortex, as well as the anterior part of the MTG/ITG.	Significant **interaction effects** between Number Congruency and Type of Word Pair emerged in three left-lateralized clusters: ▪ Left pars opercularis within the IFG ▪ Left anterior part of the MTG/STG ▪ Left and right precuneus/Cuneus
Experiment IV	**Main effect of Agreement Congruency**: Subjects classified word pairs as grammatically incorrect more easily and accurately than congruent items. This differentiation was evident for both person and number agreement violations.	***Ungrammatical* relative to Grammatical sentences**: the medial superior frontal gyrus, the middle frontal gyrus, the postcentral gyrus, the middle cingulate cortex, as well as the inferior and superior parietal cortices. ***Grammatical* relative to Ungrammatical sentences***:* the pars orbitalis and triangularis within the left IFG, the superior frontal gyrus, as well as the posterior and anterior portions of the left MTG/STG and the superior temporal pole.	Significant **differences** between *Number* and *Person Agreement Violation* emerged in four left-lateralized clusters: ▪ Left pars orbitalis within the IFG ▪ Left pars triangularis within the IFG ▪ Left anterior part of the MTG/STG ▪ Left posterior part of the MTG/STG
Experiment V	**Main effect of Agreement Congruency**: Subjects classified word pairs as grammatically incorrect more easily and accurately than congruent items.	***Ungrammatical* relative to Grammatical sentences**: the medial superior frontal gyrus, the middle frontal gyrus, the anterior cingulate cortex, as well as the inferior parietal cortex. ***Grammatical* relative to Ungrammatical sentences***:* the pars orbitalis and triangularis within the left IFG, the superior frontal gyrus, the medial orbito-frontal cortex, the pre- and post-central gyri, as well as the posterior and anterior portions of the left MTG/STG.	The **commonalities** between Person Mismatch and Unagreement emerged in: ▪ Left middle frontal gyrus The **differences** between Unagreement and Standard Agreement emerged in: ▪ Left angular gyrus

Morpho-syntactic detection processing. One of the main results of the present study is the dissociation found in the middle frontal cortex, where a differential response is shown for the two morpho-syntactic subject-verb mismatches (Unagreement and Person Mismatch). On the one hand, in a posterior portion of the middle frontal gyrus we found activation for both Person Mismatch and Unagreement. On the other hand, a more anterior part of the middle frontal cortex responds only to Person Mismatch (see Figure 6.3). Importantly, both types of stimuli involve a person mismatch, although with a different grammatical status.

The similarity in the activation pattern of Person Mismatch and Unagreement sentences is consistent with the results obtained in the ERP experiment showing that both Person Mismatch and Unagreement evoke a posterior negative effect between 300 and 500 ms compared to Standard Agreement sentences (Mancini et al., 2011b). It is therefore possible that the posterior portion of the middle frontal gyrus contributes to the generation of this early negative component, although this hypothesis requires further evidence. As we discussed in the previous chapters, this finding is consistent with previous fMRI results from a variety of languages and agreement dependencies (see Results and Discussion sections in Chapters 3, 4, 5 and 6).

As debated in the Discussion section of the Chapter 3 (Experiment I), there are two different points of view that can explain this common activation in the posterior part of the middle frontal cortex recruited by Person Mismatch and Unagreement. First (from a more domain-general perspective), it may be that this common activation reflects the involvement of more general working memory mechanisms (see Katsuki & Constantinidis, 2012a; 2012b for the involvement of the dorsolateral prefrontal regions in working memory processes) associated to the evaluation of the morpho-syntactic relation between the person feature of the (subsequently presented) subject (*"El pintor/The painter*$_{3sg.}$*"*) and verb (*"trajiste/brought*$_{2sg.}$*"*). In this sense, Murray and Ranganath (2007) explored the functional brain activity during a sequential encoding of word pairs while participants either made a semantic judgment related to the second word or a semantic judgment that involved a comparison between the second word and the previous word. This experiment demonstrated activity increases of dorsolateral prefrontal regions during relational compared with item-specific encoding, suggesting that this frontal region play a critical role for building relationships between items during on-line processing (see also Blumenfeld & Ranganath, 2006; Murray & Ranganath, 2007). This idea is consistent with previous studies that have reported the activation of this frontal region in association with more general aspects of language processing: verbal fluency tasks (Abrahams et al., 2003) and visual Stroop congruency tasks (Ye & Zhou, 2009).

As the second plausible explanation (from a more language-specific domain), this sub-region within the middle frontal gyrus would be crucially engaged in checking the morpho-syntactic match between two sentence constituents, irrespective of its grammaticality. Several models of sentence comprehension consider morpho-syntactic checking as an initial critical step for building up the syntactic structure of a sentence that depends on agreement relations (Friederici, 2011, 2012; Friederici & Gierhan, 2013). The low temporal resolution of fMRI does not clarify the chronology of the brain regions involved in the processing of these two experimental conditions (Person Mismatch and Unagreement): thus, we cannot temporally determine if the posterior part of the left middle frontal gyrus is activated earlier compared to the other brain regions that are significantly activated for these conditions. Nonetheless, the fact that Unagreement and Person Mismatch *only* share the morpho-syntactic subject-verb incongruency (Unagreement differs from person violations because it can be successfully integrated) supports the idea that this common brain activation for the two conditions would reflect processes involved in the evaluation of morpho-syntax consistency.

These two apparently different perspectives are not necessarily exclusive. On reading Unagreement and Person Mismatch sentences, the system detects the presence of a morpho-syntactic mismatch between subject and verb, a process that is reflected in the common activation of the posterior portion of the middle frontal cortex. However, the system subsequently recognizes that while Unagreement verbal and nominal information can be further integrated, the person feature violation included in the Person Mismatch condition cannot be integrated into the current sentence context. The posterior part of the middle frontal cortex can mediate the processing of agreement computation via a) afferent connections providing information to regulate the detection of a morpho-syntactic mismatch, and b) efferent projections sending such information to regions involved in subsequent processing stages for resolving the grammaticality of the sentence (see Xiang et al., 2010 for a functional connectivity study; an also see Yeterian et al., 2012, for a description of the anatomical connectivity of this frontal region in the primate brain). Despite the fact that this hypothesis needs further investigation (for instance, to establish the directionality of the information flow between the different nodes within this fronto-parieto-temporal network), the activation of the left middle frontal gyrus associated to sentences with morpho-syntactic incongruities points to the important role of this region during sentence comprehension and more specifically in the processing of agreement computation, probably as part as a more general (not-language specific) hub.

Additional discourse-semantic integration processing. According to the feature anchoring hypothesis (Mancini et al., 2013a, 2013b), successful integration of the different speech roles in Unagreement sentences (speaker and non-participants) requires the activation of regions related to semantic integration processes, to overcome the feature mismatch between subject and verb ("Los pintores trajimos/The painters$_{3.pl}$ brought$_{1.pl}$"). Based on previous findings, we identified the angular gyrus and the anterior temporal cortex as plausible candidates for this processing stage. Our experimental design has allowed us to discriminate between these two neuro-anatomical candidates: a) The anterior part of the left middle temporal gyrus and the left anterior temporal cortex exhibited a greater response to grammatical sentences compared to the anomalous ones without differences between Unagreement and Standard Agreement; b) The left angular gyrus is selectively activated only by Unagreement sentences (both for Unagreement relative to Standard Agreement and for Unagreement, Person Mismatch and Standard Agreement relative to the baseline condition); c) Participants with greater activation in the left angular gyrus showed faster reaction time and a higher percentage of accuracy. These results suggest that both the left angular gyrus and anterior temporal regions mediate semantic-integration processes during the computation of subject-verb agreement. However, only the left angular gyrus is activated for the more semantically complex condition that can be successfully integrated [i.e., in the case of Unagreement, where the person value of the referent shifts from third to first person plural (from "they" to "they + myself")].

Language-related neuroimaging findings have pointed to the involvement of this region during semantic processing (see reviews in Binder et al., 2009; Lau et al., 2008; Price, C. J., 2012; Seghier, 2013; Seghier et al., 2010; Vigneau et al., 2006), particularly in tasks that require concept retrieval and conceptual integration (Bemis & Pylkkänen, 2012a), as well as sentence integration into discourse (Bambini et al., 2011; Kuperberg et al., 2003; Kuperberg, Sitnikova, et al., 2008; Luke et al., 2002; Menenti et al., 2009). These findings have been replicated across multiple studies with different semantic tasks and stimuli (for meta-analysis reviews, see Binder & Desai, 2011; Binder et al., 2009; Vigneau et al., 2006). For instance, Binder et al. (2009) found that the most consistent semantic activation across 120 functional neuroimaging studies was located within the left angular gyrus, strengthening the heteromodal character of this region. Using magnetoencephalography, Bemis and Pylkkänen (2012a) measured neural activity elicited by the comprehension of adjective-noun pairs to highlight the neural substrates involved in basic linguistic composition across different modalities (auditory and visual). Interestingly, they found significant angular gyrus activation for compositional (e.g., *red-boat*) vs. non-compositional stimuli (e.g., *xlq-boat*) in both modalities, and interpreted this result as evidence for the crucial role of this region in conceptual integration processes[32].

At the sentence level, Kuperberg et al. (2006) found activity increases in the left and right angular gyri in association with reading sentences that were partially related to their preceding contexts, relative to highly related or unrelated sentences. In their study, participants were asked to evaluate the semantic relation between subsequent sentences. These authors found that the greater the difficulty in judging the semantic relationship

---

[32] It is important to note that the functional interpretation of this magnetoencephalography result is mediated by the temporality of the effects, based on the available models of sentence comprehension that assume initial syntactic composition followed by later semantic combinatorial operations. These authors found that the increased left anterior temporal cortex activity always preceded increased left angular gyrus activity in both auditory and visual modality (Bemis & Pylkkänen, 2012a, pp. 10-11).

between sentences, the greater the activity of the angular gyrus (the effect only emerged for intermediate semantic relation, Kuperberg et al., 2006). Similarly, Nieuwland et al. (2007) manipulated the referential ambiguity between a pronoun and its referent in a sentence comprehension paradigm (e.g., **Ronald told Frank that <u>he</u> had a positive attitude towards life/*Rose told Emily that <u>he</u>...*): the right and left angular gyrus were strongly activated with higher amplitude for referential ambiguities than referential anomalies. These findings highlight the specificity of the angular gyrus in dealing with high-level discourse representation. Interestingly, similar activity increases of the angular gyrus have been also found in fMRI studies that explored the neuro-anatomical correlates of metaphor processing (Bambini et al., 2011; Mashal et al., 2007; Shibata et al., 2012), which requires accessing a metaphorical meaning that extends beyond the literal meaning expressed by the linguistic input. This additional semantic processing recalls the additional semantic resources required to interpret Unagreement patterns: in fact, comprehension of both metaphors and Unagreement requires integrating the subject and verb forms at a higher conceptual level, overcoming the literal (discordant) meaning. Finally, neurological lesions in the angular gyrus have been previously associated with difficulties in processing complex sentences such as "*It was the niece that the father kicked*" (Dronkers et al., 2004; Newhart et al., 2012). Thus, it appears that the angular gyrus plays a crucial role in the processing of semantic complexity, whatever its source (both within sentences and beyond the sentence processing domain). In the present study we additionally show that this region is activated even when an agreement-relevant morpho-syntactic scenario is the source of semantic complexity. Possible replications of our findings could therefore have strong implications for neuro-anatomical models of sentence processing.

Taking into account these coherent findings, it seems plausible that neuro-cognitive models of sentence comprehension should take this parietal region as a key node for semantic integration processing. Currently, no existing neuro-cognitive models of sentence comprehension have considered parietal regions as mediating semantic functions (but see Binder & Desai, 2011; Binder et al., 2009 for a neuro-anatomical model of semantic processing). For instance, Bornkessel-Schlesewsky and Schlesewsky (2013) proposed that parietal regions are part of a dorsal pathway that mediates different aspects of syntactic processing: time-dependent segmentation, constituent combination into well-formed syntactic structure, and assessment of the elements in this structure in action-related terms. On the other hand, these authors pointed to the anterior middle temporal cortex as a key region mediating semantic integration processes. In contrast, Friederici (2011) argued that the role of inferior parietal regions as part as a dorsal stream ("dorsal pathway II mediating syntactic operations dealing with complex sentence structures") is an open issue and suggests phonological working memory storage as the most likely function of these regions. This author considers that semantic processing engages the middle and posterior superior temporal gyrus, as well as BA 45/47 within the inferior frontal gyrus ("ventral pathway I").

In this sense, the correlation between the behavioral results and the angular gyrus activity is a crucial piece of evidence: participants with greater activation in this region were more efficient (faster and more accurate) in the Unagreement grammaticality judgment. The neural response pattern of this region with respect to the baseline condition varied between participants: only the participants who exhibited activation in the angular gyrus during the Unagreement grammaticality judgment showed high task performance, while the ones exhibiting either no activation or deactivation showed lower performance. This inter-subject variability in the functional recruitment of parietal neural regions during reading processes has been previously reported (Bolger, Hornickel, et al., 2008; Bolger, Minas, et al., 2008; Levy, J. et al., 2009; Seghier et al., 2008), and may reflect their association with the Standard network (see Seghier, 2013 for a review). The fact that only the angular gyrus shows task-related modulation, as opposed to the frontal regions that did not show such variability, casts doubts on the theoretical proposal of Bornkessel-Schlesewsky and Schlesewsky (2013) indicating that only frontal regions are involved in domain-general cognitive control. The present correlation between the activation pattern for the angular gyrus and its relation with behavioral measures suggests that this parietal region influences the observed behavior of the participants in the experimental task.

Interim conclusions. Taken together, the present findings suggest that different brain networks are involved in language comprehension depending on i) the grammaticality of the sentence (Unagreement/Standard Agreement vs. Person Mismatch) and the subsequent possibility of integrating morpho-syntactic information at a semantic-discourse level; and ii) overcoming (or not) an apparent morpho-syntactic mismatch (Person Mismatch vs. Unagreement). Many accounts of subject-verb agreement fMRI findings derive from studies on the processing of feature mismatches and the results have provided a very fragmented scenario. Here, we used an experimental design that allowed us to distinguish the fine-grained neural circuitry within a fronto-temporal-parietal network recruited by different aspects of subject-verb agreement computation. The results indicate that the evaluation of morpho-syntactic subject-verb match correlates with activity in the posterior part of the left middle frontal gyrus, while syntactic-semantic integration is pursued by an extended left fronto-temporal network. Additional semantic complexity due to the re-interpretation of speech-act participants at the discourse level was observed to increase activity in the left angular gyrus. Overall, the present findings point out the central role of activity and interactivity between the classic fronto-temporal network and two additional nodes: the posterior part of the left middle frontal gyrus and the left angular gyrus.

Chapter 8.

General Discussion

Before concluding, I would like to come back to the phrase that opens the current thesis: *“When we are reading a text such as “...como si sobre sus cabezas hubiera caído la gota de agua que forman las estalactitas...”(literally: “…as if on their heads$_{plural}$had$_{singular}$ fallen [the drop of water] $_{singular}$ that form$_{plural}$ stalactites…”) (Lezama Lima in Paradiso, page 486-487) with apparent incongruities between different sentence constituents, we become aware of the constant computation of grammatical relations (i.e., agreement) that is necessary to combine the different words and grasp the idea that the author wants to convey.”* Using this statement we tried to point out *“the what”*, *“the why”* and *“the how”* of the current dissertation. What is the main subject of this document, what is the motivation for investigating this topic and how will it be explored to provide new empirical evidence that can be translated into novel claims?

In the current modern society, we are constantly exposed to written linguistic material – e.g., from basic thinks like signage systems to more complex material like poetry. The comprehension of this type of stimulus is an automatic process essential for our daily life. Nevertheless, the more automatic a process is, the less aware we are of the cost associated with the process. Despite its automaticity, sentence comprehension is a very complex and costly neural process that encompasses different mechanisms. One of these critical mechanisms is the computation of agreement dependencies. The investigation of this phenomenon from a neuro-cognitive perspective has been overlooked, maybe due to its intrinsic variability across languages or the complexity to isolate it from other mechanisms underlying sentences comprehension. This is the reason – i.e., *“the why”*– why we chose ***agreement*** as *“the what”* of this dissertation. The richness this phenomenon has in Spanish was what made the ***Spanish Agreement System*** the perfect tool to isolate the neural circuit specialized in the establishment of grammatical relations – i.e., *“the how”*. These three points – i.e., *“the what”*, *“the why”* and *“the how”* – were the central focus of the Chapter 1. Specifically, we started by critically reviewing the main linguistic theories about agreement and the most relevant empirical neuro-cognitive evidence concerning this topic. In addition, since the significance agreement comprehension has for the sentence processing literature, we also included in this section some theoretical details about the most recent neuro-anatomical models proposed on this theme. Critically, this part tried to put forward the main unresolved questions regarding agreement processing, emphasizing the lack of consensus in the existing empirical evidence.

Three principal goals were pinpointed in the Introduction section: [1]does the brain have a circuit specialized in the computation of grammatical relations among words, [2]whether this neural circuit, if indeed found, is fine-tuned depending on syntactic or semantic signals embedded in our linguistic code, and [3]whether the interaction between these two different types of information leaves a trace in the brain response. In order to address these questions, five independent experiments were designed and organized according to the syntactic and semantic complexity characterizing the grammatical dependency (or dependencies) manipulated in each case (from Chapter 3 to Chapter 7). Thus, these three general questions were the guiding thread connecting these studies. Each one of these experimental chapters included a discussion section, where the main results were contrasted with the previous evidence and the major claims were extensively debated. In this final chapter, we will focus on the commonalities and differences emerging across the five experiments. Establishing commonalities and differences across experiments we will be able to better characterize the neural circuit underlying the comprehension of agreement relations. The starting point of this comparison will be the Table 1S, which set out with an illustration of the main behavioral and fMRI findings resulting from each one of these five experiments. The commonalities and differences per main result were represented using a color code: while the commonalities were coded with similar colors, the differences were coded with different colors.

Table S1. Main Findings

	Behavioral results	Neuro-anatomical results	
		Grammaticality effects	**Effects related with the critical manipulation**
Experiment I (determiner-noun pairs)	**Main effect of Agreement Congruency**: Subjects classified determiner-noun pairs as grammatically correct more easily and accurately than incongruent pairs. This differentiation was evident for both transparent and opaque nouns. **Interaction effect**: Regarding RT, this effect was larger for opaque than for transparent nouns.	***Gender Mismatch*** **relative to** ***Gender Match***: the dorsal striatum, the middle and medial superior frontal gyrus, the medial orbito-frontal cortex, the pre- and post-central gyrus, as well as the anterior cingulate cortex. ***Gender Match*** **as compared to** ***Gender Mismatch****:* the pars opercularis and triangularis within the left IFG and the posterior part of the left MTG/STG.	Significant **interaction effects** between Gender Congruency and Gender-marking emerged in five left-lateralized clusters: ▪ Pars triangularis within the IFG ▪ Posterior part of the MTG/STG ▪ Hippocampus ▪ Angular Gyrus ▪ Supramarginal Gyrus
Experiment II	**Null effects** for RT and error rates.	***Gender Mismatch*** **relative to** ***Gender Match***: the pars triangularis, orbitalis and opercularis within the left IFG, the middle frontal gyrus, as well as the inferior parietal gyrus and the supramarginal and the angular gyri. ***Gender Match*** **as compared to** ***Gender Mismatch****:* the middle and medial superior frontal gyrus, the medial orbito-frontal cortex, the anterior cingulate cortex, as well as the anterior part of the left MTG/STG and the superior and middle temporal pole.	Significant **interaction effects** between Gender Congruency and Type of Gender emerged in two left-lateralized clusters: ▪ Inferior Parietal ▪ Angular Gyrus

Experiment III	**Main effect of Agreement Congruency**: Subjects classified word pairs as grammatically correct more easily and accurately than incongruent pairs. This differentiation was evident for both determiner-noun and subject-verb pairs. **Interaction effect**: Regarding RT, this effect was larger for determiner-noun pairs than for subject-verb pairs.	***Number Mismatch* relative to *Number Match***: the right and left insula, the pars orbitalis, opercularis and triangularis within the left IFG, the pre- and post-central gyrus, as well as the inferior parietal cortex. ***Number Match* as compared to *Number Mismatch****:* the middle and superior frontal gyrus, the anterior cingulate cortex, the medial orbito-frontal cortex, as well as the anterior part of the MTG/ITG.	Significant **interaction effects** between Number Congruency and Type of Word Pair emerged in three left-lateralized clusters: ▪ Left pars opercularis within the IFG ▪ Left anterior part of the MTG/STG ▪ Left and right precuneus/cuneus
Experiment IV	**Main effect of Agreement Congruency**: Subjects classified word pairs as grammatically incorrect more easily and accurately than congruent items. This differentiation was evident for both person and number agreement violations.	***Ungrammatical* relative to Grammatical sentences**: the medial superior frontal gyrus, the middle frontal gyrus, the postcentral gyrus, the middle cingulate cortex, as well as the inferior and superior parietal cortices. ***Grammatical* relative to Ungrammatical sentences***:* the pars orbitalis and triangularis within the left IFG, the superior frontal gyrus, as well as the posterior and anterior portions of the left MTG/STG and the superior temporal pole.	Significant **differences** between *Number* and *Person Agreement Violation* emerged in four left-lateralized clusters: ▪ Left pars orbitalis within the IFG ▪ Left pars triangularis within the IFG ▪ Left anterior part of the MTG/STG ▪ Left posterior part of the MTG/STG
Experiment V	**Main effect of Agreement Congruency**: Subjects classified word pairs as grammatically incorrect more easily and accurately than congruent items.	***Ungrammatical* relative to Grammatical sentences**: the medial superior frontal gyrus, the middle frontal gyrus, the anterior cingulate cortex, as well as the inferior parietal cortex. ***Grammatical* relative to Ungrammatical sentences***:* the pars orbitalis and triangularis within the left IFG, the superior frontal gyrus, the medial orbito-frontal cortex, the pre- and post-central gyri, as well as the posterior and anterior portions of the left MTG/STG.	The **commonalities** between Person Mismatch and Unagreement emerged in: ▪ Left middle frontal gyrus The **differences** between Unagreement and Standard Agreement emerged in: ▪ Left angular gyrus

With respect to the first question (***i.e., does the brain have a circuit specialized in the computation of grammatical relations among words?***), the five experiments consistently revealed a functional dissociation between a bilateral distributed fronto-parietal network that was associated to amodal conflict-monitoring operations, and a left-lateralized fronto-temporal network that seems to be specifically related to different aspects of phrase and sentence processing (see Table 1S for the results listed in the column *Grammaticality effects*). We take this finding to suggest that for the comprehension of grammatical relations a complex system, which includes language-specific and domain-general circuits, is boosted.

Specifically, in line with previous ERPs and fMRI findings, we identified the anterior cingulate cortex as a critical epicenter of the conflict-monitoring system aimed at control the consistency between the expected and the perceived signal (Botvinick et al., 2004; van de Meerendonk et al., 2011; van de Meerendonk et al., 2009; van de Meerendonk et al., 2010; Ye & Zhou, 2009). Irrespectively of the experiment, this region exhibited higher response for incongruent than for congruent items, suggesting that the detection of grammatical incongruities between two different sentence elements boost the response of this system (see Figure 8.1). According to our data, apart from the anterior cingulate cortex, we consistently found a bilateral fronto-parietal network that seems to be related with the same mechanism. This network includes areas such as the superior and medial frontal gyri, the superior parietal cortex and the precuneus/cuneus. However, in contrast with the anterior cingulate cortex, the response of this network was related with the difficulty of the task: the larger the reaction times were, the greater the neural response in these areas. Interestingly, this finding goes in line with previous empirical evidence which identified these areas as crucial nodes for task-dependent attentional mechanisms. In consonance with this result, as we outlined in Chapter 3, previous studies have suggested that attentional mechanisms are biased by this conflict-monitoring system through bottom-up control mechanisms (van de Meerendonk et al., 2011; van de Meerendonk et al., 2009; van de Meerendonk et al., 2010). Interestingly, with regard to this bilateral network, we identified a clear difference across experiments: while the BOLD response in the experiments I, IV and V were positive, the BOLD response in the experiments II and III were negative. Throughout the document, we provided some plausible hypothesis for this difference; nonetheless it could be interestingly for further studies to identify the specific factors modulating the neural response of this circuit.

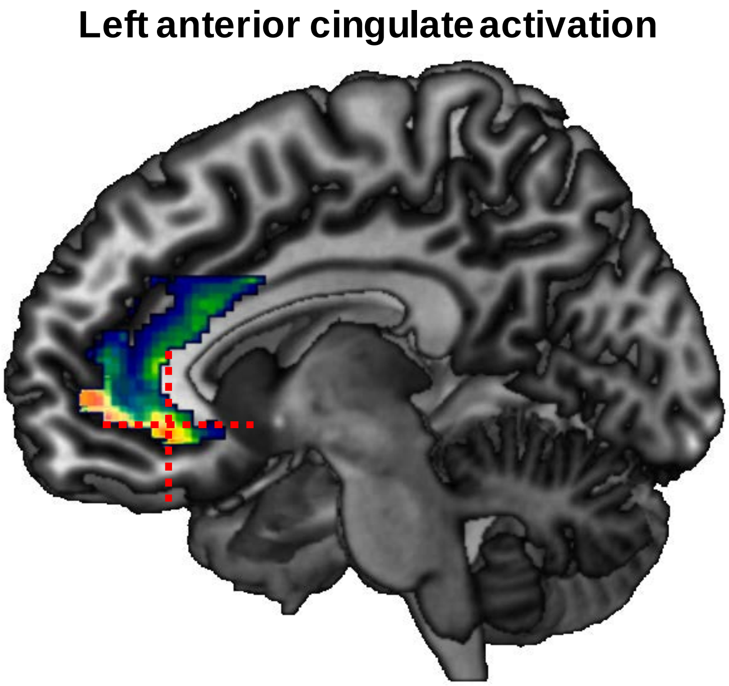

Left anterior cingulate activation

Figure 8.1. Left anterior cingulate activation resulting from the combination of the five experiments was projected on the MNI single-subject T1 image (sagittal view). Red dotted lines represent the maximum peak of response. Note that brain activity in this region is extended from the most anterior and ventral part to the most posterior portion.

In parallel, we isolated a left-lateralized fronto-temporal network that also showed high sensitivity to the congruency pattern (see Table 1S for the results listed in the column *Grammaticality effects*). This network encompassed the left pars opercularis, triangularis and orbitalis within the IFG, the left MTG/STG and the middle frontal gyrus. As we have pointed out throughout this document, all the classical neurobiological models of language have considered the interplay between the IFG and the MTG/STG as critical for the processing of linguistic material (see Bornkessel-Schlesewsky & Schlesewsky, 2013; Friederici, 2011 for two recent and divergence points of view). Nonetheless, despite the huge amount of empirical evidence concerning this topic (for contradictory perspectives see Bornkessel-Schlesewsky & Schlesewsky, 2013; Friederici, 2011, 2012; Friederici & Gierhan, 2013; Hagoort, 2005, 2013, 2014), the specific role played by these areas during language comprehension and more specifically during agreement processing still remains an unsettled issue (Fedorenko et al., 2011; Fedorenko, Duncan, et al., 2012; Fedorenko & Thompson-Schill, 2014). Similarly, the engagement of other frontal areas, such as the middle frontal gyrus, during the comprehension of linguistic material is a controversial issue (see Friederici, 2011; Friederici, 2012; Friederici & Gierhan, 2013; and Hagoort, 2005; Hagoort, 2013; 2014 for contradictory points of view). The vast majority of neurobiological models of sentence processing do not consider this region as part of this system. With respect to the response of this left-lateralized fronto-temporal network, three critical similarities were identified from our studies.

- The pars orbitalis, triangularis and opercularis within the left inferior frontal gyrus were recruited for the processing of congruent and incongruent constructions. However, the neural responses of these areas were dependent on the congruency between the different elements involved in the corresponding grammatical relation (see Figure 8.2A).

- The left temporal cortex consistently exhibited greater response for grammatically correct constructions than for the ungrammatical ones (see Figure 8.2B). This temporal region encompassed the anterior, the middle and the posterior portions of the left MTG/STG and the temporal pole.

- A region within the left middle frontal gyrus showed marked sensitivity (i.e., greater neural responses) to morpho-syntactic mismatches independently of the grammatical pattern (see Table 1S for the results derived from the Experiment V and Figure 8.2C). Based on previous findings, we associated this neural activity with morpho-syntactic feature checking mechanisms that should be enhanced for incongruent items.

Overall, the recruitment of these three different nodes and more importantly the interfacing between them, seem to be crucial for the comprehension of grammatical relations independently of their semantic or syntactic complexity. Critically, these areas showed similar responses for different types of agreement dependencies (i.e., nominal agreement as for the experiments I and II and verbal agreement as for the experiments III, IV and V), different morpho-syntactic features (i.e., gender agreement as for the experiments I and II, number agreement as for the experiments III and IV and person agreement as for the experiments IV and V) and different contexts (i.e., word-pairs as for the experiments I and III and sentence context as for the experiments II, IV and V).

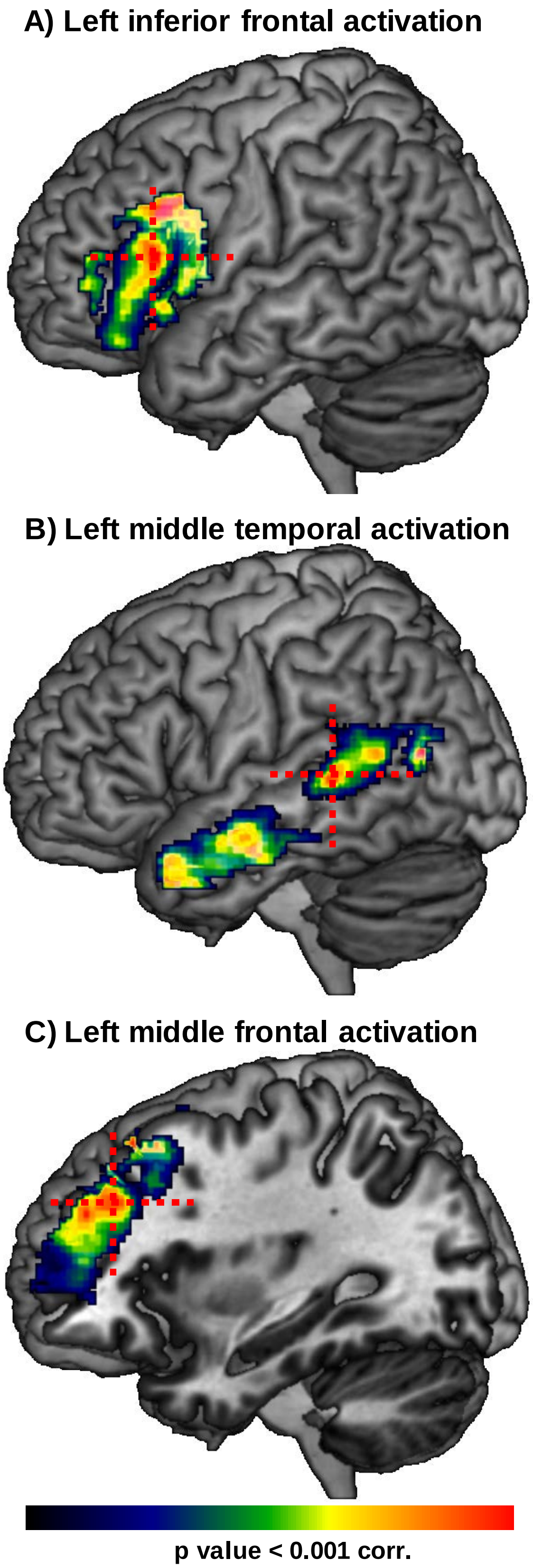


Figure 8.2. Brain activations of the left inferior frontal gyrus (A), the left middle temporal gyrus (B) and the left middle frontal gyrus (C) resulting from the combination of the five experiments was projected on the MNI single-subject T1 image (sagittal view). Red dotted lines represent the maximum peak of response. Note that brain activity in these areas is markedly distributed, especially for the middle temporal gyrus where the significant response is extended from the most anterior part (i.e., including the temporal pole) to the most posterior portion.

Regarding the second and third questions (***i.e.*, [2]whether this neural circuit is fine-tuned depending on syntactic or semantic signals embedded in our linguistic code and [3]whether the interaction between these two different types of information leaves a trace in the brain response**), the present studies provide crucial evidence suggesting that the neural circuit underlying agreement comprehension is flexible enough to consider and integrate the formal and conceptual signals characterizing the different sentential elements. With regard to this point, in contrast with the regularities in the neural responses of the regions associated with the conflict-monitoring system or the activity in the middle frontal gyrus, the neural responses of the left IFG and the left MTG/STG varied as a function of the different factors manipulated in each experiment (see Table 1S for the results listed in the column *Effects related with the critical manipulation*). However, the flexibility of this circuit is not circumscribed to variations in the responses of the different nodes within this left-lateralized perisylvian network. In contrast, when the integration between formal and conceptual signals is required to properly interpret an agreement relation, the system seems to recruit additional parietal nodes (see Table 1S for the results of the experiments II and V). Based on the pattern of response exhibiting by these areas and establishing a link between our results and previous findings, we associated each one of these nodes with the different processing stages that have been related to agreement computation (see Chapter 1, *Neuro-cognitive Mechanisms Underlying Agreement Processing*). In the following we will go through the main results regarding the singularities across experiments.

- As far as the responses of the left IFG, our data parallel the empirical evidence that have been previously observed in other fMRI studies (Hagoort, 2005, 2013, 2014). A functional anterior-ventral to posterior-dorsal gradient was found within the left inferior frontal gyrus. However, in contrast with previous claims and in line with our data, this gradient distinguishes between two different functionally-defined clusters, the pars opercularis in the anterior-ventral part, and the pars triangularis/orbitalis in the posterior-dorsal part. While the pars opercularis seems to be involved in coordinating syntactic processes, the orbital/triangular part of the left IFG seems to support semantic operations.

- Critically, in line with previous neurobiological models of sentence processing, a posterior to anterior functional gradient emerged for the left middle/superior temporal gyrus (Friederici, 2011, 2012; Friederici & Gierhan, 2013; but see Hagoort, 2005; Hagoort, 2013; 2014 for contrasting approaches). However, in the context of agreement comprehension this is the first study demonstrating this gradient. Specifically, while the posterior part of the MTG/STG seems to be related with the storage and retrieval of lexical and morpho-syntactic information (see Table 1S for the results of the experiments I), the anterior portion of this region appears to reflect syntactic-combinatorial building mechanisms. On the other hand, activity in the temporal pole was associated with the mapping between form and meaning, especially boosted during the assignment of interpretively discourse relevant roles (see Table 1S for the results of the experiments IV).

- Left parietal regions such as the angular gyrus and adjacent inferior parietal areas showed increased activation for those manipulations involving lexico-semantic factors (see Table 1S for the results of the experiments I, II and V and Figure 8.3). As we highlighted in previous chapters, the angular gyrus has been postulated as a central hub of the highly heteromodal conceptual associative system (Binder & Desai, 2011; Binder et al., 2009; Bonner et al., 2013; Price, A. R. et al., 2015; Seghier, 2013; Seghier et al., 2010). The engagement of this left parietal cluster for the comprehension of grammatical relations was taken as a critical finding reflecting how the agreement system is fine-tuned depending on the available conceptual information (see the Discussion sections of the Chapter 3, 4 and 7 for more details).

In sum, the data discussed here show that two different but closely related systems seem to be working in parallel during the processing of agreement: a) a bilateral fronto-parietal conflict-monitoring system not language specific and b) a left fronto-temporal system that seems to be specifically related to different aspects of agreement processing Within this fronto-temporal system, a functional coupling between the left MTG/STG and the left IFG seems to be crucial for the comprehension of grammatical relations. In addition to this core system, parietal areas are enhanced when the integration of different formal and lexico-semantic signals are required.

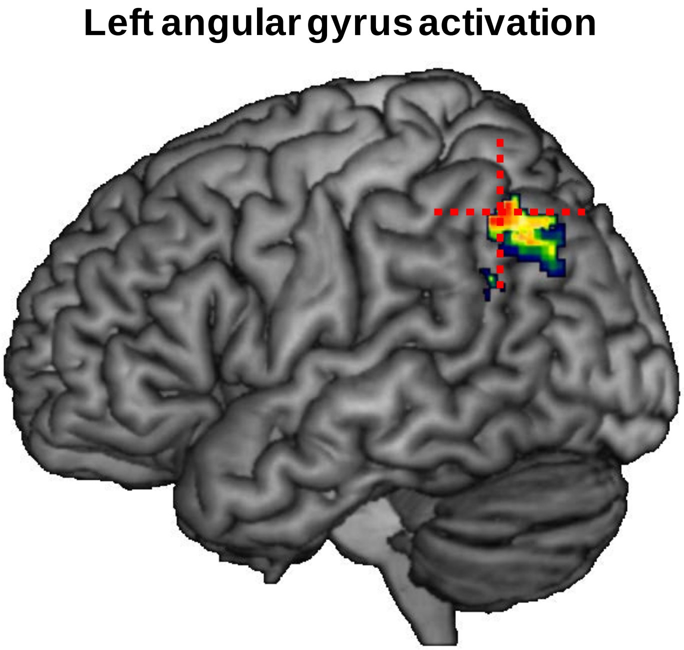


Figure 8.3. Left angular gyrus activation resulting from the combination of the experiments I, II and V was projected on the MNI single-subject T1 image (sagittal view). Red dotted lines represent the maximum peak of response.

To what extent the present findings impact on the linguistic theoretical frameworks of agreement?

In Chapter 1 (*Linguistic Theoretical Frameworks of Agreement*) we described two divergent theoretical perspectives of agreement highlighting the differences between them: the *strictly syntactic approach* (Chomsky, 1955a, 1995, 2000, 2001) and the *lexicalist approach* (Pollard & Sag, 1994; Wechsler, 2009; Wechsler, 2011; Wechsler & Zlatić, 2000; Wechsler & Zlatić, 2003). The debate revolved around three main questions: 1) whether the interaction between syntactic and semantic information modulated the comprehension of agreement; 2) whether the agreement system relies on the type of morpho-syntactic features and 3) whether the comprehension of nominal and verbal agreement entail different neuro-cognitive operations. In addition we pointed out how these two frameworks have influenced the neuro-cognitive investigations regarding sentence comprehension and more specifically agreement processing.

With respect to the first question, our data suggest that during the comprehension of an agreement relation, the formal and conceptual signals equally contribute and also interact during the comprehension process (see Table 1S for the results of the experiments I, II and V). As demonstrated in the Experiment II, even in the case of Conceptual Gender (e.g., El abuel<u>o</u> es sabi<u>o</u>), where it is possible to integrate the noun and the predicative adjective based on the formal information, the conceptual knowledge modulate the syntactic-structure building process. Crucially, in accordance with the *lexicalist approach*, we interpreted this result as relevant for arguing that the agreement system needs to assign semantic interpretations to the formal structure, in order to comprehend this type of grammatical relations (Pollard & Sag, 1994; Wechsler, 2009; Wechsler, 2011; Wechsler & Zlatić, 2000; Wechsler & Zlatić, 2003). However, given the poor temporal resolution of the fMRI data, we cannot rule out the alternative hypothesis proposed by the *strictly syntactic approach* (Chomsky, 1955a, 1995, 2000, 2001): the interaction between syntactic and semantic information occurs after the syntactic building-up processes. This point should be addressed in further studies in order to determine when the interaction between conceptual and formal properties occurs.

As far as the processing of different types of morpho-syntactic features, the results of the Experiment IV revealed that agreement comprehension operates in a feature-specific fashion, in which the nodes of the language network are differentially involved. The direct contrast between person and number violations showed significant differences in the anterior and posterior part of the left middle temporal gyrus, as well as in pars orbitalis and triangularis of the inferior frontal gyrus. In this case, the MTG-IFG coupling differentiating between person and number violation was related with the feature-sensitive mechanism of form-to-meaning mapping. This interpretation had disagreed with the *strictly syntactic approach* (Chomsky, 1955a, 1995, 2000, 2001) which emphasized that the morpho-syntactic feature values are extracted from the controller without differentiating among person, number, and gender. Nonetheless, as previously mentioned (Chapter 6, Experiment IV), we cannot discard that the computation of different features is a late process preceded by an early “agree” computation blind to feature modulation.

Critically, regarding the third question, the comparison between verbal and nominal agreement included in the Experiment III, shows that the processing of these two types of dependencies relies on common mechanisms, as shown by the overlapping activated networks. However, at the same time, brain activation in some critical areas was modulated by the specific type of agreement. The major difference between these two dependencies was found in the anterior portion of the left MTG-STG and the pars opercularis within the left IFG. The findings derived from this study were taken to suggest that these two theoretical frameworks are not mutually exclusive. In accordance with Chomsky (2000, 2001), the computation of nominal and subject-verb agreement implies similar computational processes supported by an overlapping neural network, as evidenced by the failure to find *qualitative* differences between the two patterns. However, in partial agreement with Wechsler and Zlatić (2003), some nodes within this network show differences between nominal and subject-verb agreement, although this difference is *quantitative* in nature and may reflect the structural difference between them (within-constituent vs. sentence-level structure), and not the type of features involved (index and concord features).

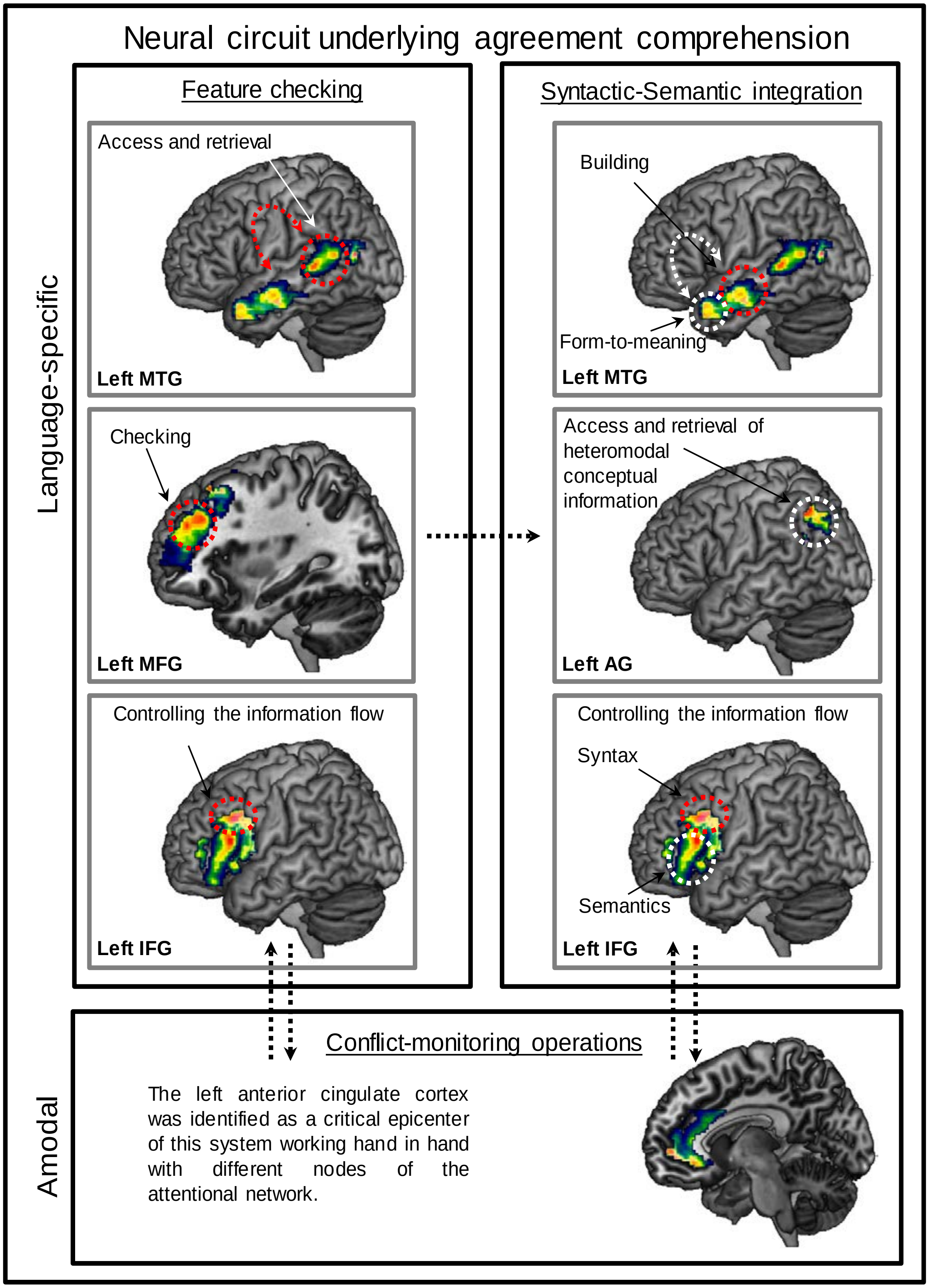
To what extent the present findings impact on the neuro-cognitive models of sentence processing?

In line with the previous neurobiological models of sentences processing, our study has differentiated between three different components: a *Memory-related Hub – i.e.,* from which the underlying morpho-syntactic and lexico-semantic representations associated with the input can be accessed and retrieved –, an *Integration Hub – i.e.,* which combines the incoming signals with previously encountered information –, and a *Monitoring Hub* – i.e., responsible for preventing behavioral mistakes. Crucially, the present findings provide valuable information describing how these components operate during the establishment of an agreement relation. The discussion sections included in each experimental chapter extensively debated the similarities and the differences between our results and the theoretical models of sentence processing. Overall, according with our data, agreement comprehension is underpinned by neural regions that have been traditionally related with sentence processing. However, the functionality of each node within the agreement circuit and its involvement within each component does not always match with what the theoretical models of sentence processing propose. In order to generalize our results, it could be important for future works to explore how this agreement network operates in sentence production. This could facilitate the comparison between our proposals and the currently available theoretical neurobiological models of sentences processing.

General conclusions: Nuero-anatomical basis of agreement processing.

Through this document we will briefly lay out what we consider the most important insights of the neurobiology of agreement comprehension. By combining the data provided by the present fMRI study with previous evidence it is possible to characterize the neural mechanisms underlying agreement comprehension in a fine-grained way. A summary of our proposal is illustrated in Figure 8.4. This proposal summarizes the main claims of the current dissertation. It is based on the specific functional role each neuro-anatomical region within these circuits was related to. Importantly, as the discussion sections of each experimental chapter, the currently available empirical ERP evidence on agreement comprehension was consider as the started point of this proposal (see Molinaro, Barber, et al., 2011 for a review). This assumption implies a distinction between three functionally distinct processing stages: I) Feature consistency checking; II) Integration of incoming information and III) Conflict-monitoring resolution (see Chapter 1, *Neuro-cognitive Mechanisms Underlying Agreement Processing*). Therefore, following this distinction we postulated the most plausible candidate(s) for each one of these operations.

Our results provide the first neuro-cognitive approach of agreement comprehension serving to identify the core neural areas behind this process and open important windows for future studies. Crucially, this study showed that agreement comprehension relies on neural mechanisms that transcend the linguistic domain. We broadly demonstrated that the interfacing between different language-specific and domain-general neural systems is essential for the proper interpretation of grammatical relations. Interestingly, we also segregated within this network the areas related with semantic and syntactic operations. Importantly, the close relationship between these two domains was also disclosed. In sum, this dissertation provides valuable empirical data that represents a turning point in the characterization of the neurobiology of agreement, opening new windows to the study of agreement computation and language comprehension.



The left anterior cingulate cortex was identified as a critical epicenter of this system working hand in hand with different nodes of the attentional network.

Figure 8.4. Neural circuit underlying agreement comprehension. This figure summarizes the main claims resulting from the previous five experimental chapters. The three black boxes represent the processing stages previously proposed for agreement comprehension: I) Feature consistency checking; II) Integration of incoming information and III) Conflict-monitoring resolution. The grey boxes encompass the neural regions postulated as the most plausible candidates for each one of these processes. MTG: Middle temporal gyrus; IFG: Inferior frontal gyrus; AG: Angular gyrus; MFG: Middle frontal gyrus.

Chapter 9.

References

A

Abrahams, S., Goldstein, L. H., et al. (2003). Functional magnetic resonance imaging of verbal fluency and confrontation naming using compressed image acquisition to permit overt responses. *Hum Brain Mapp, 20*(1), 29-40.

Acheson, D. J., & Hagoort, P. (2013). Stimulating the brain's language network: syntactic ambiguity resolution after TMS to the inferior frontal gyrus and middle temporal gyrus. *J Cogn Neurosci, 25*(10), 1664-1677. doi: 10.1162/jocn_a_00430

Acheson, D. J., & Hagoort, P. (2014). Twisting tongues to test for conflict-monitoring in speech production. *Front Hum Neurosci, 8*, 206.

Afonso, O., Domínguez, A., et al. (2013). Sublexical and Lexico-Syntactic Factors in Gender Access in Spanish. *J Psycholinguist Res*, 1-13.

Akhutina, T., Kurgansky, A., et al. (1999). Processing of grammatical gender in a three-gender system: Experimental evidence from Russian. *J Psycholinguist Res, 28*(6), 695-713.

Anderson, J. M. (1961). The morphophonemics of gender in Spanish nouns. *Lingua, 10*, 285-296.

Aron, A. R., Fletcher, P. C., et al. (2003). Stop-signal inhibition disrupted by damage to right inferior frontal gyrus in humans. *Nat Neurosci, 6*(2), 115-116.

Aron, A. R., & Poldrack, R. A. (2006). Cortical and subcortical contributions to stop signal response inhibition: role of the subthalamic nucleus. *J Neurosci, 26*(9), 2424-2433.

Aron, A. R., Robbins, T. W., et al. (2004). Inhibition and the right inferior frontal cortex. *Trends Cogn Sci, 8*(4), 170-177. doi: 10.1016/j.tics.2004.02.010

B

Badecker, W., Miozzo, M., et al. (1995). The two-stage model of lexical retrieval: evidence from a case of anomia with selective preservation of grammatical gender. *Cognition, 57*(2), 193-216.

Baggio, G., & Hagoort, P. (2011). The balance between memory and unification in semantics: A dynamic account of the N400. *Lang Cogn Process, 26*(9), 1338-1367. doi: 10.1080/01690965.2010.542671

Baldo, J. V., Wilson, S. M., et al. (2012). Uncovering the neural substrates of language: A voxel-based lesion symptom mapping approach. *Advances in the Neural Substrates of Language: Toward a Synthesis of Basic Science and Clinical Research. Oxford: Wiley-Blackwell*.

Bambini, V., Gentili, C., et al. (2011). Decomposing metaphor processing at the cognitive and neural level through functional magnetic resonance imaging. *Brain Res Bull, 86*(3-4), 203-216. doi: 10.1016/j.brainresbull.2011.07.015

Barber, H. A., & Carreiras, M. (2003). Integrating gender and number information in Spanish word pairs: An ERP study. *Cortex, 39*(3), 465-482.

Barber, H. A., & Carreiras, M. (2005). Grammatical gender and number agreement in Spanish: an ERP comparison. *J Cogn Neurosci, 17*(1), 137-153. doi: 10.1162/0898929052880101

Barber, H. A., Salillas, E., et al. (2004). Gender or Genders Agreement? *On-line study of sentence comprehension* (pp. 309-328): Taylor & Francis.

Baron, R. M., & Kenny, D. A. (1986). The moderator–mediator variable distinction in social psychological research: Conceptual, strategic, and statistical considerations. *Journal of personality and social psychology, 51*(6), 1173.

Baron, S. G., Thompson-Schill, S. L., et al. (2010). An early stage of conceptual combination: Superimposition of constituent concepts in left anterolateral temporal lobe. *Cogn Neuosci, 1*(1), 44-51.

Bartels, A., Logothetis, N. K., et al. (2008). fMRI and its interpretations: an illustration on directional selectivity in area V5/MT. *Trends Neurosci, 31*(9), 444-453.

Bates, E., Devescovi, A., et al. (1996). Gender priming in Italian. *Atten Percept Psychophys, 58*(7), 992-1004.

Bates, E., Devescovi, A., et al. (1995). Gender and lexical access in Italian. *Percept Psychophys, 57*(6), 847-862.

Bayley, P. J., & Squire, L. R. (2002). Medial temporal lobe amnesia: gradual acquisition of factual information by nondeclarative memory. *J Neurosci, 22*(13), 5741-5748.

Becher, A. L., & Oka, G. N. (1974). Person in Kawi: Exploration of an elementary semantic dimension. *Oceanic Linguistic, 13*, 229-255.

Bemis, D. K., & Pylkkänen, L. (2011). Simple composition: A magnetoencephalography investigation into the comprehension of minimal linguistic phrases. *J Neurosci, 31*(8), 2801-2814.

Bemis, D. K., & Pylkkänen, L. (2012a). Basic linguistic composition recruits the left anterior temporal lobe and left angular gyrus during both listening and reading. *Cereb Cortex, 23*(8), 1859-1873. doi: 10.1093/cercor/bhs170

Bemis, D. K., & Pylkkänen, L. (2012b). Combination Across Domains: An MEG Investigation into the Relationship between Mathematical, Pictorial, and Linguistic Processing. *Front Psychol, 3*, 583. doi: 10.3389/fpsyg.2012.00583

Benveniste, E. (1966). *Problèmes de linguistique générale* (Vol. 2). France: Paris: Gallimard.

Berg, T. (1998). *Linguistic structure and change: An explanation from language processing*. New York: Oxford University Press.

Bianciardi, M., Fukunaga, M., et al. (2011). Negative BOLD-fMRI signals in large cerebral veins. *J Cereb Blood Flow Metab, 31*(2), 401-412.

Bianchi, V. (2006). On the syntax of personal arguments. *Lingua, 116*(12), 2023-2067. doi: 10.1016/j.lingua.2005.05.002

Binder, J. R., & Desai, R. H. (2011). The neurobiology of semantic memory. *Trends Cogn Sci, 15*(11), 527-536. doi: 10.1016/j.tics.2011.10.001

Binder, J. R., Desai, R. H., et al. (2009). Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cereb Cortex, 19*(12), 2767-2796. doi: 10.1093/cercor/bhp055

Binder, J. R., Gross, W. L., et al. (2011). Mapping anterior temporal lobe language areas with fMRI: a multicenter normative study. *NeuroImage, 54*(2), 1465-1475.

Bizzi, A., Blasi, V., et al. (2008). Presurgical Functional MR Imaging of Language and Motor Functions: Validation with Intraoperative Electrocortical Mapping 1. *Radiology*, *248*(2), 579-589.

Blackwell, A. (1996). The time course of grammaticality judgement. *Lang Cogn Process, 11*(4), 337-406.

Blumenfeld, R. S., & Ranganath, C. (2006). Dorsolateral prefrontal cortex promotes long-term memory formation through its role in working memory organization. *J Neurosci, 26*(3), 916-925. doi: 10.1523/JNEUROSCI.2353-05.2006

Boas, D. A., Jones, S. R., et al. (2008). A vascular anatomical network model of the spatio-temporal response to brain activation. *NeuroImage, 40*(3), 1116-1129.

Bock, K., Eberhard, K. M., et al. (2001). Some attractions of verb agreement. *Cogn Psychol, 43*(2), 83-128. doi: 10.1006/cogp.2001.0753

Bock, K., & Miller, C. A. (1991). Broken agreement. *Cogn Psychol, 23*(1), 45-93.

Bolger, D. J., Hornickel, J., et al. (2008). Neural correlates of orthographic and phonological consistency effects in children. *Hum Brain Mapp, 29*(12), 1416-1429. doi: 10.1002/hbm.20476

Bolger, D. J., Minas, J., et al. (2008). Differential effects of orthographic and phonological consistency in cortex for children with and without reading impairment. *Neuropsychologia*, *46*(14), 3210-3224. doi: 10.1016/j.neuropsychologia.2008.07.024

Bonner, M. F., Peelle, J. E., et al. (2013). Heteromodal conceptual processing in the angular gyrus. *NeuroImage, 71*, 175-186.

Bonvento, G., Sibson, N., et al. (2002). Does glutamate image your thoughts? *Trends in Neurosciences, 25*(7), 359-364.

Booth, J. R., Burman, D. D., et al. (2004). Development of brain mechanisms for processing orthographic and phonologic representations. *J Cogn Neurosci, 16*(7), 1234-1249.

Bornkessel-Schlesewsky, I., & Schlesewsky, M. (2009). *Processing Syntax and Morphology: A Neurocognitive Perspective*. New York: Oxford University Press.

Bornkessel-Schlesewsky, I., & Schlesewsky, M. (2013). Reconciling time, space and function: a new dorsal-ventral stream model of sentence comprehension. *Brain Lang, 125*(1), 60-76. doi: 10.1016/j.bandl.2013.01.010

Bornkessel, I., & Schlesewsky, M. (2006). The extended argument dependency model: a neurocognitive approach to sentence comprehension across languages. *Psychological Review, 113*(4), 787-821. doi: 10.1037/0033-295X.113.4.787

Bornkessel, I., Zysset, S., et al. (2005). Who did what to whom? The neural basis of argument hierarchies during language comprehension. *NeuroImage, 26*(1), 221-233. doi: 10.1016/j.neuroimage.2005.01.032

Botvinick, M. M., Cohen, J. D., et al. (2004). Conflict monitoring and anterior cingulate cortex: an update. *Trends Cogn Sci, 8*(12), 539-546. doi: 10.1016/j.tics.2004.10.003

Božić, M., & Marslen-Wilson, W. D. (2013). Neurocognitive mechanisms for processing inflectional and derivational complexity in English. *Psihologija, 46*(4), 439-454.

Božić, M., Marslen-Wilson, W. D., et al. (2007). Differentiating morphology, form, and meaning: Neural correlates of morphological complexity. *J Cogn Neurosci, 19*(9), 1464-1475.

Božić, M., Tyler, L. K., et al. (2013). Neurobiological systems for lexical representation and analysis in English. *J Cogn Neurosci, 25*(10), 1678-1691.

Braun, M., Hutzler, F., et al. (2015). The neural bases of the pseudohomophone effect: Phonological constraints on lexico-semantic access in reading. *Neuroscience, 295*, 151-163.

Brennan, J., Nir, Y., et al. (2012). Syntactic structure building in the anterior temporal lobe during natural story listening. *Brain Lang, 120*(2), 163-173. doi: 10.1016/j.bandl.2010.04.002

Brennan, J., & Pylkkanen, L. (2012). The time-course and spatial distribution of brain activity associated with sentence processing. *NeuroImage, 60*(2), 1139-1148. doi: 10.1016/j.neuroimage.2012.01.030

Brouwer, H., Fitz, H., et al. (2012). Getting real about semantic illusions: rethinking the functional role of the P600 in language comprehension. *Brain Res, 1446*, 127-143. doi: 10.1016/j.brainres.2012.01.055

Brouwer, H., & Hoeks, J. C. (2013). A time and place for language comprehension: mapping the N400 and the P600 to a minimal cortical network. *Front Hum Neurosci, 7*, 758. doi: 10.3389/fnhum.2013.00758

Buchsbaum, B. R., & D'Esposito, M. (2008). The search for the phonological store: from loop to convolution. *J Cogn Neurosci, 20*(5), 762-778.

Burock, M. A., & Dale, A. M. (2000). Estimation and detection of event-related fMRI signals with temporally correlated noise: a statistically efficient and unbiased approach. *Hum Brain Mapp, 11*(4), 249-260.

Buxton, R. B. (2012). Dynamic models of BOLD contrast. *NeuroImage, 62*(2), 953-961.

Buxton, R. B., Uludag, K., et al. (2004). *Investigating the physiology of brain activation with MRI.* Paper presented at the Medical Imaging 2004.

Buxton, R. B., Uludağ, K., et al. (2004). Modeling the hemodynamic response to brain activation. *NeuroImage, 23*, S220-S233.

C

Cacciari, C., Corradini, P., et al. (2011). Pronoun resolution in Italian: The role of grammatical gender and context. *J Cogn Psychol (Hove), 23*(4), 416-434. doi: 10.1080/20445911.2011.526599

Cacciari, C., & Cubelli, R. (2003). The neuropsychology of grammatical gender: An introduction. *Cortex, 39*(3), 377-382.

Cacciari, C., & Padovani, R. (2007). Further evidence of gender stereotype priming in language: Semantic facilitation and inhibition in Italian role nouns. *Appl Psycholinguist, 28*(02), 277-293.

Caffarra, S., & Barber, H. A. (2015). Does the ending matter? The role of gender-to-ending consistency in sentence reading. *Brain Res, 1605*, 83-92. doi: 10.1016/j.brainres.2015.02.018., 83-92. doi: 10.1016/j.brainres.2015.02.018.

Caffarra, S., Janssen, N., et al. (2014). Two sides of gender: ERP evidence for the presence of two routes during gender agreement processing. *Neuropsychologia*, *63*, 124-134. doi: 10.1016/j.neuropsychologia.2014.08.016

Caffarra, S., Siyanova-Chanturia, A., et al. (2015). Is the noun ending a cue to grammatical gender processing? An ERP study on sentences in Italian. *Psychophysiology*, *52*, 1019-1030. doi: 10.1111/psyp.12429

Carnap, R. (1948). *Introduction to semantics* (Vol. 1042): Harvard University Press Cambridge, Massachusetts.

Carreiras, M., Carr, L., et al. (2010). Where syntax meets math: right intraparietal sulcus activation in response to grammatical number agreement violations. *NeuroImage, 49*(2), 1741-1749. doi: 10.1016/j.neuroimage.2009.09.058

Carreiras, M., Garnham, A., et al. (1993). The use of superficial and meaning-based representations in interpreting pronouns: Evidence from Spanish. *Eur J Cogn Psychol, 5*(1), 93-116.

Carreiras, M., & Gernsbacher, M. A. (1992). Comprehending conceptual anaphors in Spanish. *Lang Cogn Process, 7*(3-4), 281-299.

Carreiras, M., Pattamadilok, C., et al. (2012). Broca's area plays a causal role in morphosyntactic processing. *Neuropsychologia, 50*(5), 816-820. doi: 10.1016/j.neuropsychologia.2012.01.016

Carreiras, M., Quinones, I., et al. (2014). Orthographic Coding: Brain Activation for Letters, Symbols, and Digits. *Cereb Cortex*, bhu163. doi: 10.1093/cercor/bhu163

Carreiras, M., Salillas, E., et al. (2004). Event-related potentials elicited during parsing of ambiguous relative clauses in Spanish. *Brain Res Cogn Brain Res, 20*(1), 98-105. doi: 10.1016/j.cogbrainres.2004.01.009

Carstens, V. (2000). Concord in minimalist theory. *Linguist Inq, 31*(2), 319-355.

Carstens, V. (2001). Multiple Agreement and Case Deletion: Against φ-incompleteness. *Syntax, 4*(3), 147-163.

Carter, C. S., & van Veen, V. (2007). Anterior cingulate cortex and conflict detection: an update of theory and data. *Cogn Affect Behav Neurosci, 7*(4), 367-379.

Catani, M., Dell'Acqua, F., et al. (2012). Short frontal lobe connections of the human brain. *Cortex, 48*(2), 273-291.

Catani, M., & Mesulam, M. (2008). The arcuate fasciculus and the disconnection theme in language and aphasia: history and current state. *Cortex, 44*(8), 953-961.

Catani, M., & Thiebaut de Schotten, M. (2008). A diffusion tensor imaging tractography atlas for virtual in vivo dissections. *Cortex., 44*(8), 1105-1132. doi: 1110.1016/j.cortex.2008.1105.1004. Epub 2008 May 1123.

Clements-Stephens, A. M., Materek, A. D., et al. (2012). Neural circuitry associated with two different approaches to novel word learning. *Dev Cogn Neurosci, 2 Suppl 1*, S99-113. doi: 10.1016/j.dcn.2011.06.001

Colé, P., Pynte, J., et al. (2003). Effect of grammatical gender on visual word recognition: Evidence from lexical decision and eye movement experiments. *Percept Psychophys, 65*(3), 407-419.

Collignon, A., Vandermeulen, D., et al. (1995). *3D multi-modality medical image registration using feature space clustering.* Paper presented at the Computer Vision, Virtual Reality and Robotics in Medicine.

Copland, D. (2003). The basal ganglia and semantic engagement: potential insights from semantic priming in individuals with subcortical vascular lesions, Parkinson's disease, and cortical lesions. *J Int Neuropsychol Soc, 9*(07), 1041-1052.

Corbett, G. G. (1991). *Gender*. New York: Cambridge University Press.

Corbett, G. G. (2000). *Number*. New York: Cambridge University Press.

Corbett, G. G. (2003). *Agreement: Terms and boundaries.* Paper presented at the The Role of Agreement in Natural Language. Proceedings of the 2001 Texas Linguistic Society Conference, Austin, Texas.

Corbett, G. G. (2006). *Agreement*. Cambridge: Cambridge University Press.

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci, 3*(3), 201-215. doi: 10.1038/nrn755

Corbetta, M., & Shulman, G. L. (2011). Spatial neglect and attention networks. *Annu Rev Neurosci, 34,* 569.

Crosson, B., Rao, S. M., et al. (1999). Mapping of semantic, phonological, and orthographic verbal working memory in normal adults with functional magnetic resonance imaging. *Neuropsychology, 13*(2), 171-187.

Chierchia, G., & McConnell-Ginet, S. (2000). *Meaning and grammar: An introduction to semantics*: MIT press.

Choi, Y.-H., Park, H. K., et al. (2015). Role of the posterior temporal lobe during language tasks: a virtual lesion study using repetitive transcranial magnetic stimulation. *NeuroReport, 26*(6), 314-319.

Chomsky, N. (1955a). *The logical structure of linguistic theory.* (Ms.), Harvard University and MIT.

Chomsky, N. (1955b). Logical syntax and semantics: Their linguistic relevance. *Language*, 36-45.

Chomsky, N. (1995) The minimalist program. *Vol. 28* (pp. 420): Cambridge Univ Press.

Chomsky, N. (2000). Minimalist inquiries: the framework. Step by step: essays on minimalist syntax in honor of Howard Lasnik (pp. 89–156): Cambridge, MA: MIT Press.

Chomsky, N. (2001). Derivation by phase. Ken Hale: a life in language (pp. 1–52): Cambridge, MA: MIT Press.

Church, J. A., Coalson, R. S., et al. (2008). A developmental fMRI study of reading and repetition reveals changes in phonological and visual mechanisms over age. *Cereb Cortex, 18*(9), 2054-2065.

D

Dale, A. M. (1999). Optimal experimental design for event-related fMRI. *Hum Brain Mapp, 8*(2-3), 109-114.

Dapretto, M., & Bookheimer, S. Y. (1999). Form and content: dissociating syntax and semantics in sentence comprehension. *Neuron, 24*(2), 427-432.

De Martino, M., Bracco, G., et al. (2011). The activation of grammatical gender information in processing Italian nouns. *Lang Cogn Process, 26*(4-6), 745-776.

De Vincenzi, M., Job, R., et al. (2003). Differences in the perception and time course of syntactic and semantic violations. *Brain Lang, 85*(2), 280-296.

DeLong, K. A., Urbach, T. P., et al. (2005). Probabilistic word pre-activation during language comprehension inferred from electrical brain activity. *Nat Neurosci, 8*(8), 1117-1121.

Demuth, K. (2007). *Acquisition at the prosody-morphology interface.* Paper presented at the Proceedings of the 2nd conference on generative approaches to language acquisition North America (GALANA).

Desrochers, A., Gélinas, C., et al. (1989). An application of the mnemonic keyword method to the acquisition of German nouns and their grammatical gender. *Journal of Educational Psychology, 81*(1), 25.

Deutsch, A., & Bentin, S. (2001). Syntactic and semantic factors in processing gender agreement in Hebrew: Evidence from ERPs and eye movements. *J Mem Lang, 45*(2), 200-224.

Devonshire, I. M., Papadakis, N. G., et al. (2012). Neurovascular coupling is brain region-dependent. *NeuroImage, 59*(3), 1997-2006.

Diedrichsen, J., & Shadmehr, R. (2005). Detecting and adjusting for artifacts in fMRI time series data. *NeuroImage, 27*(3), 624-634. doi: 10.1016/j.neuroimage.2005.04.039

Dikker, S., Rabagliati, H., et al. (2010). Early occipital sensitivity to syntactic category is based on form typicality. *Psychol Sci, 21*(5), 629-634.

Dirnagl, U. (1997). Metabolic aspects of neurovascular coupling *Optical Imaging of Brain Function and Metabolism 2* (pp. 155-159): Springer.

Dronkers, N. F., Wilkins, D. P., et al. (2004). Lesion analysis of the brain areas involved in language comprehension. *Cognition, 92*(1-2), 145-177. doi: 10.1016/j.cognition.2003.11.002

Du, X., Qin, Y., et al. (2013). Differentiation of stages in joke comprehension: Evidence from an ERP study. *Int J Psychol, 48*(2), 149-157.

Duchon, A., Perea, M., et al. (2013). EsPal: One-stop shopping for Spanish word properties. *Behav Res Methods, 45*(4), 1246-1258. doi: 10.3758/s13428-013-0326-1

Duff, M. C., & Brown-Schmidt, S. (2012). The hippocampus and the flexible use and processing of language. *Front Hum Neurosci, 6*.

Duff, M. C., & Kurczek, J. (2013). *Hippocampal amnesia disrupts episodic memory and narrative construction.* Paper presented at the Cognitive Neuroscience Society (CNS) Conference, Cambridge, USA.

Duncan, K., Ketz, N., et al. (2012). Evidence for area CA1 as a match/mismatch detector: A high-resolution fMRI study of the human hippocampus. *Hippocampus, 22*(3), 389-398.

E

Eddington, D. (2004). *Spanish phonology and morphology: Experimental and quantitative perspectives* (Vol. 53): John Benjamins Publishing.

Evans, A. C., Collins, D. L., et al. (1993). 3D statistical neuroanatomical models from 305 MRI volumes. *Proc. IEEE-Nuclear S. Symposium, and Medical Imaging Conference*, 1813-1817.

F

Faussart, C., Jakubowicz, C., et al. (1999). Gender and number processing in spoken French and Spanish. *11*(1), 75e101.

Fedorenko, E., Behr, M. K., et al. (2011). Functional specificity for high-level linguistic processing in the human brain. *Proc Natl Acad Sci U S A*, *108*(39), 16428-16433. doi: 10.1073/pnas.1112937108

Fedorenko, E., Duncan, J., et al. (2012). Language-selective and domain-general regions lie side by side within Broca's area. *Curr Biol, 22*(21), 2059-2062. doi: 10.1016/j.cub.2012.09.011

Fedorenko, E., Nieto-Castanon, A., et al. (2012). Syntactic processing in the human brain: what we know, what we don't know, and a suggestion for how to proceed. *Brain Lang, 120*(2), 187-207. doi: 10.1016/j.bandl.2011.01.001

Fedorenko, E., & Thompson-Schill, S. L. (2014). Reworking the language network. *Trends Cogn Sci, 18*(3), 120-126. doi: 10.1016/j.tics.2013.12.006

Fedorenko, E., Woodbury, R., et al. (2013). Direct evidence of memory retrieval as a source of difficulty in non-local dependencies in language. *Cogn Sci, 37*(2), 378-394. doi: 10.1111/cogs.12021

Fiebach, C. J., Friederici, A. D., et al. (2002). fMRI evidence for dual routes to the mental lexicon in visual word recognition. *J Cogn Neurosci, 14*(1), 11-23. doi: 10.1162/089892902317205285

Folia, V., Forkstam, C., et al. (2009). *Language Comprehension: The Interplay between Form and Content.* Paper presented at the Cognitive Science Society.

Friederici, A. D. (1995). The time course of syntactic activation during language processing: A model based on neuropsychological and neurophysiological data. *Brain Lang, 50*(3), 259-281.

Friederici, A. D. (2002). Towards a neural basis of auditory sentence processing. *Trends Cogn Sci*, *6*(2), 78-84.

Friederici, A. D. (2004). Event-related brain potential studies in language. *Curr Neurol Neurosci Rep, 4*(6), 466-470.

Friederici, A. D. (2011). The brain basis of language processing: from structure to function. *Physiol Rev, 91*(4), 1357-1392. doi: 10.1152/physrev.00006.2011

Friederici, A. D. (2012). The cortical language circuit: from auditory perception to sentence comprehension. *Trends Cogn Sci, 16*(5), 262-268. doi: 10.1016/j.tics.2012.04.001

Friederici, A. D., & Alter, K. (2004). Lateralization of auditory language functions: A dynamic dual pathway model. *Brain and Language, 89*(2), 267-276. doi: 10.1016/s0093-934x(03)00351-1

Friederici, A. D., Bahlmann, J., et al. (2006). The brain differentiates human and non-human grammars: functional localization and structural connectivity. *Proc Natl Acad Sci U S A, 103*(7), 2458-2463. doi: 10.1073/pnas.0509389103

Friederici, A. D., & Gierhan, S. M. (2013). The language network. *Curr Opin Neurobiol, 23*(2), 250-254.

Friederici, A. D., Hahne, A., et al. (1996). Temporal structure of syntactic parsing: early and late event-related brain potential effects. *J Exp Psychol Learn Mem Cogn, 22*(5), 1219-1248.

Friederici, A. D., & Kotz, S. A. (2003). The brain basis of syntactic processes: functional imaging and lesion studies. *NeuroImage, 20*, S8-S17. doi: 10.1016/j.neuroimage.2003.09.003

Friederici, A. D., Rüschemeyer, S. A., et al. (2003). The Role of Left Inferior Frontal and Superior Temporal Cortex in Sentence Comprehension: Localizing Syntactic and Semantic Processes. *Cereb Cortex, 13*(2), 170-177.

Friedmann, N., & Biran, M. (2003). When is gender accessed? A study of paraphasias in Hebrew anomia. *Cortex, 39*(3), 441-463.

Friston, K. J. (2005). Models of brain function in neuroimaging. *Annu Rev Psychol, 56*, 57-87. doi: 10.1146/annurev.psych.56.091103.070311

Friston, K. J., Penny, W. D., et al. (2005). Conjunction revisited. *NeuroImage, 25*(3), 661-667. doi: 10.1016/j.neuroimage.2005.01.013

G

Garnham, A. (1981). Anaphoric reference to instances, instantiated and non-instantiated categories: A reading time study. *British Journal of Psychology, 72*(3), 377-384.

Garnham, A. (1984). Effects of specificity on the interpretation of anaphoric noun phrases. *Q J Exp Psychol, 36*(1), 1-12.

Garnham, A., & Oakhill, J. (1985). On-line resolution of anaphoric pronouns: Effects of inference making and verb semantics. *British Journal of Psychology, 76*(3), 385-393.

Genovese, C. R., Lazar, N. A., et al. (2002). Thresholding of statistical maps in functional neuroimaging using the false discovery rate. *NeuroImage, 15*(4), 870-878. doi: 10.1006/nimg.2001.1037

Gibson, E., Desmet, T., et al. (2005). Reading relative clauses in English. *Cogn Linguist, 16*(2), 313-353.

Gibson, E., & Pearlmutter, N. J. (2000). Distinguishing serial and parallel parsing. *J Psycholinguist Res, 29*(2), 231-240.

Gibson, E., Pearlmutter, N. J., et al. (1999). Recency and lexical preferences in Spanish. *Mem Cognit, 27*(4), 603-611.

Gold, B. T., Balota, D. A., et al. (2006). Dissociation of automatic and strategic lexical-semantics: functional magnetic resonance imaging evidence for differing roles of multiple frontotemporal regions. *J Neurosci, 26*(24), 6523-6532.

Gold, B. T., & Rastle, K. (2007). Neural correlates of morphological decomposition during visual word recognition. *J Cogn Neurosci, 19*(12), 1983-1993.

Gollan, T. H., & Frost, R. (2001). Two routes to grammatical gender: Evidence from Hebrew. *J Psycholinguist Res, 30*(6), 627-651.

Goucha, T., & Friederici, A. D. (2015). The language skeleton after dissecting meaning: A functional segregation within Broca's Area. *NeuroImage, 114*, 294-302.

Graves, W. W., Binder, J. R., et al. (2010). Neural correlates of implicit and explicit combinatorial semantic processing. *NeuroImage, 53*(2), 638-646. doi: 10.1016/j.neuroimage.2010.06.055

Greicius, M. D., Krasnow, B., et al. (2003). *Functional connectivity in the resting brain: a network analysis of the default mode hypothesis.* Paper presented at the Proceedings of the National Academy of Sciences.

Greicius, M. D., Supekar, K., et al. (2009). Resting-state functional connectivity reflects structural connectivity in the default mode network. *Cereb Cortex, 19*(1), 72-78.

Griffiths, J. D., Marslen-Wilson, W. D., et al. (2012). Functional organization of the neural language system: dorsal and ventral pathways are critical for syntax. *Cereb Cortex, 23*(1), 139-147. doi: 10.1093/cercor/bhr386

Grodzinsky, Y. (2000). The neurology of syntax: Language use without Broca's area. *Behav Brain Sci, 23*(01), 1-21.

Grodzinsky, Y., & Friederici, A. D. (2006). Neuroimaging of syntax and syntactic processing. *Curr Opin Neurobiol, 16*(2), 240-246. doi: 10.1016/j.conb.2006.03.007

Gunter, T. C., Friederici, A. D., et al. (2000). Syntactic gender and semantic expectancy: ERPs reveal early autonomy and late interaction. *J Cogn Neurosci, 12*(4), 556-568.

Gusnard, D. A., & Raichle, M. E. (2001). Searching for a baseline: functional imaging and the resting human brain. *Nat Rev Neurosci, 2*(10), 685-694.

H

Hagoort, P. (2003a). How the brain solves the binding problem for language: a neurocomputational model of syntactic processing. *NeuroImage, 20 Suppl 1,* S18-29.

Hagoort, P. (2003b). Interplay between syntax and semantics during sentence comprehension: ERP effects of combining syntactic and semantic violations. *J Cogn Neurosci, 15*(6), 883-899.

Hagoort, P. (2005). On Broca, brain, and binding: a new framework. *Trends Cogn Sci, 9*(9), 416-423. doi: 10.1016/j.tics.2005.07.004

Hagoort, P. (2013). MUC (Memory, Unification, Control) and beyond. *Front Psychol, 4*, 416. doi: 10.3389/fpsyg.2013.00416

Hagoort, P. (2014). Nodes and networks in the neural architecture for language: Broca's region and beyond. *Curr Opin Neurobiol, 28C*, 136-141. doi: 10.1016/j.conb.2014.07.013

Hagoort, P., Brown, C. A., et al. (1993). The syntactic positive shift (SPS) as an ERP measure of syntactic processing. *Lang Cogn Process, 8*(4), 439-483.

Hagoort, P., & Brown, C. M. (1999). Gender electrified: ERP evidence on the syntactic nature of gender processing. *J Psycholinguist Res, 28*(6), 715-728.

Hagoort, P., Hald, L., et al. (2004). Integration of word meaning and world knowledge in language comprehension. *Science, 304*(5669), 438-441.

Hagoort, P., & Indefrey, P. (2014). The neurobiology of language beyond single words. *Annu Rev Neurosci, 37,* 347-362. doi: 10.1146/annurev-neuro-071013-013847

Hagoort, P., Wassenaar, M., et al. (2003). Syntax-related ERP-effects in Dutch. *Cogn Brain Res, 16*(1), 38–50.

Hammer, A., Goebel, R., et al. (2007). When sex meets syntactic gender on a neural basis during pronoun processing. *Brain Res, 1146,* 185-198. doi: 10.1016/j.brainres.2006.06.110

Hammer, A., Jansma, B. M., et al. (2005). Pronominal reference in sentences about persons or things: An electrophysiological approach. *J Cogn Neurosci, 17*(2), 227-239.

Hammer, A., Jansma, B. M., et al. (2011). Neural mechanisms of anaphoric reference revealed by FMRI. *Front Psychol, 2*, 32. doi: 10.3389/fpsyg.2011.00032

Handy, T. C. (2005). *Event-related potentials: A methods handbook*: MIT press.

Harel, N., Lee, S.-P., et al. (2002). Origin of negative blood oxygenation level–dependent fMRI signals. *J Cereb Blood Flow Metab, 22*(8), 908-917.

Harley, H., & Ritter, E. (2002). Structuring the bundle: A universal morphosyntactic feature geometry In H. J. S. a. H. Wiese (Ed.), *Pronouns – Grammar and Representation* (pp. 23-39). Humboldt University Berlin: John Benjamins Publishing Company.

Harris, J. W. (1991). The exponence of gender in Spanish. *Linguist Inq*, 27-62.

Hasselmo, M. E., Schnell, E., et al. (1995). A model of the hippocampus combining self-organization and associative memory function. *Adv Neural Inf Process Syst*, 77-84.

Heim, S. (2008). Syntactic gender processing in the human brain: a review and a model. *Brain Lang, 106*(1), 55-64. doi: 10.1016/j.bandl.2007.12.006

Heim, S., Alter, K., et al. (2005). The role of the left Brodmann's areas 44 and 45 in reading words and pseudowords. *Brain Res Cogn Brain Res, 25*(3), 982-993. doi: 10.1016/j.cogbrainres.2005.09.022

Heim, S., Eickho¡a, S. B., et al. (2006). BA 44 in Broca’s area supports syntactic gender decisions in language production. *NeuroReport, 17*(11), 1097-1110.

Heim, S., van Ermingen, M., et al. (2010). Left cytoarchitectonic BA 44 processes syntactic gender violations in determiner phrases. *Hum Brain Mapp, 31*(10), 1532-1541. doi: 10.1002/hbm.20957

Hernandez, A. E., Kotz, S. A., et al. (2004). The neural correlates of grammatical gender decisions in Spanish. *NeuroReport, 15*(5), 863-866.

Hernandez, A. E., Woods, E. A., et al. (2015). Neural correlates of single word reading in bilingual children and adults. *Brain Lang, 143*, 11-19.

Hickock, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Reviews Neuroscience*.

Hillert, D., & Bates, E. (1996). Morphological constraints on lexical access: Gender priming in German *Gender in German*. La Jolla, San Diego: Center for Research in Language, University of California.

Hoeks, J., & Brouwer, H. (2014). *Electrophysiological Research on Conversation and Discourse Processing*. Oxford: Oxford University Press.

Hofmann, J., Kotz, S. A., et al. (2007). Lesion-site affects grammatical gender assignment in German: Perception and production data. *Neuropsychologia, 45*(5), 954-965.

Hofmann, J., Marschhauser, A., et al. (2003). Grammatical gender processing in aphasic patients. *Brain and Language, 87*(1), 57-58. doi: 10.1016/s0093-934x(03)00196-2

Hohlfeld, A., Sangals, J., et al. (2004). Effects of additional tasks on language perception: an event-related brain potential investigation. *J Exp Psychol Learn Mem Cogn, 30*(5), 1012.

Höhn, G. (2012). *Unagreement is an Illusion: The structure of the extended nominal projection and apparent agreement mismatches.* (Unpublish Doctoral Thesis), University College of London.

Holmes, V. M., & Segui, J. (2004). Sublexical and lexical influences on gender assignment in French. *J Psycholinguist Res, 33*(6), 425-457.

Holmes, V. M., & Segui, J. (2006). Assigning grammatical gender during word production. *J Psycholinguist Res, 35*(1), 5-30.

Huang, J., Zhu, Z., et al. (2012). The role of left inferior frontal gyrus in explicit and implicit semantic processing. *Brain Res, 1440*, 56-64. doi: 10.1016/j.brainres.2011.11.060

Huber, L., Goense, J., et al. (2014). Investigation of the neurovascular coupling in positive and negative BOLD responses in human brain at 7T. *NeuroImage, 97,* 349-362.

Huettel, S. A. (2004). *Non-linearities in the blood-oxygenation-level dependent (BOLD) response measured by functional magnetic resonance imaging (fMRI).* Paper presented at the Engineering in Medicine and Biology Society, 2004. IEMBS'04. 26th Annual International Conference of the IEEE.

Huettel, S. A. (2012). Event-related fMRI in cognition. *NeuroImage, 62*(2), 1152-1156.

Huettel, S. A., McKeown, M. J., et al. (2004). Linking hemodynamic and electrophysiological measures of brain activity: evidence from functional MRI and intracranial field potentials. *Cereb Cortex, 14*(2), 165-173.

Huettel, S. A., Obembe, O. O., et al. (2004). The BOLD fMRI refractory effect is specific to stimulus attributes: evidence from a visual motion paradigm. *NeuroImage, 23*(1), 402-408.

Huettel, S. A., Song, A. W., et al. (2004). *Functional magnetic resonance imaging* (Vol. 1): Sinauer Associates Sunderland.

Humphries, C., Binder, J. R., et al. (2006). Syntactic and semantic modulation of neural activity during auditory sentence comprehension. *J Cogn Neurosci, 18*(4), 665-679. doi: 10.1162/jocn.2006.18.4.665

Humphries, C., Binder, J. R., et al. (2007). Time course of semantic processes during sentence comprehension: an fMRI study. *NeuroImage, 36*(3), 924-932. doi: 10.1016/j.neuroimage.2007.03.059

Hyönä, J., Lorch Jr, R. F., et al. (2002). Individual differences in reading to summarize expository text: Evidence from eye fixation patterns. *J Educ Psychol, 94*(1), 44.

I

Igoa, J. M., Carreiras, M., et al. (1998). A study on late closure in Spanish: Principle-grounded vs. frequency-based accounts of attachment preferences. *Q J Exp Psychol-A, 51*(3), 561-592.

Imai, K., Keele, L., et al. (2010). A general approach to causal mediation analysis. *Psychol Methods, 15*(4), 309-334. doi: 10.1037/a0020761

Imai, K., Keele, L., et al. (2010). Identification, inference and sensitivity analysis for causal mediation effects. *Stat Sci*, 51-71.

Indefrey, P., & Levelt, W. J. (2004). The spatial and temporal signatures of word production components. *Cognition, 92*(1-2), 101-144. doi: 10.1016/j.cognition.2002.06.001

J

Jaiswal, M. K. (2015). Toward a High-Resolution Neuroimaging Biomarker for Mild Traumatic Brain Injury: From Bench to Bedside. *Frontiers in Neurology, 6*, 148.

Janssen, N., & Caramazza, A. (2003). The selection of closed-class words in noun phrase production: The case of Dutch determiners. *J Mem Lang, 48*(3), 635-652.

Jefferies, E. (2013). The neural basis of semantic cognition: converging evidence from neuropsychology, neuroimaging and TMS. *Cortex, 49*(3), 611-625. doi: 10.1016/j.cortex.2012.10.008

Jueptner, M., & Weiller, C. (1995). Review: does measurement of regional cerebral blood flow reflect synaptic activity?—Implications for PET and fMRI. *NeuroImage, 2*(2PA), 148-156.

Just, M. A., & Carpenter, P. A. (1980). A theory of reading: from eye fixations to comprehension. *Psychol Rev, 87*(4), 329.

K

Kaan, E., Harris, A., et al. (2000). The P600 as an index of syntactic integration difficulty. *Lang Cognit Process, 15*(2), 159-201.

Kaan, E., & Swaab, T. Y. (2003). Repair, revision, and complexity in syntactic analysis: an electrophysiological differentiation. *J Cogn Neurosci, 15*(1), 98-110. doi: 10.1162/089892903321107855

Kail, M., Bassano, D., et al. (2010). *Early comprehension of syntactic constructions: transitive structures in French.* Paper presented at the Grammaticalization and Language Acquisition, Paris, France.

Katsuki, F., & Constantinidis, C. (2012a). Early involvement of prefrontal cortex in visual bottom-up attention. *Nat Neurosci, 15*(8), 1160-1166.

Katsuki, F., & Constantinidis, C. (2012b). Unique and shared roles of the posterior parietal and dorsolateral prefrontal cortex in cognitive functions. *Front Integr Neurosci, 6*.

Kerns, J. G., Cohen, J. D., et al. (2004). Anterior cingulate conflict monitoring and adjustments in control. *Science, 303*(5660), 1023-1026. doi: 10.1126/science.1089910

Kim, A., & Osterhout, L. (2005). The independence of combinatory semantic processing: Evidence from event-related potentials. *Journal of Memory and Language, 52*(2), 205-225. doi: 10.1016/j.jml.2004.10.002

Kim, S. G., & Ogawa, S. (2012). Biophysical and physiological origins of blood oxygenation level-dependent fMRI signals. *J Cereb Blood Flow Metab, 32*(7), 1188-1206.

Koelsch, S. (2005). Neural substrates of processing syntax and semantics in music. *Curr Opin Neurobiol, 15*(2), 207-212. doi: 10.1016/j.conb.2005.03.005

Koelsch, S., Gunter, T. C., et al. (2005). Interaction between syntax processing in language and in music: An ERP study. *J Cogn Neurosci, 17*(10), 1565-1577.

Koelsch, S., Kasper, E., et al. (2004). Music, language and meaning: brain signatures of semantic processing. *Nat Neurosci, 7*(3), 302-307. doi: 10.1038/nn1197

Kolk, H. H. J., Chwilla, D. J., et al. (2003). Structure and limited capacity in verbal working memory: A study with event-related potentials. *Brain Lang, 85*(1), 1-36. doi: 10.1016/s0093-934x(02)00548-5

Koshino, H., Minamoto, T., et al. (2014). Coactivation of the default mode network regions and working memory network regions during task preparation. *Sci Rep, 4*.

Kotz, S. A., & Schmidt-Kassow, M. (2015). Basal ganglia contribution to rule expectancy and temporal predictability in speech. *Cortex*.

Kotz, S. A., & Schwartze, M. (2010). Cortical speech processing unplugged: a timely subcortico-cortical framework. *Trends Cogn Sci, 14*(9), 392-399. doi: 10.1016/j.tics.2010.06.005

Kotz, S. A., Schwartze, M., et al. (2009). Non-motor basal ganglia functions: a review and proposal for a model of sensory predictability in auditory language perception. *Cortex, 45*(8), 982-990.

Kumaran, D. (2008). Short-term memory and the human hippocampus. *J Neurosci, 28*(15), 3837-3838.

Kumaran, D., & Maguire, E. A. (2005). The human hippocampus: cognitive maps or relational memory? *J Neurosci, 25*(31), 7254-7259.

Kumaran, D., & Maguire, E. A. (2006). An unexpected sequence of events: mismatch detection in the human hippocampus. *PLoS Biol, 4*(12), e424.

Kumaran, D., & Maguire, E. A. (2007). Which computational mechanisms operate in the hippocampus during novelty detection? *Hippocampus, 17*(9), 735-748.

Kuperberg, G. R. (2007). Neural mechanisms of language comprehension: challenges to syntax. *Brain Res, 1146*, 23-49. doi: 10.1016/j.brainres.2006.12.063

Kuperberg, G. R., Halgren, E., et al. (2000). Event-related fMRI reveals distinct patterns of neural modulation during semantic and syntactic processing of sentences. *NeuroImage, 11*(5), S263.

Kuperberg, G. R., Holcomb, P. J., et al. (2003). Distinct patterns of neural modulation during the processing of conceptual and syntactic anomalies. *J Cogn Neurosci, 15*(2), 272-293.

Kuperberg, G. R., Kreher, D. A., et al. (2007). The role of animacy and thematic relationships in processing active English sentences: evidence from event-related potentials. *Brain Lang, 100*(3), 223-237. doi: 10.1016/j.bandl.2005.12.006

Kuperberg, G. R., Lakshmanan, B. M., et al. (2006). Making sense of discourse: an fMRI study of causal inferencing across sentences. *NeuroImage, 33*(1), 343-361. doi: 10.1016/j.neuroimage.2006.06.001

Kuperberg, G. R., Sitnikova, T., et al. (2008). Neuroanatomical distinctions within the semantic system during sentence comprehension: evidence from functional magnetic resonance imaging. *NeuroImage, 40*(1), 367-388. doi: 10.1016/j.neuroimage.2007.10.009

Kuperberg, G. R., West, W. C., et al. (2008). Functional magnetic resonance imaging reveals neuroanatomical dissociations during semantic integration in schizophrenia. *Biol Psychiatry, 64*(5), 407-418. doi: 10.1016/j.biopsych.2008.03.018

Kurczek, J. (2014). *Hippocampal contributions to language: an examination of referential processing and narrative in amnesia.* (Doctor of Philosophy), University of Iowa, Iowa, USA.

Kurczek, J., Brown-Schmidt, S., et al. (2013). Hippocampal contributions to language: Evidence of referential processing deficits in amnesia. *J Exp Psychol Gen, 142*(4), 1346.

Kutas, M., & Federmeier, K. D. (2000). Electrophysiology reveals semantic memory use in language comprehension. *Trends in Cognitive Sciences, 4*(12), 463-470.

Kutas, M., & Hillyard, S. A. (1983). Event-related brain potentials to grammatical errors and semantic anomalies. *Mem Cognit, 11*(5), 539-550.

Kutas, M., & Hillyard, S. A. (1984). Brain potentials during reading reflect word expectancy and semantic association. *Nature, 307*(5947), 161-163.

L

Laiacona, M., Luzzatti, C., et al. (2001). Lexical and semantic factors influencing picture naming in aphasia. *Brain Cogn, 46*(1), 184-187.

Lau, E. F., Gramfort, A., et al. (2013). Automatic semantic facilitation in anterior temporal cortex revealed through multimodal neuroimaging. *J Neurosci, 33*(43), 17174-17181. doi: 10.1523/JNEUROSCI.1018-13.2013

Lau, E. F., Phillips, C., et al. (2008). A cortical network for semantics: (de)constructing the N400. *Nat Rev Neurosci, 9*(12), 920-933. doi: 10.1038/nrn2532

Lauro, L. J., Tettamanti, M., et al. (2008). Idiom comprehension: a prefrontal task? *Cereb Cortex, 18*(1), 162-170. doi: 10.1093/cercor/bhm042

Leh, S. E., Chakravarty, M. M., et al. (2007). The connectivity of the human pulvinar: a diffusion tensor imaging tractography study. *Int J Biomed Imaging, 2008*.

Leh, S. E., Ptito, A., et al. (2007). Fronto-striatal connections in the human brain: a probabilistic diffusion tractography study. *Neurosci Lett, 419*(2), 113-118.

Lemhöfer, K., Schriefers, H., et al. (2006). The processing of free and bound gender-marked morphemes in speech production: Evidence from Dutch. *J Exp Psychol Learn Mem Cogn, 32*(2), 437.

Levelt, W. J. (2001). Spoken word production: a theory of lexical access. *Proc Natl Acad Sci U S A, 98*(23), 13464-13471. doi: 10.1073/pnas.231459498

Levelt, W. J., Roelofs, A., et al. (1999). A theory of lexical access in speech production. *Behav and brain sci, 22*(01), 1-38.

Levy, B. J., & Wagner, A. D. (2011). Cognitive control and right ventrolateral prefrontal cortex: reflexive reorienting, motor inhibition, and action updating. *Ann N Y Acad Sci, 1224*(1), 40-62.

Levy, J., Pernet, C., et al. (2009). Testing for the dual-route cascade reading model in the brain: an fMRI effective connectivity account of an efficient reading style. *PLoS One, 4*(8), e6675. doi: 10.1371/journal.pone.0006675

Lewis, G., Solomyak, O., et al. (2011). The neural basis of obligatory decomposition of suffixed words. *Brain Lang, 118*(3), 118-127. doi: 10.1016/j.bandl.2011.04.004

Libertus, K., & Needham, A. (2010). Teach to reach: the effects of active vs. passive reaching experiences on action and perception. *Vision Res, 50*(24), 2750-2757. doi: 10.1016/j.visres.2010.09.001

Lisman, J. E., & Grace, A. A. (2005). The hippocampal-VTA loop: controlling the entry of information into long-term memory. *Neuron, 46*(5), 703-713.

Logothetis, N. K. (2002). The neural basis of the blood-oxygen-level-dependent functional magnetic resonance imaging signal. *Philos Trans R Soc Lond B Biol Sci, 357*(1424), 1003-1037. doi: 10.1098/rstb.2002.1114

Logothetis, N. K., Pauls, J., et al. (2001). Neurophysiological investigation of the basis of the fMRI signal. *Nature, 412*(6843), 150-157.

Logothetis, N. K., & Pfeuffer, J. (2004). On the nature of the BOLD fMRI contrast mechanism. *Magn Reson Imaging, 22*(10), 1517-1531.

Lu, X. Y., Cai, Q., et al. (2011). Recent developments in the third generation inhibitors of Bcr-Abl for overriding T315I mutation. *Curr Med Chem, 18*(14), 2146-2157.

Luke, K. K., Liu, H. L., et al. (2002). Functional anatomy of syntactic and semantic processing in language comprehension. *Hum Brain Mapp, 16*(3), 133-145. doi: 10.1002/hbm.10029

Lum, J. A., Conti-Ramsden, G., et al. (2012). Working, declarative and procedural memory in specific language impairment. *Cortex, 48*(9), 1138-1154.

Lum, J. A., Ullman, M. T., et al. (2015). Verbal declarative memory impairments in specific language impairment are related to working memory deficits. *Brain Lang, 142*, 76-85.

Lutcke, H., & Frahm, J. (2008). Lateralized anterior cingulate function during error processing and conflict monitoring as revealed by high-resolution fMRI. *Cereb Cortex, 18*(3), 508-515. doi: 10.1093/cercor/bhm090

Luzzatti, C., & De Bleser, R. (1999). Gender an number processing in italiabn agrammatic speakers: futher evidence for dual route models of processing. *Rivista di Linguistica, 11*(1), 103-132.

Lyons, J. (1995). *Linguistic semantics: An introduction*: Cambridge University Press.

M

Macey, P. M., Macey, K. E., et al. (2004). A method for removal of global effects from fMRI time series. *NeuroImage, 22*(1), 360-366. doi: 10.1016/j.neuroimage.2003.12.042

MacKinnon, D. P. (2008). *Introduction to statistical mediation analysis*: Routledge.

MacWhinney, B., Leinbach, J., et al. (1989). Language learning: Cues or rules? *J Mem Lang, 28*(3), 255-277.

Maess, B., Koelsch, S., et al. (2001). Musical syntax is processed in Broca's area: an MEG study. *Nature neuroscience, 4*(5), 540-545.

Maguire, E. A., Vargha-Khadem, F., et al. (2001). The effects of bilateral hippocampal damage on fMRI regional activations and interactions during memory retrieval. *Brain, 124*(6), 1156-1170.

Mancini, S., Molinaro, N., et al. (2013a). Anchoring agreement. In M. T. M. Sanz, M. & I. Laka (Ed.), *Language Down the Garden Path: The Cognitive and Biological Basis for Linguistic Structures* (pp. 280-293). Oxford: Oxford University Press.

Mancini, S., Molinaro, N., et al. (2013b). Anchoring Agreement in Comprehension. *Lang Linguist Compass, 7*(1), 1–21. doi: 10.1111/lnc3.12008

Mancini, S., Molinaro, N., et al. (2011a). A person is not a number: Discourse involvement in subject–verb agreement computation. *Brain Res, 1410*, 64-76.

Mancini, S., Molinaro, N., et al. (2011b). When persons disagree: an ERP study of Unagreement in Spanish. *Psychophysiology, 48*(10), 1361-1371. doi: 10.1111/j.1469-8986.2011.01212.x

Mancini, S., Postiglione, F., et al. (2014). On the person-number distinction: Subject-verb agreement processing in Italian. *Lingua, 146*, 28-38.

Marslen-Wilson, W. D., & Tyler, L. K. (2007). Morphology, language and the brain: the decompositional substrate for language comprehension. *Philos Trans R Soc Lond B Biol Sci, 362*(1481), 823-836.

Martin-Loeches, M., Nigbur, R., et al. (2006). Semantics prevalence over syntax during sentence processing: a brain potential study of noun-adjective agreement in Spanish. *Brain Res, 1093*(1), 178-189. doi: 10.1016/j.brainres.2006.03.094

Mashal, N., Faust, M., et al. (2007). An fMRI investigation of the neural correlates underlying the processing of novel metaphoric expressions. *Brain Lang, 100*(2), 115-126. doi: 10.1016/j.bandl.2005.10.005

Mehta, R. K., & Parasuraman, R. (2013). Neuroergonomics: a review of applications to physical and cognitive work. *Front Hum Neurosci, 7*.

Menenti, L., Petersson, K. M., et al. (2009). When elephants fly: differential sensitivity of right and left inferior frontal gyri to discourse and world knowledge. *J Cogn Neurosci, 21*(12), 2358-2368. doi: 10.1162/jocn.2008.21163

Mestres-Missé, A., Bazin, P.-L., et al. (2014). Dorsomedial striatum involvement in regulating conflict between current and presumed outcomes. *NeuroImage, 98*, 159-167.

Mestres-Missé, A., Càmara, E., et al. (2008). Functional neuroanatomy of meaning acquisition from context. *J Cogn Neurosci, 20*(12), 2153-2166.

Mestres-Missé, A., Turner, R., et al. (2012). An anterior-posterior gradient of cognitive control within the dorsomedial striatum. *NeuroImage, 62*(1), 41-47. doi: 10.1016/j.neuroimage.2012.05.021

Meyer-Lindenberg, A. (2010). From maps to mechanisms through neuroimaging of schizophrenia. *Nature, 468*(7321), 194-202.

Miceli, G., Turriziani, P., et al. (2002). The Neural Correlates of Grammatical Gender: An fMRI Investigation. *J Cogn Neurosci, 14*(4), 618-628.

Michael, G. A., Garcia, S., et al. (2006). The ventral premotor cortex (vPM) and resistance to interference. *Behav Neurosci, 120*(2), 447.

Miyagawa, S. (2010). *Why Agree? Why Move: Unifying Agreement-Based and Discourse Configurational Languages*: MIT Press.

Miyagawa, S., Ojima, S., et al. (2014). The integration hypothesis of human language evolution and the nature of contemporary languages. *Front Psychol, 5*, 564. doi: 10.3389/fpsyg.2014.00564

Molinaro, N., Barber, H. A., et al. (2013). Left fronto-temporal dynamics during agreement processing: evidence for feature-specific computations. *NeuroImage, 78*, 339-352. doi: 10.1016/j.neuroimage.2013.04.025

Molinaro, N., Barber, H. A., et al. (2011). Grammatical agreement processing in reading: ERP findings and future directions. *Cortex, 47*(8), 908-930. doi: 10.1016/j.cortex.2011.02.019

Molinaro, N., Carreiras, M., et al. (2012). Semantic combinatorial processing of non-anomalous expressions. *Neuroimage, 59*(4), 3488-3501. doi: 10.1016/j.neuroimage.2011.11.009

Molinaro, N., Conrad, M., et al. (2010). On the functional nature of the N400: Contrasting effects related to visual word recognition and contextual semantic integration. *Cognitive Neuroscience, 1*(1), 1-7. doi: 10.1080/17588920903373952

Molinaro, N., Kim, A., et al. (2008). Anaphoric agreement violation: an ERP analysis of its interpretation. *Cognition, 106*(2), 963-974. doi: 10.1016/j.cognition.2007.03.006

Molinaro, N., Paz-Alonso, P. M., et al. (2015). Combinatorial semantics strengthens angular-anterior temporal coupling. *Cortex, 65*, 113-127.

Molinaro, N., Vespignani, F., et al. (2008). A deeper reanalysis of a superficial feature: an ERP study on agreement violations. *Brain Res, 1228*, 161-176. doi: 10.1016/j.brainres.2008.06.064

Molinaro, N., Vespignani, F., et al. (2011). Why brother and sister are not just siblings: Repair processes in agreement computation. *J Mem Lang, 64*(3), 211-232. doi: 10.1016/j.jml.2010.12.002

Mueller, J. L., Rueschemeyer, S.-A., et al. (2014). Neural networks involved in learning lexical-semantic and syntactic information in a second language. *Front Psychol, 5*.

Munte, T. F., Heinze, H. J., et al. (1993). Dissociation of brain activity related to syntactic and semantic aspects of language. *J Cogn Neurosci, 5*(3), 335-344.

Murray, L. J., & Ranganath, C. (2007). The dorsolateral prefrontal cortex contributes to successful relational memory encoding. *J Neurosci, 27*(20), 5515-5522. doi: 10.1523/JNEUROSCI.0406-07.2007

N

Nadeau, S. E., & Crosson, B. (1997). Subcortical aphasia. *Brain Lang, 58*(3), 355-402.

Nevins, A., Dillon, B., et al. (2007). The role of feature-number and feature-type in processing Hindi verb agreement violations. *Brain Res, 1164*, 81-94. doi: 10.1016/j.brainres.2007.05.058

Newhart, M., Trupe, L. A., et al. (2012). Asyntactic comprehension, working memory, and acute ischemia in Broca's area versus angular gyrus. *Cortex, 48*(10), 1288-1297. doi: 10.1016/j.cortex.2011.09.009

Newman, S. D., Just, M. A., et al. (2003). Differential effects of syntactic and semantic processing on the subregions of Broca’s area. *Cogn Brain Res, 16*(2), 297-307. doi: 10.1016/s0926-6410(02)00285-9

Ni, W., Constable, R. T., et al. (2000). An event-related neuroimaging study distinguishing form and content in sentence processing. *J Cogn Neurosci, 12*(1), 120-133.

Nicol, J. L., Forster, K. I., et al. (1997). Subject–verb agreement processes in comprehension. *J Mem Lang, 36*(4), 569-587.

Nichols, T., Brett, M., et al. (2005). Valid conjunction inference with the minimum statistic. *NeuroImage, 25*(3), 653-660. doi: 10.1016/j.neuroimage.2004.12.005

Nichols, T., & Hayasaka, S. (2003). Controlling the familywise error rate in functional neuroimaging: a comparative review. *Stat Methods Med Res, 12*(5), 419-446.

Nieuwland, M. S., Martin, A. E., et al. (2012). Brain regions that process case: evidence from Basque. *Hum Brain Mapp, 33*(11), 2509-2520. doi: 10.1002/hbm.21377

Nieuwland, M. S., Petersson, K. M., et al. (2007). On sense and reference: examining the functional neuroanatomy of referential processing. *NeuroImage, 37*(3), 993-1004. doi: 10.1016/j.neuroimage.2007.05.048

Nir, Y., Dinstein, I., et al. (2008). BOLD and spiking activity. *Nat Neurosci, 11*(5), 523-524.

Nir, Y., Fisch, L., et al. (2007). Coupling between neuronal firing rate, gamma LFP, and BOLD fMRI is related to interneuronal correlations. *Curr Biol, 17*(15), 1275-1285.

Novick, J. M., Trueswell, J. C., et al. (2005). Cognitive control and parsing: reexamining the role of Broca's area in sentence comprehension. *Cogn Affect Behav Neurosci, 5*(3), 263-281.

O

O'Kane, G., Insler, R. Z., et al. (2005). Conceptual and perceptual novelty effects in human medial temporal cortex. *Hippocampus, 15*(3), 326-332.

O'Kane, G., Kensinger, E. A., et al. (2004). Evidence for semantic learning in profound amnesia: an investigation with patient HM. *Hippocampus, 14*(4), 417-425.

Obleser, J., & Kotz, S. A. (2009). Expectancy constraints in degraded speech modulate the language comprehension network. *Cereb Cortex*, bhp128.

Ogawa, S., Lee, T.-M., et al. (1990). *Brain magnetic resonance imaging with contrast dependent on blood oxygenation.* Paper presented at the Proceedings of the National Academy of Sciences.

Ogawa, S., Lee, T.-M., et al. (1990). Oxygenation-sensitive contrast in magnetic resonance image of rodent brain at high magnetic fields. *Magn Reson Med, 14*(1), 68-78.

Ogawa, S., Menon, R., et al. (1998). On the characteristics of functional magnetic resonance imaging of the brain. *Annu Rev Biophys Biomol Struct, 27*(1), 447-474.

Ogawa, S., Menon, R., et al. (1993). Functional brain mapping by blood oxygenation level-dependent contrast magnetic resonance imaging. A comparison of signal characteristics with a biophysical model. *Biophys J, 64*(3), 803.

Ogawa, S., Tank, D. W., et al. (1992). *Intrinsic signal changes accompanying sensory stimulation: functional brain mapping with magnetic resonance imaging.* Paper presented at the Proceedings of the National Academy of Sciences.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychologia, 9,* 97-113.

Olichney, J. M., Taylor, J. R., et al. (2010). fMRI congruous word repetition effects reflect memory variability in normal elderly. *Neurobiol Aging, 31*(11), 1975-1990. doi: 10.1016/j.neurobiolaging.2008.10.010

Osterhout, L., & Mobley, L. A. (1995). Event-related brain potentials elicited by failure to agree. *J Mem Lang, 34*(6), 739-773.

P

Padovani, R., Calandra-Buonaura, G., et al. (2005). Grammatical gender in the brain: evidence from an fMRI study on Italian. *Brain Res Bull, 65*(4), 301-308.

Pallier, C., Devauchelle, A.-D., et al. (2011). *Cortical representation of the constituent structure of sentences.* Paper presented at the Proceedings of the National Academy of Sciences.

Papoutsi, M., Stamatakis, E. A., et al. (2011). Is left fronto-temporal connectivity essential for syntax? Effective connectivity, tractography and performance in left-hemisphere damaged patients. *Neuroimage, 58*(2), 656-664. doi: 10.1016/j.neuroimage.2011.06.036

Pardo, J. V., Pardo, P. J., et al. (1990). *The anterior cingulate cortex mediates processing selection in the Stroop attentional conflict paradigm.* Paper presented at the National Academy of Sciences.

Pascual, B., Masdeu, J. C., et al. (2015). Large-scale brain networks of the human left temporal pole: a functional connectivity MRI study. *Cereb Cortex, 25*(3), 680-702.

Pasley, B. N., Inglis, B. A., et al. (2007). Analysis of oxygen metabolism implies a neural origin for the negative BOLD response in human visual cortex. *NeuroImage, 36*(2), 269-276.

Patterson, K., Nestor, P. J., et al. (2007). Where do you know what you know? The representation of semantic knowledge in the human brain. *Nat Rev Neurosci, 8*(12), 976-987. doi: 10.1038/nrn2277

Pearlmutter, N. J. (2000). Linear versus hierarchical agreement feature processing in comprehension. *J Psycholinguist Res, 29*(1), 89-98.

Pearlmutter, N. J., Garnsey, S. M., et al. (1999). Agreement processes in sentence comprehension. *Journal of Memory and Language, 41*(3), 427-456.

Pearlmutter, N. J., & Mendelsohn, A. A. (1999). Serial versus parallel sentence comprehension. *Unpublished manuscript*.

Pérez, A., Molinaro, N., et al. (2012). Oscillatory dynamics related to the Unagreement pattern in Spanish. *Neuropsychologia, 50*(11), 2584-2597. doi: 10.1016/j.neuropsychologia.2012.07.009

Petersen, S. E., & Posner, M. I. (2012). The attention system of the human brain: 20 years after. *Annu Rev Neurosci, 35*, 73-89. doi: 10.1146/annurev-neuro-062111-150525

Petersson, K. M., Folia, V., et al. (2012). What artificial grammar learning reveals about the neurobiology of syntax. *Brain Lang, 120*(2), 83-95. doi: 10.1016/j.bandl.2010.08.003

Petersson, K. M., & Hagoort, P. (2012). The neurobiology of syntax: beyond string sets. *Philos Trans R Soc Lond B Biol Sci, 367*(1598), 1971-1983. doi: 10.1098/rstb.2012.0101

Pollard, C. J., & Sag, I. A. (1994). *Head-driven phrase structure grammar*: Univ Chic Press.

Prabhakaran, R., Blumstein, S. E., et al. (2006). An event-related fMRI investigation of phonological–lexical competition. *Neuropsychologia, 44*(12), 2209-2221.

Price, A. R., Bonner, M. F., et al. (2015). Converging evidence for the neuroanatomic basis of combinatorial semantics in the angular gyrus. *J Neurosci, 35*(7), 3276-3284.

Price, C. J. (2010). The anatomy of language: a review of 100 fMRI studies published in 2009. *Ann N Y Acad Sci, 1191*, 62-88. doi: 10.1111/j.1749-6632.2010.05444.x

Price, C. J. (2012). A review and synthesis of the first 20 years of PET and fMRI studies of heard speech, spoken language and reading. *NeuroImage, 62*(2), 816-847. doi: 10.1016/j.neuroimage.2012.04.062

Price, C. J., Moore, C. J., et al. (1997). Segregating semantic from phonological processes during reading. *J Cogn Neurosci, 9*(6), 727-733.

Pylkkänen, L., Bemis, D. K., et al. (2014). Building phrases in language production: An MEG study of simple composition. *Cognition, 133*(2), 371-384.

Pylkkänen, L., Stringfellow, A., et al. (2002). Neuromagnetic Evidence for the Timing of Lexical Activation: An MEG Component Sensitive to Phonotactic Probability but Not to Neighborhood Density. *Brain and Language, 81*(1-3), 666-678. doi: 10.1006/brln.2001.2555

R

Radeau, M., & van Berkum, J. J. A. (1996). Gender decision. *Lang Cogn Process, 11*(6), 605-610.

Radford, A. (1997). *Syntax: A minimalist introduction*: Cambridge University Press.

Radford, A. (2004). *Minimalist Syntax. Exploring the Structure of English*. New York: Cambridge University Press.

Raichle, M. E. (2015). The Brain's Default Mode Network. *Annu Rev Neurosci, 38*, 433-447. doi: 10.1146/annurev-neuro-071013-014030

Raichle, M. E., MacLeod, A. M., et al. (2001). A default mode of brain function. *Proc Natl Acad Sci U S A, 98*(2), 676-682. Retrieved from

Raichle, M. E., & Snyder, A. Z. (2007). A default mode of brain function: a brief history of an evolving idea. *NeuroImage, 37*(4), 1083-1090.

Raizada, R. D., & Poldrack, R. A. (2007). Selective amplification of stimulus differences during categorical processing of speech. *Neuron, 56*(4), 726-740.

Ravizza, S. M., Delgado, M. R., et al. (2004). Functional dissociations within the inferior parietal cortex in verbal working memory. *NeuroImage, 22*(2), 562-573.

Rissman, J., Eliassen, J. C., et al. (2003). An event-related fMRI investigation of implicit semantic priming. *J Cogn Neurosci, 15*(8), 1160-1175.

Rodd, J. M., Johnsrude, I. S., et al. (2010). The role of domain-general frontal systems in language comprehension: evidence from dual-task interference and semantic ambiguity. *Brain Lang, 115*(3), 182-188. doi: 10.1016/j.bandl.2010.07.005

Rogalsky, C., & Hickok, G. (2009). Selective attention to semantic and syntactic features modulates sentence processing networks in anterior temporal cortex. *Cereb Cortex, 19*(4), 786-796. doi: 10.1093/cercor/bhn126

Rogalsky, C., & Hickok, G. (2011). The Role of Broca's Area in Sentence Comprehension. *J Cogn Neurosci, 23*(7), 1664-1680.

Rolheiser, T., Stamatakis, E. A., et al. (2011). Dynamic processing in the human language system: synergy between the arcuate fascicle and extreme capsule. *J Neurosci, 31*(47), 16949-16957.

Rosengarten, B., Huwendiek, O., et al. (2001). Neurovascular coupling in terms of a control system: validation of a second-order linear system model. *Ultrasound Med Biol, 27*(5), 631-635.

Rugg, M. D., & Coles, M. G. (1995). *Electrophysiology of mind: Event-related brain potentials and cognition*: Oxford University Press.

Rugg, M. D., Kok, A., et al. (1986). ERPs associated with language and hemispheric specialization. A review. *Electroencephalogr Clin Neurophysiol Suppl, 38*, 273-300.

S

Santi, A., & Grodzinsky, Y. (2012). Broca's area and sentence comprehension: a relationship parasitic on dependency, displacement or predictability? *Neuropsychologia, 50*(5), 821-832. doi: 10.1016/j.neuropsychologia.2012.01.017

Saur, D., Kreher, B. W., et al. (2008). Ventral and dorsal pathways for language. *Proc Natl Acad Sci U S A, 105*(46), 18035-18040. doi: 10.1073/pnas.0805234105

Schiller, N. O., & Caramazza, A. (2003). Grammatical feature selection in noun phrase production: Evidence from German and Dutch. *J Mem Lang, 48*(1), 169-194.

Schiller, N. O., Munte, T. F., et al. (2003a). The influence of semantic and phonological factors on syntactic decisions: an event-related brain potential study. *Psychophysiology, 40*(6), 869-877.

Schiller, N. O., Munte, T. F., et al. (2003b). The influence of semantic and phonological factors on syntactic decisions: An event-related brain potential study. *Psychophysiology, 40*(6), 869-877. doi: 10.1111/1469-8986.00105

Schmolck, H., Kensinger, E. A., et al. (2002). Semantic knowledge in patient HM and other patients with bilateral medial and lateral temporal lobe lesions. *Hippocampus, 12*(4), 520-533.

Schriefers, H., Jescheniak, J. D., et al. (2002). Determiner selection in noun phrase production. *J Exp Psychol Learn Mem Cogn, 28*(5), 941.

Schriefers, H., Jescheniak, J. D., et al. (2005). Selection of gender-marked morphemes in speech production. *J Exp Psychol Learn Mem Cogn, 31*(1), 159.

Seghier, M. L. (2013). The angular gyrus: multiple functions and multiple subdivisions. *Neuroscientist, 19*(1), 43-61. doi: 10.1177/1073858412440596

Seghier, M. L., Fagan, E., et al. (2010). Functional subdivisions in the left angular gyrus where the semantic system meets and diverges from the default network. *J Neurosci, 30*(50), 16809-16817. doi: 10.1523/JNEUROSCI.3377-10.2010

Seghier, M. L., Lazeyras, F., et al. (2004). Variability of fMRI activation during a phonological and semantic language task in healthy subjects. *Hum Brain Mapp, 23*(3), 140-155.

Seghier, M. L., Lee, H. L., et al. (2008). Inter-subject variability in the use of two different neuronal networks for reading aloud familiar words. *NeuroImage, 42*(3), 1226-1236. doi: 10.1016/j.neuroimage.2008.05.029

Seghier, M. L., Neufeld, N. H., et al. (2012). Reading without the left ventral occipito-temporal cortex. *Neuropsychologia, 50*(14), 3621-3635. doi: 10.1016/j.neuropsychologia.2012.09.030

Sharp, D. J., Awad, M., et al. (2010). The neural response to changing semantic and perceptual complexity during language processing. *Hum Brain Mapp, 31*(3), 365-377. doi: 10.1002/hbm.20871

Shibata, M., Toyomura, A., et al. (2012). Does simile comprehension differ from metaphor comprehension? A functional MRI study. *Brain Lang, 121*(3), 254-260. doi: 10.1016/j.bandl.2012.03.006

Shlonsky, U. (1989). The hierarchical representation of subject-verb agreement. *Ms., Haifa University*.

Shulman, G. L., Corbetta, M., et al. (1997). Common blood flow changes across visual tasks: I. Increases in subcortical structures and cerebellum but not in nonvisual cortex. *Journal of Cognitive Neuroscience, 9*(5), 624-647.

Siewierska, A. (2004). *Person*: Cambridge University Press.

Sigurdsson, H. A. (2004). The syntax of person, tense and speech features. *Italian Journal of Linguistics, 16*, 219-251.

Sigurdsson, H. A. (2009). *Remarks on features* (K. Grohman Ed.). Berlin, Mouton de Gruyter.

Sigurdsson, H. A. (2011). Uniformity and diversity: A minimalist perspective. *Linguistic Variation, 11*(2), 189-222.

Silva-Pereyra, J. F., & Carreiras, M. (2007). An ERP study of agreement features in Spanish. *Brain Res, 1185*, 201-211. doi: 10.1016/j.brainres.2007.09.029

Silva-Pereyra, J. F., Gutierrez-Sigut, E., et al. (2012). An ERP study of coreference in Spanish: semantic and grammatical gender cues. *Psychophysiology, 49*(10), 1401-1411. doi: 10.1111/j.1469-8986.2012.01446.x

Silva, S., Branco, P., et al. (2014). Musical phrase boundaries, wrap-up and the closure positive shift. *Brain Res, 1585*, 99-107.

Sliwinska, M. W., Khadilkar, M., et al. (2012). Early and sustained supramarginal gyrus contributions to phonological processing. *Front Psychol, 3*.

Sohn, M. H., Albert, M. V., et al. (2007). Anticipation of conflict monitoring in the anterior cingulate cortex and the prefrontal cortex. *Proc Natl Acad Sci U S A, 104*(25), 10330-10334. doi: 10.1073/pnas.0703225104

Solomyak, O., & Marantz, A. (2010). Evidence for early morphological decomposition in visual word recognition. *Journal of Cognitive Neuroscience, 22*(9), 2042-2057.

Speas, M. (2004a). Evidential paradigms, world variables and person agreement features. *Italian Journal of Linguistics, 16*(4), 253-280.

Speas, M. (2004b). Evidentiality, logophoricity and the syntactic representation of pragmatic features. *Lingua, 114*(3), 255-276.

Steele, S. (1978). Word order variation: A typological study. In J. H. G. C. A. F. E. A. Moravcsik (Ed.), *Universals of Human Language IV: Syntax* (Vol. 4, pp. 585-623). Stanford: Stanford University Press.

Stefanovic, B., Warnking, J. M., et al. (2004). Hemodynamic and metabolic responses to neuronal inhibition. *NeuroImage, 22*(2), 771-778.

T

Taft, M., & Meunier, F. (1998). Lexical representation of gender: A quasiregular domain. *J Psycholinguist Res, 27*(1), 23-45.

Taylor, S. F., Stern, E. R., et al. (2007). Neural systems for error monitoring: recent findings and theoretical perspectives. *Neuroscientist, 13*(2), 160-172. doi: 10.1177/1073858406298184

Teichmann, M., Rosso, C., et al. (2015). A cortical–subcortical syntax pathway linking Broca's area and the striatum. *Hum Brain Mapp, 36*(6), 2270-2283.

Thiebaut de Schotten, M., Dell’Acqua, F., et al. (2012). Monkey to human comparative anatomy of the frontal lobe association tracts. *Cortex, 48*(1), 82-96.

Thompson-Schill, S. L., Bedny, M., et al. (2005). The frontal lobes and the regulation of mental activity. *Curr Opin Neurobiol, 15*(2), 219-224. doi: 10.1016/j.conb.2005.03.006

Thompson-Schill, S. L., D'Esposito, M., et al. (1997). Role of left inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation. *Proc Natl Acad Sci U S A, 94*(26), 14792-14797.

Tingley, D., Yamamoto, T., et al. (2013). Mediation: R package for causal mediation analysis. *R package version, 4*(3), 1-39.

Turken, A. U., & Dronkers, N. F. (2011). The neural architecture of the language comprehension network: converging evidence from lesion and connectivity analyses. *Front Syst Neurosci, 5*, 1. doi: 10.3389/fnsys.2011.00001

U

Uddin, L. Q., Clare Kelly, A., et al. (2009). Functional connectivity of default mode network components: correlation, anticorrelation, and causality. *Hum Brain Mapp, 30*(2), 625-637.

Uludağ, K., Dubowitz, D. J., et al. (2004). Coupling of cerebral blood flow and oxygen consumption during physiological activation and deactivation measured with fMRI. *NeuroImage, 23*(1), 148-155.

Ullman, M. T. (1999). The functional neuroanatomy of inflectional morphology. *Behav and brain sci, 22*(06), 1041-1042.

Ullman, M. T. (2004). Contributions of memory circuits to language: the declarative/procedural model. *Cognition, 92*(1-2), 231-270. doi: 10.1016/j.cognition.2003.10.008

Ullman, M. T., Corkin, S., et al. (1997). A neural dissociation within language: Evidence that the mental dictionary is part of declarative memory, and that grammatical rules are processed by the procedural system. *J Cogn Neurosci, 9*(2), 266-276.

Utevsky, A. V., Smith, D. V., et al. (2014). Precuneus is a functional core of the default-mode network. *J Neurosci, 34*(3), 932-940.

V

van Berkum, J. J. A. (1996). *The psycholinguistics of grammatical gender: Studies in language comprehension and production.* University of Nijmegen.

van Berkum, J. J. A., Brown, C. M., et al. (1999). Early referential context effects in sentence processing: Evidence from event-related brain potentials. *J Mem Lang, 41*(2), 147-182.

van de Meerendonk, N., Indefrey, P., et al. (2011). Monitoring in language perception: Electrophysiological and hemodynamic responses to spelling violations. *Neuroimage, 54*(3), 2350-2363.

van de Meerendonk, N., Kolk, H. H., et al. (2009). Monitoring in Language Perception. *Lang Linguist Compass, 3*(5), 1211-1224.

van de Meerendonk, N., Kolk, H. H., et al. (2010). Monitoring in Language Perception: Mild and Strong Conflict Elicit Different ERP Patterns. *J Cogn Neurosci, 22*(1), 67-82.

van der Lely, H. K., & Pinker, S. (2014). The biological basis of language: insight from developmental grammatical impairments. *Trends Cogn Sci*. doi: 10.1016/j.tics.2014.07.001

Vigliocco, G., Butterworth, B., et al. (1996). Subject-verb agreement in Spanish and English: differences in the role of conceptual constraints. *Cognition, 61*(3), 261-298.

Vigliocco, G., & Franck, J. (1999). When Sex and Syntax Go Hand in Hand: Gender Agreement in Language Production. *J Mem Lang, 40*, 455–478.

Vigliocco, G., & Hartsuiker, R. J. (2002). The interplay of meaning, sound, and syntax in sentence production. *Psychol Bull, 128*(3), 442-472.

Vigliocco, G., Lauer, M., et al. (2002). Semantic and syntactic forces in noun phrase production. *J Exp Psychol Learn Mem Cogn, 28*(1), 46-58.

Vigliocco, G., Vinson, D. P., et al. (2011). Nouns and verbs in the brain: a review of behavioural, electrophysiological, neuropsychological and imaging studies. *Neurosci Biobehav Rev, 35*(3), 407-426. doi: 10.1016/j.neubiorev.2010.04.007

Vigneau, M., Beaucousin, V., et al. (2006). Meta-analyzing left hemisphere language areas: phonology, semantics, and sentence processing. *NeuroImage, 30*(4), 1414-1432. doi: 10.1016/j.neuroimage.2005.11.002

Vigneau, M., Beaucousin, V., et al. (2011). What is right-hemisphere contribution to phonological, lexico-semantic, and sentence processing? Insights from a meta-analysis. *NeuroImage, 54*(1), 577-593. doi: 10.1016/j.neuroimage.2010.07.036

Villringer, A. (1997). Understanding functional neuroimaging methods based on neurovascular coupling *Optical Imaging of Brain Function and Metabolism 2* (pp. 177-193): Springer.

Visser, M., Jefferies, E., et al. (2012). Both the middle temporal gyrus and the ventral anterior temporal area are crucial for multimodal semantic processing: distortion-corrected fMRI evidence for a double gradient of information convergence in the temporal lobes. *J Cogn Neurosci, 24*(8), 1766-1778.

Visser, M., & Lambon Ralph, M. A. (2011). Differential Contributions of Bilateral Ventral Anterior Temporal Lobe and Left Anterior Superior Temporal Gyrus to Semantic Processes. *J Cogn Neurosci, 23*(10), 3121-3131.

Vissers, C. T., Chwilla, D. J., et al. (2006). Monitoring in language perception: The effect of misspellings of words in highly constrained sentences. *Brain Res, 1106*(1), 150-163. doi: 10.1016/j.brainres.2006.05.012

W

Wager, T. D., & Barrett, L. F. (2004). From affect to control: Functional specialization of the insula in motivation and regulation. *Published online at PsycExtra*.

Wager, T. D., Lindquist, M., et al. (2007). Meta-analysis of functional neuroimaging data: current and future directions. *Soc Cogn Affect Neurosci, 2*(2), 150-158. doi: 10.1093/scan/nsm015

Wager, T. D., Sylvester, C. C., et al. (2005). Common and unique components of response inhibition revealed by fMRI. *NeuroImage, 27*(2), 323-340.

Wagers, M. W., Lau, E. F., et al. (2009). Agreement attraction in comprehension: Representations and processes. *J Mem Lang, 61*(2), 206-237.

Wagers, M. W., & Phillips, C. (2009). Multiple dependencies and the role of the grammar in real-time comprehension. *J Linguist, 45*(02), 395-433.

Weber, K., & Lavric, A. (2008). Syntactic anomaly elicits a lexico-semantic (N400) ERP effect in the second language but not the first. *Psychophysiology, 45*(6), 920-925.

Wechsler, S. (2009). Agreement features. *Lang Linguist Compass, 3*(1), 384-405.

Wechsler, S. (2011). Mixed agreement, the person feature, and the index/concord distinction. *Natural Language & Linguistic Theory, 29*(4), 999-1031. doi: 10.1007/s11049-011-9149-x

Wechsler, S., & Zlatić, L. (2000). A theory of agreement and its application to Serbo-Croatian. *Language*, 799-832.

Wechsler, S., & Zlatić, L. (2003). *The many faces of agreement*: Center for the Study of Language and Information Stanford.

Wei, T., Liang, X., et al. (2012). Predicting conceptual processing capacity from spontaneous neuronal activity of the left middle temporal gyrus. *J Neurosci, 32*(2), 481-489. doi: 10.1523/JNEUROSCI.1953-11.2012

Wicha, N. Y., Bates, E., et al. (2003). Potato not Pope: human brain potentials to gender expectation and agreement in Spanish spoken sentences. *Neurosci Lett, 346*(3), 165–168.

Wicha, N. Y., Moreno, E. M., et al. (2004). Anticipating words and their gender: an event-related brain potential study of semantic integration, gender expectancy, and gender agreement in Spanish sentence reading. *J Cogn Neurosci, 16*(7), 1272-1288. doi: 10.1162/0898929041920487

Wilson, S. M., Galantucci, S., et al. (2012). The neural basis of syntactic deficits in primary progressive aphasia. *Brain Lang, 122*(3), 190-198. doi: 10.1016/j.bandl.2012.04.005

Wilson, S. M., Galantucci, S., et al. (2011). Syntactic processing depends on dorsal language tracts. *Neuron, 72*(2), 397-403. doi: 10.1016/j.neuron.2011.09.014

X

Xiang, H.D., Fonteijn, H. M., et al. (2010). Topographical functional connectivity pattern in the perisylvian language networks. *Cerebral Cortex, 20*(3), 549-560.

Xu, X., Jiang, X., et al. (2013). Processing biological gender and number information during Chinese pronoun resolution: ERP evidence for functional differentiation. *Brain Cogn, 81*(2), 223-236. doi: 10.1016/j.bandc.2012.11.002

Y

Ye, Z., & Zhou, X. (2009). Conflict control during sentence comprehension: fMRI evidence. *NeuroImage, 48*(1), 280-290. doi: 10.1016/j.neuroimage.2009.06.032

Yeterian, E. H., Pandya, D. N., et al. (2012). The cortical connectivity of the prefrontal cortex in the monkey brain. *Cortex, 48*(1), 58-81.

Z

Zevin, J. D., & McCandliss, B. D. (2005). Dishabituation of the BOLD response to speech sounds. *Behav Brain Funct, 1*(4).

Zhang, S., & Li, C. S. (2012). Functional connectivity mapping of the human precuneus by resting state fMRI. *NeuroImage, 59*(4), 3548-3562. doi: 10.1016/j.neuroimage.2011.11.023

Zhang, Y., Li, P., et al. (2013). Syntax does not necessarily precede semantics in sentence processing: ERP evidence from Chinese. *Brain Lang, 126*(1), 8-19.

Zhang, Y., Yu, J., et al. (2010). Semantics does not need a processing license from syntax in reading Chinese. *J Exp Psychol Learn Mem Cogn, 36*(3), 765.

Zhu, Z., Hagoort, P., et al. (2012). The anterior left inferior frontal gyrus contributes to semantic unification. *NeuroImage, 60*(4), 2230-2237. doi: 10.1016/j.neuroimage.2012.02.036

Chapter 10.

Resulting Publications

1. **Quiñones, I.**, Molinaro, N., Hernández-Cabrera, J. A., Barber H. & Carreiras, M. How word transparency mediates lexical access: Left anterior temporal role. In preparation. (Chapter 3)
2. **Quiñones, I.**, Mancini, S., Molinaro, N., Caballero C., Hernández-Cabrera, J. A., Barber H. & Carreiras, M. Parietal circuit distinguishing between feminine and masculine entities: an fMRI study of gender agreement processing. In preparation. (Chapter 4)
3. Carreiras, M., **Quiñones, I.**, Mancini, S. Hernández-Cabrera, J. A., Barber H. (2015). Verbal and nominal agreement: An fMRI study. Neuroimage, in press. (Chapter 5)
4. Mancini, S., **Quiñones, I.**, Molinaro, N., Hernández-Cabrera, J. A., & Carreiras, M. Who is doing what? Left temporal involvement for sentence reading. Human Brain Mapping, submitted. (Chapter 6)
5. **Quiñones, I.**, Molinaro, N., Mancini, S., Hernández-Cabrera, J. A., & Carreiras, M. (2014). Where agreement merges with disagreement: fMRI evidence of subject–verb integration. NeuroImage, 88, 188-201. (Chapter 7)
6. **Quiñones, I.**, Molinaro, N., Mancini, S. & Carreiras, M. Functional dynamic of the agreement network: A new neuro-cognitive approach. In preparation. (Chapter 8)

Chapter 11.

Appendices

Appendix 1. Word pairs used in the Experiment I (Chapter 3) including information about the gender-marking (transparent [1] or opaque [2]), the agreement congruency pattern (Match [4] or Mismatch [1]) and the gender values (masculine [1] or feminine [2]).

	Transparent - Opaque	Agreement Pattern	Masculine - Femenine	Stimuli	
Transparent (Match Condition)	1	4	1	el	dedo
	1	4	1	el	lago
	1	4	1	el	sótano
	1	4	1	el	carro
	1	4	1	el	labio
	1	4	1	el	olfato
	1	4	1	el	lavabo
	1	4	1	el	escudo
	1	4	1	el	techo
	1	4	1	el	cráneo
	1	4	1	el	vídeo
	1	4	1	el	hígado
	1	4	1	el	metro
	1	4	1	el	rebaño
	1	4	1	el	trofeo
	1	4	2	la	costa
	1	4	2	la	hierba
	1	4	2	la	deuda
	1	4	2	la	pasta
	1	4	2	la	sopa
	1	4	2	la	rama
	1	4	2	la	película
	1	4	2	la	cola
	1	4	2	la	pierna
	1	4	2	la	misa
	1	4	2	la	risa
	1	4	2	la	oreja
	1	4	2	la	pista
	1	4	2	la	meta
	1	4	2	la	navaja

	Transparent - Opaque	Agreement Pattern	Masculine - Femenine	Stimuli	
Transparent (Mismatch Condition)	1	1	1	la	luto
	1	1	1	la	vidrio
	1	1	1	la	banco
	1	1	1	la	piano
	1	1	1	la	circo
	1	1	1	la	hielo
	1	1	1	la	rayo
	1	1	1	la	beso
	1	1	1	la	torneo
	1	1	1	la	martillo
	1	1	1	la	átomo
	1	1	1	la	núcleo
	1	1	1	la	tejado
	1	1	1	la	coco
	1	1	1	la	arco
	1	1	2	el	página
	1	1	2	el	espada
	1	1	2	el	gama
	1	1	2	el	regla
	1	1	2	el	cúpula
	1	1	2	el	ventana
	1	1	2	el	franja
	1	1	2	el	boda
	1	1	2	el	colcha
	1	1	2	el	miopía
	1	1	2	el	plata
	1	1	2	el	luna
	1	1	2	el	playa
	1	1	2	el	taza
	1	1	2	el	selva

	Transparent - Opaque	Agreement Pattern	Masculine - Femenine	Stimuli	
Opaque (Match Condition)	2	4	1	el	parque
	2	4	1	el	puente
	2	4	1	el	ascensor
	2	4	1	el	portal
	2	4	1	el	camión
	2	4	1	el	taxi
	2	4	1	el	bigote
	2	4	1	el	examen
	2	4	1	el	salón
	2	4	1	el	tren
	2	4	1	el	paisaje
	2	4	1	el	cristal
	2	4	1	el	bosque
	2	4	1	el	ordenador
	2	4	1	el	avión
	2	4	2	la	navegación
	2	4	2	la	serpiente
	2	4	2	la	raíz
	2	4	2	la	catástrofe
	2	4	2	la	nube
	2	4	2	la	electricidad
	2	4	2	la	miel
	2	4	2	la	invasión
	2	4	2	la	pensión
	2	4	2	la	llave
	2	4	2	la	cruz
	2	4	2	la	fiebre
	2	4	2	la	nave
	2	4	2	la	prisión
	2	4	2	la	canción

	Transparent - Opaque	Agreement Pattern	Masculine - Femenine	Stimuli	
Opaque (Mismatch Condition)	2	1	1	la	reloj
	2	1	1	la	alcohol
	2	1	1	la	jardín
	2	1	1	la	hotel
	2	1	1	la	norte
	2	1	1	la	club
	2	1	1	la	cine
	2	1	1	la	corazón
	2	1	1	la	papel
	2	1	1	la	país
	2	1	1	la	cadáver
	2	1	1	la	rincón
	2	1	1	la	balón
	2	1	1	la	hospital
	2	1	1	la	hogar
	2	1	2	el	flor
	2	1	2	el	nación
	2	1	2	el	tesis
	2	1	2	el	universidad
	2	1	2	el	región
	2	1	2	el	oscuridad
	2	1	2	el	fuente
	2	1	2	el	cárcel
	2	1	2	el	nariz
	2	1	2	el	publicidad
	2	1	2	el	reunión
	2	1	2	el	pared
	2	1	2	el	unidad
	2	1	2	el	carne
	2	1	2	el	mitad

Appendix 2. MRI sequences used for the recording of the data.

Appendix 2A. Description of the T2*-weighted sequence's parameters used to record the functional images in Experiment I.

Parameters	Values
Field of view (Read)	192 mm
Field of view (Phase)	100%
Base resolution	64 pixels
Phase resolution	100%
Echo time (TE)	30 ms
Repetition time (TR)	2.0 s
Time gap	No
Flip angle	90°
Slices number	32
Orientation	Axial
Slice thickness	3 mm
In plane resolution	3 x 3 mm
Distance factor	25%

Appendix 2B. Description of the T2*-weighted sequence's parameters used to record the functional images in Experiment II.

Parameters	Values
Field of view (Read)	192 mm
Field of view (Phase)	100%
Base resolution	64 pixels
Phase resolution	100%
Echo time (TE)	30 ms
Repetition time (TR)	2.5 s
Time gap	No
Flip angle	90°
Slices number	32
Orientation	Axial
Slice thickness	3 mm
In plane resolution	3 x 3 mm
Distance factor	25%

Appendix 2C. Description of the T2*-weighted sequence's parameters used to record the functional images in Experiment III.

Parameters	Values
Field of view (Read)	192 mm
Field of view (Phase)	100%
Base resolution	64 pixels
Phase resolution	100%
Echo time (TE)	30 ms
Repetition time (TR)	2.0 s
Time gap	No
Flip angle	90°
Slices number	32
Orientation	Axial
Slice thickness	3 mm
In plane resolution	3 x 3 mm
Distance factor	25%

Appendix 2D. Description of the T2*-weighted sequence's parameters used to record the functional images in Experiment IV and V.

Parameters	Values
Field of view (Read)	192 mm
Field of view (Phase)	100%
Base resolution	64 pixels
Phase resolution	100%
Echo time (TE)	30 ms
Repetition time (TR)	2.0 s
Time gap	No
Flip angle	78°
Slices number	32
Orientation	Axial
Slice thickness	3 mm
In plane resolution	3 x 3 mm
Distance factor	25%

Appendix 3. Sentences used in the Experiment II including information about the agreement system (Formal [1] or Conceptual [2]), the agreement congruency pattern (Match [4] or Mismatch [1]) and the gender values (masculine [1] or feminine [2]).

	Formal - Conceptual	Agreement Pattern	Masculine - Femenine	Stimuli			
Formal Gender (Match Condition)	1	4	1	El	suelo	está	plano.
	1	4	1	El	título	estaba	oculto.
	1	4	1	El	mundo	será	justo.
	1	4	1	El	caso	era	cierto.
	1	4	1	El	pelo	estaba	teñido.
	1	4	1	El	faro	es	alto.
	1	4	1	El	fuego	está	flojo.
	1	4	1	El	llanto	fue	amargo.
	1	4	1	El	bocado	es	tierno.
	1	4	1	El	estilo	era	maduro.
	1	4	1	El	pueblo	era	bélico.
	1	4	1	El	sonido	parecía	lejano.
	1	4	1	El	arroyo	estuvo	helado.
	1	4	1	El	libro	era	único.
	1	4	1	El	ruido	fue	brusco.
	1	4	2	La	cabeza	era	menuda.
	1	4	2	La	pieza	es	hueca.
	1	4	2	La	lucha	fue	fiera.
	1	4	2	La	vida	es	sana.
	1	4	2	La	senda	era	recta.
	1	4	2	La	basura	era	nociva.
	1	4	2	La	teoría	era	exacta.
	1	4	2	La	prosa	fue	aguda.
	1	4	2	La	piedra	era	áspera.
	1	4	2	La	visita	fue	rápida.
	1	4	2	La	guerra	fue	mítica.
	1	4	2	La	lluvia	era	escasa.
	1	4	2	La	bolsa	fue	usada.
	1	4	2	La	madera	estaba	blanda.
	1	4	2	La	droga	era	tóxica.

	Formal - Conceptual	Agreement Pattern	Masculine - Femenine	Stimuli			
Formal Gender (Mismatch Condition)	1	1	1	El	jugo	está	fría.
	1	1	1	El	museo	es	bella.
	1	1	1	El	vuelo	fue	larga.
	1	1	1	El	dibujo	es	bonita.
	1	1	1	El	velero	es	ligera.
	1	1	1	El	cuero	es	falsa.
	1	1	1	El	juicio	fue	severa.
	1	1	1	El	deseo	era	mutua.
	1	1	1	El	teatro	es	lujosa.
	1	1	1	El	piso	será	pagada.
	1	1	1	El	coro	está	sola.
	1	1	1	El	cielo	está	clara.
	1	1	1	El	empleo	era	penosa.
	1	1	1	El	equipo	está	completa.
	1	1	1	El	charco	estaba	espesa.
	1	1	2	La	cena	está	malo.
	1	1	2	La	tarea	es	arduo.
	1	1	2	La	época	fue	grato.
	1	1	2	La	comida	estuvo	jugoso.
	1	1	2	La	sombra	era	oscuro.
	1	1	2	La	prensa	era	pésimo.
	1	1	2	La	cocina	estaba	limpio.
	1	1	2	La	norma	era	tonto.
	1	1	2	La	dama	era	culto.
	1	1	2	La	copa	estaba	tapado.
	1	1	2	La	altura	será	idóneo.
	1	1	2	La	renta	era	digno.
	1	1	2	La	falda	era	negro.
	1	1	2	La	papaya	está	fresco.
	1	1	2	La	leña	está	seco.

	Formal - Conceptual	Agreement Pattern	Masculine - Femenine	Stimuli			
Conceptual Gender (Match Condition)	2	4	1	El	novio	está	nervioso.
	2	4	1	El	casero	era	austero.
	2	4	1	El	soltero	era	gracioso.
	2	4	1	El	granjero	es	minucioso.
	2	4	1	El	filólogo	estaba	informado.
	2	4	1	El	pastelero	es	tranquilo.
	2	4	1	El	tendero	estaba	delgado.
	2	4	1	El	decano	es	honrado.
	2	4	1	El	sobrino	parece	antipático.
	2	4	1	El	cuñado	es	quisquilloso.
	2	4	1	El	peluquero	estaba	insatisfecho.
	2	4	1	El	biólogo	parece	avispado.
	2	4	1	El	tío	es	bueno.
	2	4	1	El	alumno	parecía	aplicado.
	2	4	1	El	primo	parece	pesado.
	2	4	2	La	vendedora	era	desinteresada.
	2	4	2	La	locutora	parece	persuasiva.
	2	4	2	La	abuela	era	sabia.
	2	4	2	La	empleada	parecía	íntegra.
	2	4	2	La	filósofa	es	excéntrica.
	2	4	2	La	científica	parece	ambiciosa.
	2	4	2	La	conductora	era	precavida.
	2	4	2	La	camarera	parecía	efectiva.
	2	4	2	La	compañera	era	risueña.
	2	4	2	La	alcaldesa	es	justa.
	2	4	2	La	jugadora	es	alta.
	2	4	2	La	profesora	parecía	abatida.
	2	4	2	La	doctora	era	famosa.
	2	4	2	La	amiga	es	sincera.
	2	4	2	La	ministra	era	estricta.

	Formal - Conceptual	Agreement Pattern	Masculine - Femenine	Stimuli			
Conceptual Gender (Mismatch Condition)	2	1	1	El	cocinero	es	exquisita.
	2	1	1	El	suegro	parecía	testaruda.
	2	1	1	El	becario	estaba	atenta.
	2	1	1	El	ahijado	era	caprichosa.
	2	1	1	El	muchacho	es	hermosa.
	2	1	1	El	modisto	era	virtuosa.
	2	1	1	El	carnicero	era	chismosa.
	2	1	1	El	panadero	era	despistada.
	2	1	1	El	psicólogo	era	activa.
	2	1	1	El	esposo	era	considerada.
	2	1	1	El	chico	era	atrevida.
	2	1	1	El	viudo	parecía	apenada.
	2	1	1	El	enfermero	era	cariñosa.
	2	1	1	El	tesorero	era	sensata.
	2	1	1	El	discípulo	era	perezosa.
	2	1	2	La	vecina	era	malo.
	2	1	2	La	nieta	estaba	enfermo.
	2	1	2	La	escultora	es	prolífico.
	2	1	2	La	fotógrafa	era	creativo.
	2	1	2	La	funcionaria	era	serio.
	2	1	2	La	ejecutiva	era	agresivo.
	2	1	2	La	pintora	era	osado.
	2	1	2	La	diputada	era	corrupto.
	2	1	2	La	maestra	parecía	ilustrado.
	2	1	2	La	abogada	parece	listo.
	2	1	2	La	secretaria	es	orgulloso.
	2	1	2	La	escritora	era	conocido.
	2	1	2	La	niña	estaba	contento.
	2	1	2	La	hija	era	pequeño.
	2	1	2	La	directora	estaba	sereno.

	Formal - Conceptual	Agreement Pattern	Masculine - Femenine	Stimuli			
Fillers	3	4	1	El	humo	era	gris.
	3	4	1	El	trato	fue	hostil.
	3	4	1	El	paseo	fue	breve.
	3	4	1	El	peso	era	grande.
	3	4	1	El	hecho	es	real.
	3	4	1	El	vaso	es	frágil.
	3	4	1	El	dato	fue	útil.
	3	4	1	El	pecado	fue	venial.
	3	4	1	El	verdugo	será	implacable.
	3	4	1	El	regalo	fue	ideal.
	3	4	1	Los	textos	eran	formales.
	3	4	1	Los	pactos	fueron	audaces.
	3	4	1	Los	himnos	eran	alegres.
	3	4	1	Los	cursos	serán	fáciles.
	3	4	1	Los	ritmos	eran	simples.
	3	4	1	Los	brillos	eran	tenues.
	3	4	1	Los	castigos	serán	leves.
	3	4	1	Los	plazos	fueron	razonables.
	3	4	1	Los	métodos	fueron	fiables.
	3	4	1	Los	proyectos	son	posibles.
	3	4	2	La	oferta	fue	amable.
	3	4	2	La	mezcla	era	original.
	3	4	2	La	raza	era	fuerte.
	3	4	2	La	broma	fue	cruel.
	3	4	2	La	obra	quedó	impecable.
	3	4	2	La	década	fue	feliz.
	3	4	2	La	marcha	continuó	imparable.
	3	4	2	La	sala	era	azul.
	3	4	2	La	trampa	fue	feroz.
	3	4	2	La	venganza	fue	brutal.
	3	4	2	Las	dichas	son	fugaces.
	3	4	2	Las	modas	son	vulgares.
	3	4	2	Las	letras	eran	ilegibles.
	3	4	2	Las	poesías	eran	tristes.
	3	4	2	Las	sedas	son	suaves.
	3	4	2	Las	ironías	fueron	geniales.
	3	4	2	Las	células	eran	inmunes.
	3	4	2	Las	carpetas	eran	verdes.
	3	4	2	Las	peras	eran	enormes.
	3	4	2	Las	monedas	eran	legales.

Appendix 4. Word pairs used in the Experiment III including information about the type of sentence constituent (determiner-nouns [1] or subject-verb [2]), the agreement congruency pattern (Match [4] or Mismatch [1]), the number values (plural [1] or singular [2]) and the gender values (masculine [1] or feminine [2]).

	Constituents	Agreement Pattern	Masculine - Femenine	Plural - Singular	Stimuli	
Determiner-Noun (Mismatch Condition)	1	1	1	1	los	abrigo
	1	1	1	1	los	barco
	1	1	1	1	los	ciclo
	1	1	1	1	los	disco
	1	1	1	1	los	hombro
	1	1	1	1	los	juego
	1	1	1	1	los	plato
	1	1	1	1	los	sodio
	1	1	1	2	el	frutos
	1	1	1	2	el	grupos
	1	1	1	2	el	hilos
	1	1	1	2	el	huevos
	1	1	1	2	el	muros
	1	1	1	2	el	quesos
	1	1	1	2	el	tipos
	1	1	1	2	el	zapatos
	1	1	2	1	las	cinta
	1	1	2	1	las	etapa
	1	1	2	1	las	jarra
	1	1	2	1	las	mesa
	1	1	2	1	las	placa
	1	1	2	1	las	prenda
	1	1	2	1	las	roca
	1	1	2	1	las	sábana
	1	1	2	2	la	burlas
	1	1	2	2	la	minas
	1	1	2	2	la	ondas
	1	1	2	2	la	plantas
	1	1	2	2	la	retinas
	1	1	2	2	la	sillas
	1	1	2	2	la	sotanas
	1	1	2	2	la	urnas

	Constituents	Agreement Pattern	Masculine - Femenine	Plural - Singular	Stimuli	
Determiner-Noun (Match Condition)	1	4	1	1	el	cuerpo
	1	4	1	1	el	exilio
	1	4	1	1	el	hierro
	1	4	1	1	el	horno
	1	4	1	1	el	litro
	1	4	1	1	el	pozo
	1	4	1	1	el	puerto
	1	4	1	1	el	sábado
	1	4	1	2	los	anillos
	1	4	1	2	los	brazos
	1	4	1	2	los	brazos
	1	4	1	2	los	brazos
	1	4	1	2	los	brazos
	1	4	1	2	los	brazos
	1	4	1	2	los	brazos
	1	4	1	2	los	brazos
	1	4	2	1	la	brazos
	1	4	2	1	la	brazos
	1	4	2	1	la	brazos
	1	4	2	1	la	brazos
	1	4	2	1	la	brazos
	1	4	2	1	la	brazos
	1	4	2	1	la	brazos
	1	4	2	1	la	brazos
	1	4	2	2	las	brazos
	1	4	2	2	las	brazos
	1	4	2	2	las	brazos
	1	4	2	2	las	brazos
	1	4	2	2	las	brazos
	1	4	2	2	las	brazos
	1	4	2	2	las	brazos
	1	4	2	2	las	brazos

	Constituents	Agreement Pattern	Masculine - Femenine	Plural - Singular	Stimuli	
Subject-Verb (Mismatch Condition)	2	1	1	1	él	ayunan
	2	1	1	1	él	calculan
	2	1	1	1	él	consultan
	2	1	1	1	él	dibujan
	2	1	1	1	él	lanzan
	2	1	1	1	él	ofenden
	2	1	1	1	él	suplican
	2	1	1	1	él	transmiten
	2	1	1	2	ellos	apoya
	2	1	1	2	ellos	desconfía
	2	1	1	2	ellos	entrega
	2	1	1	2	ellos	extrapolan
	2	1	1	2	ellos	inspira
	2	1	1	2	ellos	logra
	2	1	1	2	ellos	patina
	2	1	1	2	ellos	urde
	2	1	2	1	ella	comprenden
	2	1	2	1	ella	deben
	2	1	2	1	ella	dejan
	2	1	2	1	ella	explican
	2	1	2	1	ella	llegan
	2	1	2	1	ella	rascan
	2	1	2	1	ella	suspenden
	2	1	2	1	ella	votan
	2	1	2	2	ellas	cierra
	2	1	2	2	ellas	convoca
	2	1	2	2	ellas	empuja
	2	1	2	2	ellas	escupe
	2	1	2	2	ellas	limpia
	2	1	2	2	ellas	lleva
	2	1	2	2	ellas	quema
	2	1	2	2	ellas	usa

	Constituents	Agreement Pattern	Masculine - Femenine	Plural - Singular	Stimuli	
Subject-Verb (Match Condition)	2	4	1	1	él	abrocha
	2	4	1	1	él	cepilla
	2	4	1	1	él	corre
	2	4	1	1	él	lava
	2	4	1	1	él	protege
	2	4	1	1	él	respira
	2	4	1	1	él	toma
	2	4	1	1	él	vive
	2	4	1	2	ellos	aportan
	2	4	1	2	ellos	besan
	2	4	1	2	ellos	disfrutan
	2	4	1	2	ellos	flotan
	2	4	1	2	ellos	imitan
	2	4	1	2	ellos	molestan
	2	4	1	2	ellos	reciben
	2	4	1	2	ellos	viajan
	2	4	2	1	ella	baila
	2	4	2	1	ella	corta
	2	4	2	1	ella	distingue
	2	4	2	1	ella	llora
	2	4	2	1	ella	nada
	2	4	2	1	ella	observa
	2	4	2	1	ella	saca
	2	4	2	1	ella	teme
	2	4	2	2	ellas	abusan
	2	4	2	2	ellas	almacenan
	2	4	2	2	ellas	avisan
	2	4	2	2	ellas	chocan
	2	4	2	2	ellas	completan
	2	4	2	2	ellas	demandan
	2	4	2	2	ellas	exceden
	2	4	2	2	ellas	pescan

Basque Center on Cognition, Brain and Language

Donostia-San Sebastian, Basque Country

November, 2015