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Mecanismos corporizados en el procesamiento de la información relacionada a acciones: conexiones entre circuitos neurales y experiencia personal

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1. PREFACIO

Para Gallese y Lakoff (2005), cualquier intento de explicar científicamente cómo el cerebro procesa información conceptual enfrenta el desafío de entender cómo los patrones de activación en los circuitos cerebrales permiten distinguir, reconocer y comprender objetos, eventos y situaciones en el mundo. Este conocimiento, acumulado a lo largo de la vida en la memoria semántica, nos permite no solo entender y producir lenguaje, sino también interpretar nuestro entorno y fundamentar nuestras acciones cotidianas (Patterson et al., 2007; Ralph et al., 2017; Tulving, 1972). Aunque la neuropsicología clínica y la neurociencia cognitiva han avanzado significativamente en esta área, aún no se ha alcanzado una teoría unificada que explique plenamente estos procesos (Gallese & Lakoff, 2005).

Aunque las ciencias cognitivas han avanzado significativamente en las últimas décadas, las preguntas fundamentales sobre la naturaleza del conocimiento humano y su vínculo con las experiencias corporales tienen raíces históricas profundas. Este debate, que se remonta a la filosofía griega, adquirió forma explícita durante el período moderno con los filósofos empiristas y racionalistas. Mientras los empiristas defendían la experiencia sensorial como base del conocimiento, los racionalistas argumentaban a favor del rol central de la razón (Markie, 2021). Estas ideas dieron forma a muchos de los paradigmas modernos y han influido directamente en las teorías contemporáneas sobre la representación conceptual.

Con el auge de las ciencias cognitivas en el siglo XX, las propuestas filosóficas tradicionales fueron desafiadas por nuevas corrientes que promovían la necesidad de representaciones amodales. Inspiradas en el desarrollo de la lógica, la lingüística y la computación, estas teorías buscaban explicar cómo los conceptos podían ser representados a través de símbolos abstractos, independientes de las experiencias sensoriales o motoras (Meteyard et al., 2012). Sin embargo, estas propuestas enfrentaron críticas importantes debido a la falta de evidencia empírica que respaldara sus postulados, y al surgimiento de hallazgos neurocientíficos y comportamentales que demostraban la influencia de los procesos sensoriomotores en el conocimiento conceptual (Barsalou, 2008; Meteyard et al., 2012).

Por ejemplo, numerosos estudios han mostrado que conceptos con un componente sensorial o motor fuerte activan regiones específicas del cerebro asociadas con estas modalidades (González et al., 2006; Simmons et al., 2007). Estas evidencias han fortalecido las teorías semánticas corporizadas, que plantean que los procesos sensoriomotores y conceptuales comparten un sistema subyacente común (Binder & Desai, 2011; Conca & Tettamanti, 2018). Así, las ideas que durante siglos fueron relegadas por corrientes más abstractas resurgen hoy como una base para entender la cognición humana.

Aunque aún existe debate sobre cómo interactúan los sistemas modales y amodales para generar representaciones semánticas estables, la mayoría de los investigadores coinciden en que estas representaciones son distribuidas y dependen de múltiples regiones corticales. En este marco, el estudio de categorías conceptuales específicas, como las relacionadas con acciones corporales, resulta clave para avanzar en la comprensión de los mecanismos subyacentes a estas interacciones. Este trabajo se enfoca precisamente en esta categoría, explorando cómo los circuitos motores, el contexto motor y la historia motora de los individuos influyen en el procesamiento de conceptos relacionados con acciones.

2. INTRODUCCIÓN

2.1. Introducción general

¿De qué manera los circuitos motores contribuyen al procesamiento de conceptos relacionados con acciones? Aunque esta relación ha sido explorada desde múltiples abordajes, tres enfoques principales han aportado evidencia clave: 1) los estudios neurológicos que examinan los efectos de daños en circuitos motores sobre la semántica de la acción, 2) los paradigmas de acoplamiento semántico-motor que evalúan la interacción funcional entre acción y lenguaje en tiempo real, y 3) los estudios pre/post que analizan cómo nuevas experiencias motoras modifican el procesamiento semántico. Sin embargo, estos enfoques aún dejan preguntas abiertas, lo que motiva las tres investigaciones que conforman esta tesis.

Estos abordajes han sido importantes para demostrar: 1) que las regiones motoras (corticales y subcorticales) están implicadas en la semántica de la acción en un amplio espectro de modalidades, por ej.: verbos, frases, narraciones, e imágenes; 2) que los procesos motores y semánticos operan en circuitos compartidos, generando facilitación o interferencia cuando ambos son puestos a funcionar en simultáneo; y 3) que la experiencia motora personal modula diferencialmente la semántica de acción, generando mejoras o interfiriendo en el desempeño conductual, así como también una activación distintiva de circuitos corticales.

Sin embargo, estas investigaciones dejan muchas preguntas sin responder. Los modelos de lesión se han enfocado en circuitos puramente corticales o fronto-estriatales, dejando un vacío en otra importante estructura del sistema motor: el cerebelo. Por otro lado, los estudios de interacción funcional entre semántica y acción son fundamentalmente comportamentales, por lo que se hace necesario el estudio de sus correlatos cerebrales. Y por último, las investigaciones que intentan explorar posibles vínculos entre experiencia motora y los procesos semánticos, son muy incipientes y en su mayoría conductuales, lo que demanda mayor evidencia y particularmente estudios neurofisiológicos.

Para superar estas limitaciones, esta tesis se estructura en tres investigaciones complementarias. En primer lugar, exploramos una estructura motora extracortical menos estudiada, el cerebelo, y su rol en la semántica de la acción a través de un estudio de caso. En segundo lugar, analizamos cómo la ejecución simultánea de tareas motoras y semánticas puede modular la actividad cerebral, proporcionando un enfoque funcional sobre la interacción entre estos procesos. Finalmente, evaluamos cómo la adquisición de nuevas experiencias motoras impacta en el acceso y procesamiento de información de acción contenida en narraciones naturalistas. De este modo, cada investigación aborda un vacío específico, sumando evidencia crítica para comprender la relación entre sistemas motores y semánticos. Estas investigaciones han llevado a la publicación de tres artículos científicos que se incorporan en la tesis.

2.2. La semántica de la acción como elemento clave de la cognición corporizada

La semántica de la acción constituye un eje crítico dentro de la perspectiva corporizada y sostiene que los conceptos no son representaciones abstractas y amodales, sino que están anclados en los circuitos sensoriomotores involucrados en la ejecución de las acciones (Barsalou, 2008; Gallese & Lakoff, 2005). Este marco teórico ha desafiado los modelos tradicionales, que sostienen que el conocimiento conceptual se organiza independientemente de las experiencias corporales (Mahon, 2015). Estudiar cómo los conceptos de acción interactúan con el sistema motor es clave no solo para validar esta perspectiva, sino también para responder a preguntas fundamentales sobre cómo se organiza y se accede al conocimiento conceptual.

En los estudios neurolingüísticos, los conceptos de acción suelen analizarse a través de una categoría denominada *verbos motores* (o *verbos de acción*). Éstos se definen como aquellos que describen acciones en las que al menos un efector corporal está claramente involucrado, en contraste con los verbos abstractos, que no poseen esta asociación directa (Dalla Volta et al., 2018). Para Pulvermüller et al. (2005), los verbos motores representan un vínculo semántico entre elementos del lenguaje y programas motores específicos, siendo una herramienta clave para analizar cómo los circuitos motores contribuyen a la representación conceptual.

Varios estudios han demostrado que las palabras relacionadas con acciones generan activaciones en áreas motoras corticales de manera somatotópica, es decir, dependiendo del efector implicado (Hauk et al., 2004; Tettamanti et al., 2005). Por ejemplo, los verbos asociados a acciones manuales activan regiones centrales de la corteza motora primaria, mientras que los relacionados con acciones faciales y podales activan sectores ventrales y dorsales, respectivamente. Sin embargo, esta hipótesis de una organización somatotópica estricta ha sido objeto de debate. Algunos trabajos han planteado que las activaciones motoras no siempre siguen un patrón topográfico claro, y que su aparición depende de múltiples factores como la tarea, el contexto, o el nivel de abstracción conceptual (Postle et al., 2008; Kemmerer, 2015a). En esta línea, Kemmerer (2015b) propone una arquitectura conceptual flexible y multinivel, en la que las áreas motoras pueden participar en la representación semántica de verbos de acción, pero su activación no es ni necesaria ni constante, sino que varía según las demandas específicas del procesamiento.

Uno de los puntos más controvertidos de la perspectiva corporizada es el rol de estas activaciones en la comprensión semántica. Investigadores críticos, como Mahon (2015; 2015b), han cuestionado si la activación motora no es más que un epifenómeno, es decir, un subproducto de la comprensión del lenguaje que no contribuye de manera causal al acceso semántico. Este debate ha impulsado investigaciones sobre la temporalidad de estas activaciones y sus implicancias funcionales. Por ejemplo, Papeo et al. (2015) han reportado reactivaciones corporizadas tardías en tareas de comprensión de verbos de acción, lo que complejiza la interpretación del rol de dichas activaciones en la comprensión semántica. En contraste, investigaciones como las de Sereno et al. (1998) y Dalla Volta et al. (2018) han mostrado activaciones motoras con organización somatotópica durante las fases tempranas del procesamiento semántico (aproximadamente a los 200 ms).

En síntesis, el conjunto de hallazgos sugieren que las activaciones motoras no se limitan a un momento específico, sino que son temporalmente ubicuas, pudiendo manifestarse tanto en etapas tempranas como tardías del procesamiento semántico. En consecuencia, estas activaciones no son necesaria ni exclusivamente postléxicas, sino que parecen desempeñar un papel integral en la construcción del significado, tal como han propuesto investigaciones recientes (Pulvermüller et al., 2005; Papeo et al., 2015).

Además, se han empleado técnicas de estimulación cerebral no invasiva para investigar la causalidad en la relación entre el sistema motor y la semántica de la acción. Por ejemplo, Pulvermüller et al. (2005) utilizaron la estimulación magnética transcraneal (TMS) para modular la actividad en áreas motoras específicas como las regiones asociadas a la representación manual y podal. Los resultados mostraron que la estimulación de estas áreas alteraba selectivamente los tiempos de reacción en tareas semánticas relacionadas con acciones correspondientes, sugiriendo un vínculo funcional directo entre la activación motora y el procesamiento semántico de acciones. Este tipo de evidencia apoya la noción de que los circuitos motores no solo se activan durante la comprensión de conceptos de acción, sino que también desempeñan un papel causal en la construcción del significado, más allá de ser un mero epifenómeno.

En resumen, existe abundante evidencia a favor de que el sistema motor participa activamente en la comprensión de conceptos relacionados con acciones. Sus patrones de activación no sólo reflejan una organización somatotópica sino también dinámicas más complejas y funcionales en la integración semántica. Sin embargo, persisten interrogantes fundamentales que limitan nuestra comprensión de este fenómeno. En particular, la interacción entre redes corticales y subcorticales en la semántica de la acción no está elucidada. Además, la influencia del contexto y la experiencia personal en la modulación de estas activaciones neuronales es un área que requiere mayor investigación. Abordar estas brechas es esencial para avanzar en el entendimiento de cómo los sistemas motores y semánticos interactúan y se modulan mutuamente en la cognición humana.

Estas cuestiones se abordan en las siguientes secciones, que introducen los tres artículos que conforman esta tesis. Cada uno de ellos explora un aspecto clave de la relación entre el sistema motor y la semántica de la acción: la sección 2.3 aborda el impacto de la disfunción cerebelosa en la semántica de la acción, la sección 2.4 analiza la interacción funcional entre procesos cerebrales motores y semánticos, y la sección 2.5 explora modulaciones en el desempeño semántico resultantes de la adquisición de nuevas experiencias motoras.

2.3. La semántica de la acción puede ser afectada por la disrupción de circuitos extracorticales

La organización del conocimiento conceptual, y en particular la semántica de la acción, ha sido ampliamente estudiada desde diversas perspectivas, con un fuerte aporte de la neuropsicología experimental basado en casos de lesión neurológica (Warrington, 1975; Capitani et al., 2003; Cree & McCrae, 2003; Conca & Tettamanti, 2018). Estos enfoques han permitido identificar estructuras neurales clave involucradas en el procesamiento de conceptos de acción, desafiando la visión tradicionalmente centrada en la corteza cerebral. Los ganglios basales y el cerebelo (componentes centrales de los circuitos motores) cumplen roles críticos en la planificación, ejecución y aprendizaje de acciones físicas. Los ganglios basales, por ejemplo, modulan la selección y secuenciación de movimientos voluntarios, mientras que el cerebelo ajusta la coordinación y precisión motora mediante mecanismos de realimentación predictiva (Albin et al., 1989; Koziol et al., 2014; Strick et al., 2009). Esta participación en el control motor los posiciona como candidatos clave para explorar cómo los sustratos neurales de la planificación y ejecución motora se integran con la representación semántica de estas acciones.

En este contexto, ambas estructuras han sido vinculadas a alteraciones en el procesamiento de conceptos de acción, aunque con dispar atención en la literatura. Los ganglios basales han sido ampliamente estudiados debido a su disfunción en patologías motoras de mayor incidencia como el

Parkinson y también en la enfermedad de Huntington, donde los déficits de movimiento coexisten con alteraciones en la semántica de la acción. Por el contrario, el cerebelo, pese a su relevancia en los procesos motores, ha recibido escaso enfoque en este campo, aún cuando su arquitectura funcional sugiere un potencial rol en la integración de información sensoriomotora y conceptual.

Los estudios sobre la disrupción de los ganglios basales han proporcionado una base sólida para entender, o al menos hipotetizar, cómo estas estructuras extracorticales pueden contribuir a la semántica de la acción. Pacientes con enfermedad de Parkinson han mostrado déficits específicos en tareas que involucran conceptos motores (Gallese & Cuccio, 2018). Éstos presentan, por ejemplo, mayores dificultades en el procesamiento de verbos y oraciones con contenido motor en comparación con verbos y oraciones con contenido abstracto (Fernandino et al., 2013a; 2013b). Además, su desempeño es inferior en la recuperación de información de acción en textos naturalistas (García et al., 2018) y en la producción de lenguaje de acción, como en tareas de nombramiento de imágenes (Bertella et al., 2002; Cotelli et al., 2006) o relatos espontáneos (García & Ibáñez, 2014). Estas alteraciones no se limitan a estímulos lingüísticos. Por ejemplo, Bocanegra et al. (2017) encontraron que pacientes parkinsonianos tienen un desempeño significativamente peor que los controles en tareas de asociación de imágenes relacionadas con objetos y acciones, siendo las acciones las más afectadas.

Las evidencias conductuales se complementan con estudios neurofisiológicos que destacan alteraciones específicas en los circuitos neurales. Por ejemplo, Abrevaya et al. (2016) encontraron que, durante la escucha de verbos motores, los pacientes parkinsonianos reclutaban vías alternativas, como conexiones entre M1 y el giro cingulado posterior, en lugar de las conexiones típicas entre M1 y el giro frontal inferior izquierdo observadas en controles neurotípicos. Estas vías alternativas se correlacionaron positivamente con el grado de atrofia en los ganglios basales. Asimismo, Melloni et al. (2015) demostraron que la abolición del efecto de compatibilidad acción-oración (ACE) en estos pacientes tuvo un correlato neurofisiológico, reflejado en la ausencia de facilitación del potencial motor y en la desconexión funcional entre regiones frontales y temporales en condiciones incongruentes.

Aunque los ganglios basales han sido el foco principal de estos estudios, el cerebelo representa otra estructura extracortical clave que merece mayor atención. Al igual que los ganglios basales, el cerebelo posee circuitos complejos que integran funciones motoras y cognitivas. Según Koziol et al. (2014), el cerebelo realiza una computación similar en estos distintos dominios debido a su arquitectura homogénea y su conectividad heterogénea con regiones sensoriomotoras, cognitivas y límbicas (Schmahmann, 2010). Estas características lo posicionan como un candidato clave para la modulación de procesos semánticos relacionados con acciones.

El paralelismo con los ganglios basales sugiere que también el cerebelo podría ser fundamental para la integración semántica-motora. En otras palabras, se puede argumentar que el cerebelo podría participar en la representación y procesamiento de la semántica de la acción mediante mecanismos análogos. Birba et al. (2017) propusieron que los circuitos frontoestriatales, originalmente diseñados para la selección y secuenciación de patrones motores, fueron reclutados evolutivamente para operaciones lingüísticas con contenido similar, como la representación léxico-semántica y la sintaxis. Extender esta hipótesis al cerebelo implica postular que sus circuitos, involucrados en la coordinación y aprendizaje motor, también podrían contribuir a operaciones semánticas mediante la integración de representaciones internas con estímulos externos. Evidencias preliminares apoyan esta idea: un estudio pionero de García et al. (2017) mostró que un paciente con atrofia cerebelosa presentó déficits selectivos en tareas de decisión léxica con verbos motores, mientras que mantuvo preservado el desempeño con verbos abstractos y sustantivos. Estos hallazgos sugieren que el cerebelo podría desempeñar un rol complementario al de los ganglios basales en el procesamiento de conceptos de acción.

Sin embargo, este campo está aún en sus primeras etapas, lo que justifica la necesidad de acumular mayor evidencia empírica. Este vacío teórico y empírico motiva el primer artículo de esta tesis, que ofrece una contribución original al evaluar el impacto de la disfunción cerebelosa en el procesamiento semántico. A través de un estudio de caso, integramos medidas conductuales y neurofisiológicas para analizar cómo el cerebelo contribuye a la representación y acceso a conceptos de acción, extendiendo el conocimiento más allá de los circuitos corticales.

2.4. El contexto motor en la semántica de la acción: Evidencias comportamentales y neurofisiológicas de interacción entre las acciones manuales y el procesamiento de verbos de acción manual

Como se discutió en secciones previas, la semántica de la acción ofrece una vía estratégica para comprender cómo los conceptos de acción se apoyan tanto en los circuitos motores como semánticos. Estudios conductuales y neurofisiológicos han reafirmado la idea de que las representaciones semánticas no son amodales, sino que están profundamente enraizadas en la experiencia corporal. Más específicamente, verbos motores como “correr” o “escribir” parecen activar circuitos cerebrales compartidos con las redes implicadas en la ejecución de esas mismas acciones (Rüschemeyer et al., 2007; Pulvermüller, 2005). Sin embargo, sigue siendo una cuestión abierta cómo estos procesos interactúan de manera funcional en tiempo real.

Una forma de avanzar en esta temática ha sido investigar cómo el procesamiento del lenguaje y la ejecución de movimientos interactúan cuando ocurren simultáneamente. Este enfoque se basa en la hipótesis de que existe una superposición parcial de las redes neurales implicadas en ambos procesos, lo que puede dar lugar a efectos de facilitación o interferencia dependiendo de ciertos factores como el grado de congruencia entre la tarea lingüística y la acción motora. Por ejemplo, cuando un verbo como “empujar” se procesa al mismo tiempo que se realiza una acción manual congruente, el acceso al significado del verbo podría facilitarse, o bien, la acción podría interferir en dicho acceso dependiendo del contexto experimental.

Esta sección aborda esta interacción funcional entre semántica y acción, revisando las principales evidencias provenientes de estudios conductuales y neurofisiológicos. Además, se presenta el modelo HANDLE (García & Ibáñez, 2016), que explica cómo la temporalidad y la complejidad de las tareas modulan estos efectos. Finalmente, se introducen las principales preguntas del segundo artículo de esta tesis, que busca llenar vacíos importantes en la literatura al explorar estas dinámicas desde una perspectiva experimental más integrada y en condiciones implícitas.

Desde un enfoque conductual, se han documentado efectos robustos de interacción semántico-motora. Uno de los paradigmas más utilizados es el "efecto de compatibilidad acción-oración" (ACE, por sus siglas en inglés), descrito inicialmente por Glenberg & Kaschak (2002). En este paradigma, se observa que los movimientos manuales son más rápidos cuando son congruentes con la dirección de la acción descrita en una oración (por ejemplo, empujar o tirar). En esta línea, Zwaan & Taylor (2006) mostraron que movimientos rotacionales manuales eran facilitados si el sentido del movimiento era congruente con una oración como “*He turned up the volume*” (giró el volumen hacia arriba).

De forma interesante, también se han observado efectos modulatorios en paradigmas que se centran en la coincidencia del efector corporal y no necesariamente en la congruencia semántica de las acciones realizadas. Buccino et al. (2005) reportaron que la respuesta manual a oraciones que describían acciones manuales era más lenta en comparación con respuestas a oraciones que describían acciones podales, indicando que el procesamiento simultáneo de estímulos relacionados con el mismo efector puede generar competencia por recursos neurales. Los autores mostraron que el efecto no se restringe únicamente para el caso de las manos y replicaron los resultados utilizando los pies como efector.

Estos efectos, aunque consistentes, muestran una gran variabilidad dependiendo de factores como la complejidad de la tarea y la temporalidad entre los estímulos, entre otros. Esta variabilidad ha motivado el desarrollo de modelos teóricos como HANDLE (García & Ibáñez, 2016), que buscan explicar y predecir cuándo se observarían efectos de facilitación o interferencia en función de estas variables.

Por otro lado, a nivel neurofisiológico, el acoplamiento entre semántica y acción ha sido explorado mediante análisis de potenciales relacionados a eventos (ERPs). Por ejemplo, Aravena et al. (2010) utilizaron el paradigma ACE, en el que los participantes realizaban movimientos manuales congruentes o incongruentes con oraciones de acción. Las condiciones congruentes generaron tiempos de reacción más rápidos, acompañados de un aumento en el potencial motor (MP) y el potencial reaferente, indicadores de la preparación y ejecución motora. Por el contrario, las condiciones incongruentes mostraron un incremento significativo del N400, asociado a una integración semántica más demandante.

Estos hallazgos fueron extendidos por Ibáñez et al. (2013), quienes, mediante registros intracorticales, mostraron que el procesamiento semántico de oraciones congruentes facilita la actividad motora, mientras que la preparación motora modula la integración semántica, reflejada en una atenuación del N400 en condiciones congruentes. De forma complementaria, Mollo et al. (2016) aportaron evidencia sobre el papel del lóbulo temporal superior posterior (pSTL) como un nodo clave en la convergencia de redes motoras y lingüísticas, aunque sin un correlato conductual directo.

Las ondas corticales, particularmente en el ritmo beta, han proporcionado otros enfoques para estudiar esta interacción. Este ritmo, caracterizado por una desincronización durante la preparación y ejecución de movimientos, ha sido vinculado a la interacción funcional entre procesos motores y semánticos (Pfurtscheller & Lopes da Silva, 1999). Klepp et al. (2015) demostraron que el procesamiento de verbos de acción manual reducía la desincronización beta en la corteza motora, sugiriendo un acoplamiento dinámico entre los procesos semánticos y motores. Visani et al. (2022) aportaron al tema al identificar modulaciones del ritmo beta tanto en la preparación como en la ejecución del movimiento durante tareas de juicio semántico. Este trabajo resalta que las oscilaciones beta no solo operan en la preparación motora, sino también la carga semántica, proporcionando una visión más integrada de la interacción semántico-motora.

El modelo HANDLE (García & Ibáñez, 2016) ofrece un marco teórico para comprender cómo las características temporales y contextuales de las tareas modulan su interacción. Según este modelo, el procesamiento explícito de conceptos de acción puede interferir con la ejecución de acciones motoras simples cuando ambas tareas coinciden en una ventana temporal de menos de 400 ms. Por el contrario, la interacción puede resultar en facilitación si las respuestas motoras ocurren dentro de un rango de 450 a 750 ms después del estímulo semántico. El efecto de interferencia es explicado por un fenómeno de competencia de recursos compartidos, con una subsecuente disponibilidad reducida del sistema motor para responder a las demandas de las acciones (Buccino et al., 2005; de Vega et al., 2013; Hommel et al., 2001; Chersi et al., 2010; Conca & Tettamanti, 2018; Visani et al., 2022). Por el contrario, el efecto de facilitación ha sido atribuido a la generación de una activación residual en las áreas motoras durante el procesamiento semántico, lo que reduciría la activación requerida para que una subsecuente acción alcance el nivel umbral (Locatelli et al., 2012). Este enfoque ha sido valioso para explicar resultados conductuales y neurofisiológicos previos, proporcionando un marco flexible para analizar la interacción entre sistemas semántico-motores.

Además, el modelo HANDLE resalta que estas predicciones son sensibles a las características específicas de las tareas implicadas. Por ejemplo, la complejidad de las acciones motoras o la profundidad del procesamiento semántico requerido puede ampliar o reducir esas ventanas temporales en las que se producen efectos de facilitación o inhibición. Tareas más complejas, como la asociación semántica entre estímulos múltiples, tienden a generar efectos de interferencia más prolongados, mientras que respuestas simples, como presionar un botón, pueden mostrar facilitación en ventanas más estrechas. Este matiz es fundamental para comprender las limitaciones del modelo en contextos naturales o más complejos.

Las dificultades que enfrentan las predicciones del modelo, son en definitiva un reflejo de las importantes limitaciones del conocimiento que aún persiste sobre la interacción funcional entre semántica y acción. La mayoría de los estudios se han centrado en tareas explícitas de procesamiento semántico con estímulos lingüísticos aislados y con un control parcial de otras categorías semánticas. Además, pocos trabajos han evaluado efectos recíprocos en marcadores cerebrales que permitan integrar dinámicas semánticas y motoras en tiempo real.

En este marco, el segundo artículo de esta tesis se propuso avanzar en el estudio de las dinámicas de acoplamiento entre tareas motoras y semánticas mediante la técnica de electroencefalografía (EEG), utilizando una tarea de procesamiento implícito de verbos de acción en comparación con verbos abstractos. Esta elección metodológica responde directamente a algunas de las limitaciones identificadas en la literatura previa. En primer lugar, el uso de EEG para registrar simultáneamente marcadores canónicos del procesamiento semántico (como el componente N400) y marcadores de preparación motora (como los MRCPs) permite investigar si existen modulaciones recíprocas entre ambos sistemas, en un análisis fino de la dinámica temporal de la interacción semántico-motora. En segundo lugar, la elección de una tarea implícita como la decisión léxica permite explorar la interacción entre procesos motores y semánticos sin exigir una atención dirigida explícitamente al contenido conceptual del estímulo. Ésto posibilita evaluar modulaciones cerebrales que ocurren de manera automática durante el procesamiento léxico, evitando el sesgo que pueden introducir las tareas semánticas explícitas. En tercer lugar, el contraste entre verbos de acción y abstractos permite evaluar si la activación motora se encuentra específicamente asociada al contenido motor del estímulo o si refleja una activación general del sistema ante cualquier tipo de palabra. A su vez, la comparación entre diferentes efectores permite explorar si existe una resonancia motora específica y somatotópica —como sugieren estudios previos de neuroimagen y potenciales evocados— o si, por el contrario, el acoplamiento semántico-motor se organiza de manera más global e indiferenciada. En suma, el segundo artículo no solo se basa en los hallazgos previos de interacción semántico-motora, sino que también propone una estrategia metodológica que permite superarlos, al integrar la dimensión temporal, la posibilidad de estudiar influencias bidireccionales, un mayor contraste entre clases semánticas, y un nivel de procesamiento lingüístico más automático y menos influenciado por demandas metalingüísticas.

2.5. La experiencia personal en la semántica de la acción: Evidencias comportamentales y neurofisiológicas del impacto de nuevas experiencias motoras en el procesamiento de información de acción

Las teorías semánticas corporizadas sostienen que los conceptos se construyen y transforman a partir de las experiencias sensoriomotoras del individuo. En este marco, la experiencia personal con acciones específicas desempeña un rol central en la formación y modulación de los conceptos de acción, vinculando los procesos semánticos con la historia motora del sujeto (Barsalou, 2005; Conca & Tettamanti, 2018). Esta idea introduce una perspectiva dinámica y situada, en la que los conceptos no son entidades estáticas, sino que evolucionan a medida que el repertorio motor y la interacción del sujeto con el entorno se modifican.

Por un lado, estudios como los de Jäncke et al. (2009) demuestran que la práctica deportiva puede generar adaptaciones estructurales en regiones fronto-parietales, las cuales están implicadas en la semántica de la acción. Particularmente esta investigación mostró un mayor volumen de la sustancia gris es la corteza premotora dorsal y el lóbulo parietal posterior, en golfistas profesionales en comparación con novatos.

Desde una perspectiva funcional, se ha visto que la experiencia motora modula la activación cerebral durante la observación de acciones. Un estudio comparativo entre bailarines de capoeira y bailarines clásicos demostró diferencias específicas en la activación de la red motora, reflejando la influencia de la experiencia previa en la percepción y conceptualización de movimientos (Calvo-Merino et al., 2005).

En el contexto del lenguaje, Beilock et al. (2008) evaluaron cómo la experiencia deportiva en hockey afecta la comprensión semántica de oraciones relacionadas con el deporte. Los resultados mostraron que los jugadores profesionales y aficionados presentaban una mayor activación de la corteza premotora dorsal en comparación con individuos sin experiencia. En cambio, los aficionados, cuya experiencia es más visual que motora, exhibían una activación reducida en la corteza sensoriomotora primaria. Estos hallazgos resaltan el papel central de la experiencia motora en el procesamiento conceptual y sugieren que la activación cerebral durante la comprensión semántica refleja un reclutamiento funcional de circuitos motores vinculados a la práctica previa.

Sin embargo, estos estudios presentan limitaciones importantes. Por un lado, resulta difícil aislar la experiencia motora de otras fuentes de experiencia, como la exposición al lenguaje especializado de las disciplinas. Por otro lado, el grado de experiencia de los participantes suele ser estimado indirectamente a partir de los años de práctica, lo que limita la precisión de los hallazgos (Conca & Tettamanti, 2018).

Para superar estas limitaciones, algunos estudios han adoptado paradigmas de intervención experimental, permitiendo evaluar de manera más controlada los efectos causales de la experiencia motora en el procesamiento semántico. Locatelli et al. (2012) entrenaron a participantes en tareas manuales novedosas y complejas (papiroflexia y nudos marineros entre otros) durante tres semanas. Los resultados mostraron una reducción significativa en los tiempos de reacción post-entrenamiento para oraciones congruentes con las acciones entrenadas, y en menor medida para las acciones no entrenadas. Estos hallazgos sugieren que la experiencia motora mejora la accesibilidad semántica fundamentalmentalmente de conceptos relacionados con las acciones practicadas, evidenciando un vínculo directo entre el entrenamiento motor y el procesamiento semántico.

Además, estos efectos de entrenamiento se han asociado con cambios en la morfometría cerebral. Bogdan et al. (2004) demostraron que la adquisición de habilidades motoras, como el malabarismo, induce un aumento progresivo en la sustancia gris en áreas como la hMT/V5 y el surco intraparietal posterior, lo que sugiere una reorganización estructural vinculada a la experiencia motora.

No obstante, la relación entre entrenamiento y procesamiento semántico no siempre resulta facilitadora. Glenberg et al. (2008) encontraron que una sesión de veinte minutos de entrenamiento en acciones repetitivas de traslado de objetos hacia o desde el cuerpo, generaron un efecto de interferencia en una tarea de decisión semántica que evaluaba oraciones congruentes con dichas acciones motoras. Específicamente, los tiempos de reacción aumentaron cuando las oraciones describían movimientos de objetos en la misma dirección que las acciones entrenadas. Los autores interpretaron este hallazgo como un efecto de saturación motora que inhibe temporalmente la disponibilidad de los circuitos motores para apoyar la comprensión semántica. Esta dualidad ha sido atribuida a la duración y la complejidad del entrenamiento, sugiriendo que los efectos facilitadores podrían estar vinculados a protocolos prolongados que promuevan una plasticidad neural estructural (Locatelli et al., 2012).

A pesar de los avances en el campo, la literatura sigue siendo limitada y en su mayoría se basa en estímulos lingüísticos artificiales, tareas de laboratorio con escasa validez ecológica y medidas puramente comportamentales. Estas restricciones dificultan la generalización de los hallazgos a contextos más complejos y naturales del procesamiento semántico. En este marco, el tercer artículo de esta tesis representa un avance significativo al examinar, mediante un protocolo de entrenamiento motor con alta validez ecológica, cómo la experiencia personal puede modular el procesamiento semántico. Combinando medidas conductuales y neurofisiológicas, se analizan cambios en la conectividad funcional entre regiones motoras y semánticas, aportando evidencia sobre la plasticidad dinámica de estos circuitos en contextos más cercanos a la vida real.

A pesar de los avances en el campo, la literatura sigue siendo limitada y en su mayoría se basa en estímulos lingüísticos artificiales, tareas de laboratorio con escasa validez ecológica y medidas puramente comportamentales. Estas restricciones dificultan la generalización de los hallazgos a contextos más complejos y naturales del procesamiento semántico. En este marco, el tercer artículo de esta tesis representa un avance significativo, al retomar y ampliar líneas de investigación previas. Particularmente, el estudio conductual de Locatelli et al. (2012) resalta que el entrenamiento motor específico facilita el acceso semántico a oraciones congruentes con las acciones practicadas, aunque también encuentra un efecto inespecífico que no lo plasma en sus implicancias teóricas. Desde estos vacíos, el tercer artículo de esta tesis explora si la activación del sistema motor, incluso en ausencia de una coincidencia semántica específica con los estímulos lingüísticos, puede inducir cambios funcionales en redes semánticas. Se implementó un protocolo de entrenamiento motor breve, inmersivo y no específico, con alta validez ecológica, y se integraron medidas conductuales de recuerdo de información de acción contenida en textos naturalistas, con registros de conectividad funcional cerebral. Este enfoque buscó analizar cómo experiencias motoras recientes, no vinculadas semánticamente al contenido verbal, pueden modular dinámicas de acoplamiento entre regiones motoras y semánticas. En conjunto, estos aportes extienden los hallazgos de estudios anteriores y proporcionan evidencia sobre la plasticidad del sistema motor-semántico en un contexto más general.

2.6. Síntesis y preguntas de investigación

A pesar de los avances significativos en la comprensión de la semántica de la acción desde una perspectiva corporizada, persisten importantes vacíos en la literatura. En primer lugar, la mayoría de los estudios neurológicos se han centrado en circuitos corticales y fronto-estriatales, relegando a un segundo plano estructuras extracorticales como el cerebelo. Esto plantea interrogantes sobre cómo la disfunción cerebelosa afecta la representación y el procesamiento de conceptos relacionados con acciones, un tema explorado en el primer artículo de esta tesis a través de un estudio de caso.

En segundo lugar, aunque se ha demostrado que los procesos motores y semánticos interactúan funcionalmente, los estudios existentes han privilegiado abordajes conductuales, dejando escasa evidencia neurofisiológica que permita caracterizar las dinámicas temporales y jerárquicas de esta interacción. Este vacío motiva el segundo artículo, que analiza la modulación bidireccional entre ambos sistemas mediante marcadores cerebrales relacionados con el movimiento y el procesamiento semántico.

Finalmente, la literatura emergente sobre el impacto de nuevas experiencias sensoriomotoras en el procesamiento semántico se basa principalmente en diseños experimentales con baja validez ecológica. Esto suscita preguntas sobre cómo entrenamientos motores inmersivos pueden reorganizar las redes semántico-motoras, una línea investigada en el tercer artículo mediante un protocolo de exergaming en escenarios naturalistas.

En conjunto, esta tesis busca abordar estos vacíos y responder preguntas clave sobre la interacción entre los sistemas motor y semántico, proporcionando un marco más completo para entender cómo las redes cerebrales y las experiencias personales moldean la cognición corporizada.

3. OBJETIVOS E HIPÓTESIS

Objetivo General

Investigar cómo los mecanismos asociados al procesamiento de conceptos relacionados con acciones se vinculan con el sistema motor y la experiencia personal, desde una perspectiva de la cognición corporizada.

Hipótesis General

El procesamiento de conceptos relacionados con acciones depende de la integración dinámica de circuitos neuronales corticales y extracorticales, modulados por la interacción entre los sistemas motor y lingüístico y la experiencia personal.

Objetivo Específico 1

Evaluar el rol del cerebelo en el procesamiento semántico de conceptos relacionados con acciones.

Hipótesis Relacionadas

- El cerebelo contribuye en el procesamiento léxico-semántico mediante mecanismos que permiten la integración de las representaciones motoras.

- La lesión cerebelosa afecta selectivamente el procesamiento de conceptos de acción, disminuyendo la eficiencia de las redes corticales asociadas.

Objetivo Específico 2

Analizar efectos modulatorios de la actividad cerebral resultantes del acoplamiento de procesos motores y semánticos relacionados con acciones.

Hipótesis Relacionada

- Partiendo de numerosas evidencias que respaldan que la ejecución de acciones manuales y el procesamiento de verbos manuales comparten circuitos de procesamiento, nostros hipotetizamos que la proximidad temporal de ambas tareas conduce a modulaciones de marcadores cerebrales canónicos de ambos procesos, aún en condiciones de procesamiento implícito de conceptos.

Objetivo Específico 3

Explorar cómo un protocolo de entrenamiento motor de corto-mediano plazo en condiciones ecológicas influye en la recuperación de información de acción y las redes neuronales asociadas.

Hipótesis Relacionadas

- La adquisición de nuevas experiencias a través de un entrenamiento motor de corto a mediano plazo puede tener un impacto en la recuperación de información de acción inmersa en un contexto naturalista e inespecífico.
- Las alteraciones conductuales podrían estar asociadas y explicadas por reorganizaciones temporales de las áreas motoras y semánticas y/o su conectividad funcional.

4. RESULTADOS

La presente tesis resultó en la elaboración y publicación de tres artículos científicos que se indican y se adjuntan a continuación.

Cervetto, S., Abrevaya, S., Martorell Caro, M., Kozono, G., Muñoz, E., Ferrari, J., ... & García, A. M. (2018). Action semantics at the bottom of the brain: Insights from dysplastic cerebellar gangliocytoma. *Frontiers in psychology*, *9*, 1194.

Cervetto, S., Díaz-Rivera, M., Petroni, A., Birba, A., Caro, M. M., Sedeño, L., ... & García, A. M. (2021). The neural blending of words and movement: event-related potential signatures of semantic and action processes during motor–language coupling. *Journal of Cognitive Neuroscience*, *33*(8), 1413-1427.

Cervetto, S., Birba, A., Pérez, G., Amoruso, L., & García, A. M. (2022). Body into narrative: Behavioral and neurophysiological signatures of action text processing after ecological motor training. *Neuroscience*, *507*, 52-63.

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Action Semantics at the Bottom of the Brain: Insights From Dysplastic Cerebellar Gangliocytoma

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Recent embodied cognition research shows that access to action verbs in shallow-processing tasks becomes selectively compromised upon atrophy of the cerebellum, a critical motor region. Here we assessed whether cerebellar damage also disturbs explicit semantic processing of action pictures and its integration with ongoing motor responses. We evaluated a cognitively preserved 33-year-old man with severe dysplastic cerebellar gangliocytoma (Lhermitte-Duclos disease), encompassing most of the right cerebellum and the posterior part of the left cerebellum. The patient and eight healthy controls completed two semantic association tasks (involving pictures of objects and actions, respectively) that required motor responses. Accuracy results via Crawford's modified *t*-tests revealed that the patient was selectively impaired in action association. Moreover, reaction-time analysis through Crawford's Revised Standardized Difference Test showed that, while processing of action concepts involved slower manual responses in controls, no such effect was observed in the patient, suggesting that motor-semantic integration dynamics may be compromised following cerebellar damage. Notably, a Bayesian Test for a Deficit allowing for Covariates revealed that these patterns remained after covarying for executive performance, indicating that they were not secondary to extra-linguistic impairments. Taken together, our results extend incipient findings on the embodied functions of the cerebellum, offering unprecedented evidence of its crucial role in processing non-verbal action meanings and integrating them with concomitant movements. These findings illuminate the relatively unexplored semantic functions of this region while calling for extensions of motor cognition models.

Keywords: cerebellar atrophy, neurodegeneration, action pictures, object pictures, embodied cognition

INTRODUCTION

Motor brain networks play critical roles in grounding action meanings (verbal and non-verbal concepts related to bodily motion) and integrating them with ongoing manual movements (Buccino et al., 2005; Ibáñez et al., 2013; García and Ibáñez, 2014, 2016a). This association has been repeatedly shown for cortical regions (e.g., the primary and supplementary motor cortices) (Pulvermüller, 2005; Fischer and Zwaan, 2008; Vukovic et al., 2017) and frontostriatal networks affected by movement disorders (Cardona et al., 2013; García and Ibáñez, 2014; Kargieman et al., 2014; Melloni et al., 2015; Birba et al., 2017a). However, the contributions of the cerebellum, another key motor hub, have received comparatively lesser attention (García et al., 2016a; Guell et al., 2017). To bridge this gap, here we report the first assessment of explicit action-semantic processing and motor-semantic integration in a rare patient with bilateral cerebellar damage due to a dysplastic gangliocytoma (Lhermitte-Duclos disease).

The two domains in question are selectively or differentially compromised in patients with movement disorders (Kotz et al., 2009; Cardona et al., 2013). In Parkinson's and Huntington's disease, atrophy of frontostriatal motor loops impairs implicit and explicit processing of words (Fernandino et al., 2013a; Bocanegra et al., 2015), sentences (Fernandino et al., 2013b; Cardona et al., 2014), and images (Ibáñez et al., 2013; Bocanegra et al., 2015; García et al., 2017b,d) evoking bodily motion, while also disrupting predictable interference or facilitation effects (García and Ibáñez, 2016a) that such stimuli produce on concomitant hand movements (Ibáñez et al., 2013; Cardona et al., 2014; Kargieman et al., 2014; Melloni et al., 2015; Buccino et al., 2018). Notably, such deficits emerge irrespective of the patients' domain-general impairments (Ibáñez et al., 2013; Bocanegra et al., 2015, 2017; García et al., 2017b) and even in preclinical disease stages (Kargieman et al., 2014; García et al., 2017d). It follows that damage to regions implicated in motor function can markedly disrupt the embodiment of action semantics.

While the above evidence comes from frontostriatal lesion models, the same could be hypothesized regarding the cerebellum, another hub critically involved in motor control and motor learning (Fabbro, 2000; Ramnani, 2006; Glickstein and Doron, 2008). Indeed, this region has been associated with the construction of internal models, or simulations (Ito, 1993, 2008; Ramnani, 2006), and it has been argued to play critical roles in embodied cognitive evolution (Barton, 2012). More particularly, cerebellar atrophy in genetic ataxia has been associated with selective action-verb impairments in lexical decision, a task that does not require explicit semantic processing (García et al., 2016a; Guell et al., 2017).

The latter finding, in particular, suggests that the cerebellum may be critical for grounding action meanings in shallow-processing verbal tasks – i.e., when semantic access is unnecessary for task completion. However, no study has assessed whether cerebellar damage also disturbs explicit action-semantic processing in non-verbal tasks, let alone its integration with ongoing motor responses. Thus, it remains unknown whether the distinct role of the cerebellum in motor semantics holds across processing modalities (verbal vs. pictorial) and levels of semantic access (implicit vs. explicit). To bridge this gap, we assessed a patient with severe dysplastic cerebellar gangliocytoma and eight healthy controls on two picture-based semantic association tasks (one involving objects, the other involving actions) requiring hand responses. In line with previous results (García et al., 2016a) and current embodied models (García and Ibáñez, 2016a), we hypothesized that cerebellar damage could selectively impair both the semantic association of actions and motor-semantic integration. In sum, we aimed to profit from this unique case to gain new insights into the contributions of the cerebellum to embodied cognitive functions.

MATERIALS AND METHODS

Case Description

Patient NA is a 35-year-old, Spanish-speaking, right-handed Argentine man with 14 years of formal education. The patient reported a family history of neurological disease (his grandfather had dementia), psychiatric disease (his grandmother suffered from depression), and an antecedent of sudden death (his older brother died 3 months after birth).

On December 20, 2015, at age 33, NA experienced vertigo, low pressure, and generalized body weakness. Four days later, he manifested progressive dysarthria. At the end of January 2016, he suffered from sudden loss of consciousness but resumed normal activities after a few days. Throughout the following month, persistent signs of dysarthria were accompanied by reduced right-hand agility and progressive gait instability – mainly due to right-leg abnormalities. FLAIR and T2 MRI sequences revealed mild hyperintensity on the cerebellum without contrast enhancement, alongside thickened folia, small cysts, and sparing of the fourth ventricle. A posterior biopsy, together with histological and immunohistochemical studies, confirmed the diagnosis of dysplastic cerebellar gangliocytoma (Lhermitte-Duclos disease) as WHO stage IV.

In March 2016, NA started pharmacological treatment, shifting between Valcas (250 mg qd), Logical (200 mg tid), and Gabapentin (100 and 200 mg tid). That same year, on September 27, NA was hospitalized after experiencing aggravated vertigo, oscillopsia, and ataxia. Motor-system impairment was variously documented. In addition to right-sided horizontal gaze nystagmus (grade 2) and hearing deficits (negative Rinne's test on the right side and left-lateralized Weber's test), neurological examination revealed mild dysarthria, loss of balance (positive Rhomberg's test), right-dominant muscular hypotonia with preserved force, motor nerve disturbances (positive Hoffman's test on the right side), and ataxic gait. A follow-up MRI revealed an expansive right cortical-subcortical cerebellar lesion, characterized by hypointensity in T1 and corresponding hyperintensity in T2 and FLAIR, weighted signals with pseudocystic formations and no contrast enhancement, perilesional edema with mass effect on adjacent structures and the fourth ventricle, a right cerebellar nodular mass corresponding to a primary neo-proliferative lesion, and a discrete intensity change on the left cerebellum. No other signs of atrophy or malformations were observed, and lesions were essentially restricted to cerebellar structures. Given the rarity of Lhermitte-Duclos disease – with roughly 220 cases reported by 2006 (Robinson and Cohen, 2006)–, alongside its highly focal compromise of the cerebellum and its pervasive impact on motor function (Marcus et al., 1996; Nowak and Trost, 2002), this case offers a unique opportunity to test our hypothesis.

Control Participants

The patient's performance on the experimental tasks was compared with that of eight right-handed healthy men with no history of neurological or psychiatric disease. This control group matched the patient in terms of age (31.6 ± 5.53, p = 0.82) and education level (15.6 ± 2.7, p = 0.58). The study was carried out in accordance with the recommendations of the Ethics Committee of the Institute of Cognitive Neurology (INECO, now a host institution of the Institute of Cognitive and Translational Neuroscience), with written informed consent from all subjects. All participants gave written informed consent in accordance with the Declaration of Helsinki, and written informed consent was obtained from patient NA for the publication of this case report. The protocol was approved by the Ethics Committee of INECO.

Neuroimaging: Lesion Localization

Following previous procedures (García-Cordero et al., 2015, 2016; Melloni et al., 2016), an expert neurologist (JF) manually traced the patient's lesion in native space. A T1 scan shows the extension of damage, comprising various parts of the cerebellum. Coordinates obtained from the Automated Anatomical Labeling software (Tzourio-Mazoyer et al., 2002) indicated that cerebellar damage included most of the right anterior and posterior hemisphere (comprising lobules VII, VIIB, VI, and IX, as well as crus I and II regions), part of the left posterior lobe (lobules VII, VIIB, IX, X, and crus II), and a few areas from the vermis (regions VII, VIII, IX, and X) (**Figure 1, panels A1–A3**).

Instruments

Neuropsychological and Psychiatric Evaluation

The assessment protocol included instruments tapping overall cognitive status, executive functions, and anxiety levels.

The participants' overall cognitive state was assessed with the Montreal Cognitive Assessment (MoCA), a sensitive tool for detecting cognitive dysfunction in populations with atrophy of motor regions, such as the basal ganglia (Gluhm et al., 2013; Bocanegra et al., 2015, 2017) and the cerebellum (Mercadillo et al., 2014; Dogan et al., 2016; García et al., 2016a). The MoCA covers eight cognitive domains, namely: visuospatial/executive skills, naming, memory, attention, language, abstraction, delayed recall, and orientation. It has a maximum of 30 points, and its total score is corrected for the participant's years of education.

In addition, executive functions were assessed through the INECO Frontal Screening (IFS) battery (Torralva et al., 2009). This tool has proved sensitive for population with damage to motor regions (Cardona et al., 2014; Bocanegra et al., 2015; García et al., 2016a, 2017a). The IFS taps domains such as motor programming, conflict resolution, inhibitory control, and working memory. This battery comprises 20 items, and its maximum score is 30.

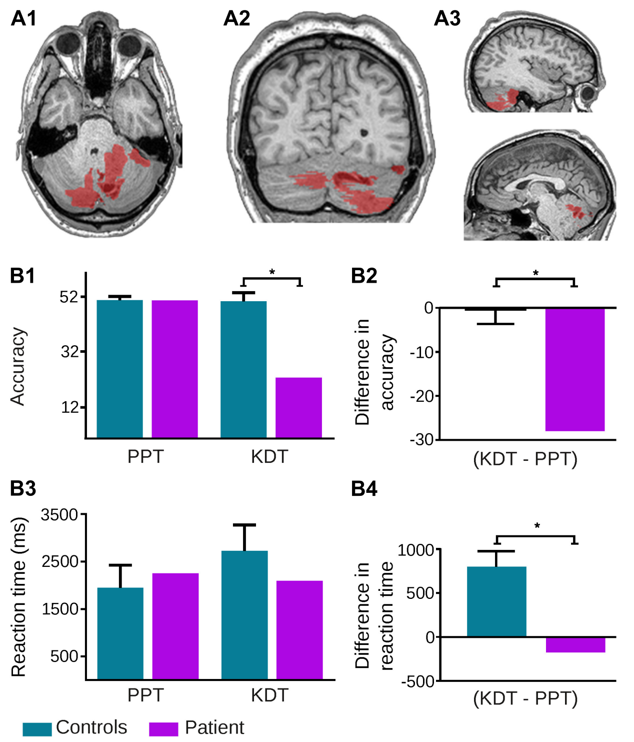

FIGURE 1 | Neuroanatomical and behavioral evidence from patient NA. **(A)** Extent of the tumor highlighted in red on the original T1 MRI scan of the patient's brain: **(A1)** axial view; **(A2)** coronal view; **(A3)** sagittal section – right (up) left (down). **(B)** Behavioral performance of patient and controls on the Pyramids and Palm Trees (PPT) test and the Kissing and Dancing Test (KDT). **(B1)** The patient showed significantly reduced accuracy on the KDT (p < 0.001) but not on the PPT test (p = 0.93). The patient's deficit on the KDT remained after covarying for global scores on the Montreal Cognitive Assessment (MoCA), the INECO Frontal Screening (IFS) battery, and the State version of the State Trait Anxiety Inventory (STAI-S) – all p-values < 0.001. **(B2)** Subtraction of PPT from KDT accuracy scores in each subject showed a difference of 28 answers for the patient and an average difference of –0.3 in controls; this difference was significant (p = 0.001) and it remained so after covarying for MoCA (p = 0.005), IFS (p = 0.01), and STAI-S (p = 0.004) scores. **(B3)** Reaction times for the patient were similar to those of controls on both the PPT test (p = 0.59) and the KDT (p = 0.32). **(B4)** However, subtraction of reaction times on the PPT test from those of the KDT in each subject revealed notably longer latencies (~800 ms more) for the latter in controls, and virtually null differences in the patient; such a difference between the patient and controls was significant (p = 0.005) and it remained so after covarying for MoCA (p < 0.001), IFS (p = 0.01), and STAI-S (p = 0.004) scores. The asterisk (*) indicates significant differences.

Anxiety levels during the cognitive tasks were assessed via the state version of the State Trait Anxiety Inventory (STAI-S; Spielberger et al., 1970). The psychometric properties of this instrument attest to its reliability and validity to detect situational anxiety (Spielberger et al., 1980) in the general population (Barnes et al., 2002). It has also been used in patients with damage in motor regions, such as the basal ganglia (Leritz et al., 2004; Tinaz et al., 2011) and the cerebellum (Zawacki et al., 2002; Orsi et al., 2011). The STAI-S comprises 20 self-report items inquiring on the examinee's current feelings. Each item rates severity on a 1–4 scale, so that the total score ranges from 20 to 80.

Semantic Association of Objects and Actions

Semantic association of objects and actions was assessed through the Pyramids and Palm Trees (PPT) test (Howard and Patterson, 1992), and the Kissing and Dancing Test (KDT) (Bak and Hodges, 2003), respectively. In both tests, participants must choose which of two pictures is most closely related to a cue picture. Each test comprises 52 trials, yielding a maximum score of 52. These instruments have revealed specific deficits in patients with damage to motor regions, such as the basal ganglia (Cardona et al., 2014; Bocanegra et al., 2015; García et al., 2017b,d), and other less focused injuries that include cerebellar atrophy (Baez et al., 2013).

The patient and all controls were tested individually in a dimly illuminated room. They sat comfortably at a desk, in front of an Intel Core i5-3470 PC equipped with a monitor (Lenovo 15.6" 16:9 HD LED backlight display) and a QWERTY keyboard (gx gaming).

For this study we implemented a computerized version of both tasks, designed and run on DMDX software[1], as to automatically record accuracy and reaction-time (RT) data and thus assess the impact of action-semantic processing on concurrent manual actions (i.e., responses made by pressing of predefined keyboard buttons). In each trial, the cue picture was located at the top of the screen and the two option pictures appeared at the bottom, in a pyramid-like arrangement. All three images were presented simultaneously and they remained on the screen for 5 s. If no response was made within this time interval, a blank screen was shown for a maximum of 5 s before the next trial appeared.

Participants were instructed to respond as fast and accurately as possible by pressing the left or the right arrow of the keyboard with two fingers of the dominant hand, indicating their choice of the picture at the corresponding location. Each key press was logged to compute accuracy and RT, and it triggered a 1-s blank screen followed by the next trial. Prior to each task, the instructions were recapped on-screen and four additional items were presented for practice purposes. The patient performed the PPT test first and then the KDT, whereas both tasks were counterbalanced across control participants.

Statistical Analysis

Demographic, neuropsychological, psychiatric, and behavioral data were compared between the patient and controls via two-tailed Crawford's modified *t*-tests (Crawford and Howell, 1998; Crawford and Garthwaite, 2002), as done in previous studies (Couto et al., 2013a,b; Sedeño et al., 2014; García et al., 2016a,b; Birba et al., 2017b). This test allows comparing test scores from one or more individuals with norms derived from small samples. It has been proved to be robust for non-normal distributions and it presents low rates of type-I error (Crawford and Howell, 1998; Crawford and Garthwaite, 2002, 2012; Crawford et al., 2009, 2011).

Also, to assess performance differences between the PPT test and the KDT, RT data from the patient and the controls were analyzed via the Revised Standardized Difference Test (RSDT) (Crawford and Garthwaite, 2005). This test examines the difference between a subject's scores on two tasks relative to the difference observed in the control group, considering the distribution of values in the latter and its correlation between tasks. As the modified *t*-test, the RSDT controls for the type-I error rate in the case of small control samples (Crawford and Garthwaite, 2005). In RT analyses, all trials exceeding 2 SDs from the subject's mean were removed as outliers (less than 10% of the trials in all cases).

Finally, to determine whether hypothesized differences between the patient and controls were influenced by the former's cognitive status, executive skills, or anxiety levels, all analyses were repeated with global MoCA, IFS, and STAI-S scores as independent covariates. These analyses were based on a Bayesian Test for a Deficit allowing for Covariates (BTD-Cov) when Crawford's *t*-test was applied, and a Bayesian Standardized Difference Test allowing for Covariates (BSDT-Cov) when the RSDT was applied (Crawford et al., 2011). Effect sizes obtained from these methods are reported as point estimates (Z_{CCC} and Z_{DCCC} for covaried results from the modified *t*-test and RSDT, respectively), as suggested in a previous study (Crawford et al., 2010). In all analyses, alpha levels were set at $p < 0.05$.

RESULTS

Cognitive Status, Executive Functions, and State Anxiety Level

No significant differences emerged between the patient and controls in the MoCA, the IFS battery, or the STAI-S (**Table 1**). Therefore, the patient showed no cognitive deficits or abnormal anxiety levels.

Semantic Performance: Accuracy Results

Compared to controls, the patient exhibited normal accuracy on the PPT test ($t = -0.09$, $Z_{CC} = -0.09$, $p = 0.93$), with a marked impairment on the KDT ($t = -8.41$, $Z_{CC} = -8.94$, $p < 0.001$). This differential pattern remained after covarying for MoCA (PPT: $Z_{CCC} = -0.1$, $p = 0.94$; KDT: $Z_{CCC} = -10.18$, $p < 0.001$),

TABLE 1 | Overall cognitive profile and anxiety levels.

	Patient	Controls (*n* = 8)	*p*-value	*t*-value	z_{CC}
MoCA	26	27.13 (1.64)	0.54	−0.65	−0.69
IFS	17	24 (3.96)	0.14	−1.68	−1.77
STAI-S	35	33.25 (6.14)	0.78	0.27	0.29

Standard deviations are indicated between parentheses. MoCA, Montreal Cognitive Assessment (Nasreddine et al., 2005); IFS, INECO Frontal Screening battery (Torralva et al., 2009); STAI-S, state version of the State Trait Anxiety Inventory (Spielberger et al., 1970). Statistical analyses were conducted with Crawford's modified t-test (Crawford and Howell, 1998; Crawford and Garthwaite, 2002).

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[1] http://www.u.arizona.edu/~kforster/dmdx/dmdx.htm

IFS (PPT: $Z_{CCC} = -0.41$, $p = 0.78$; KDT: $Z_{CCC} = -8.84$, $p < 0.001$). and STAI-S (PPT: $Z_{CCC} = -0.19$, $p = 0.88$; KDT: $Z_{CCC} = -9.74$, $p < 0.001$) scores (**Figure 1, panel B1**). Also, a comparison of between-task differences (KDT minus PPT) highlighted the markedly differential outcome for the patient in the KDT ($t = 5.29$, $Z_{DCC} = 6.51$, $p = 0.001$) and corroborated their independence from general cognitive skills (MoCA: $Z_{DCCC} = 7.5$, $p = 0.005$), executive functions (IFS: $Z_{DCCC} = 6.44$, $p = 0.01$), and state anxiety (STAI-S: $Z_{DCCC} = 7.71$, $p = 0.004$) (**Figure 1, panel B2**).

Semantic Performance: RT Results

Moreover, although RTs revealed no significant differences between the patient and controls on either the PPT test ($t = 0.58$, $Z_{CC} = 0.62$, $p = 0.59$) or the KDT ($t = -1.08$, $Z_{CC} = -1.15$, $p = 0.32$) (**Figure 1, panel B3**), analysis of between-task differences via Crawford's RSDT revealed a specific abnormality: whereas controls responded more slowly on the KDT than on the PPT test, no such difference was observed in the patient ($t = 4.08$, $Z_{DCC} = 5.58$, $p = 0.005$). This result, too, was uninfluenced by general cognitive skills (MoCA: $Z_{DCCC} = 13.47$, $p < 0.001$), executive functions (IFS: $Z_{DCCC} = 6.32$, $p = 0.01$), and state anxiety (STAI-S: $Z_{DCCC} = 7.44$, $p = 0.004$) (**Figure 1, panel B4**).

DISCUSSION

This is the first study examining explicit processing of action-related meanings and their integration with ongoing actions in a patient with extensive cerebellar damage. The patient exhibited a selective impairment of action semantics, relative to object semantics, together with a probable alteration of the predictable motor-semantic integration pattern observed in controls. Furthermore, both patterns remained after covarying for executive skills. Below we discuss these findings in turn, addressing their theoretical and clinical relevance.

Cerebellar Damage and Action Semantics

First, the patient showed selective deficits in processing action (as opposed to object) semantics. This highlights the role of the cerebellum in grounding movement-related meanings, arguably because of its critical role in motor function (Ramnani, 2006; Manto et al., 2012). In healthy subjects, action semantics is differentially related to activity in the primary motor and premotor cortices (Jirak et al., 2010; Vigliocco et al., 2011; García and Ibáñez, 2016a). Moreover, this domain is selectively affected by damage to those regions (Neininger and Pulvermüller, 2003) or to frontostriatal motor loops (García et al., 2016b, 2017a,b; Birba et al., 2017a). Our results extend these findings, showing that damage to the cerebellum, another critical motor hub, can also lead to selective deficits in action-semantic processing.

A previous report on action-verb processing in cerebellar ataxia revealed selective deficits in this category, even though more demanding lexical classes, such as abstract verbs, were preserved (García et al., 2016a). Of note, the latter study found this impairment through a lexical decision task, involving implicit semantic access. Our study shows that cerebellar damage can lead to action semantic deficits even in explicit picture-based tasks, suggesting that the cerebellum plays a crucial role in grounding action-related meanings irrespective of presentation modality (verbal vs. pictorial) or mode of access (implicit vs. explicit), as previously observed for other motor regions (Pulvermüller, 2005; Jirak et al., 2010; Birba et al., 2017a). Taken together, this finding supports the view that the cerebellum may play a transmodal role in the embodiment of action-related meanings (García and Ibáñez, 2016a; Birba et al., 2017a), alongside more general contributions to semantic processing at large (Booth et al., 2007; De Smet et al., 2007; Murdoch, 2010; Barton, 2012; Mariën et al., 2014).

Compatibly, in fact, a feasible interpretation of our RT results is that the patient was also impaired in motor-semantic integration, another relevant embodied domain (García and Ibáñez, 2014, 2016a). In healthy subjects, processing of effector-specific action meanings can predictably interfere with contiguous hand movements (as indexed by increased RTs). This has been shown in multiple experimental settings, including semantic decision via single-key presses (e.g., Dalla Volta et al., 2014), semantic congruency judgment paradigms (e.g., Bernardis and Gentilucci, 2006; Barbieri et al., 2009), and keyboard-based verb-copying tasks (García and Ibáñez, 2016b). However, in disorders characterized by motor-network atrophy, such as Parkinson's and Huntington's disease, systematic motor-semantic integration effects are abolished (Ibáñez et al., 2013; Cardona et al., 2014; Kargieman et al., 2014; Buccino et al., 2018), in the context of abnormal task-specific neural signatures (Melloni et al., 2015), and even before the onset of overt motor symptomatology (Kargieman et al., 2014). For example, in these populations, contrary to healthy controls, congruency between response-hand shape and the hand-position denoted by action verbs fails to significantly modulate RTs (Ibáñez et al., 2013; Cardona et al., 2014; Kargieman et al., 2014). Likewise, healthy individuals respond more slowly to stimuli involving motor affordances (i.e., pictures and words depicting graspable, as opposed to non-graspable, objects), but no such selective delay is observed in PD patients (Buccino et al., 2018). As proposed by (García and Ibáñez, 2018), these findings would show that motor-network atrophy disturbs the integration of manual movements with processing of action-related stimuli, due to a disruption of embodied mechanisms.

In line with this claim and its supporting evidence, our study offers the first indication that similar patterns could emerge upon damage to the cerebellum. Indeed, whereas manual responses in controls were slower for action than for object stimuli, no such interference was observed in the patient. Given that the same cerebellar regions are engaged by the execution and the observation of actions (Gazzola and Keysers, 2009), we surmise that joint recruitment of motor and action-semantic processes led to a competition for resources in controls, while such natural integrative dynamics became disturbed upon cerebellar damage in the patient. In fact, motor-network disruptions have been shown to result in the recruitment of alternative non-motor pathways during processing of action-related stimuli (Abrevaya et al., 2017), which warrants the possibility that similar abnormal grounding effects could be triggered by cerebellar compromise. In this sense, the cerebellum seems critical not only for the processing of action semantics *per se*, but also for the integration of action meanings with ongoing motoric behavior.

Admittedly, although the results support the proposed interpretation, other factors could be contributing to the observed patterns. First, larger RTs in the KDT than the PPT test in controls could be partially driven by differential stimulus-related demands in each task. Although both instruments are similar in structure and overall difficulty (Bak and Hodges, 2003), their respective images are not matched for fine-grained variables which could impact behavioral outcomes, such as visual complexity, familiarity, or age of acquisition – for examples from normative picture-based studies, see (Cycowicz et al., 1997; Manoiloff et al., 2010). Therefore, subtle differences in such variables may have partly contributed to the behavioral differences observed in controls. Second, the patient's pattern of more errors and faster RTs on the PPT test could also be influenced by a trade-off between speed and accuracy: should this task prove harder than the KDT, instruction-induced time pressure could have led the patient to respond more quickly than his actual processing speed requires, resulting in a greater propensity to errors. While these factors cannot be fully ruled out as partial contributors to the results, their impact is only speculative and could well run in parallel to (rather than in lieu of) the argued abolished action-interference effect, which has been previously reported in patients with motor-network damage (Buccino et al., 2018). Further research would be necessary to establish the relative role of these factors on the observed effects.

Of note, the two patterns of deficit exhibited by the patient emerged despite otherwise normal cognitive performance, and they survived after covariation with MoCA, IFS, and STAI-S scores. This indicates that both forms of embodied disturbances were not dependent on the patient's overall cognitive status, executive functioning, or state anxiety levels. Similar patterns have been observed in previous studies showing distinctive action-semantic deficits in Parkinson's (Bocanegra et al., 2015, 2017) and Huntington's (García et al., 2017b) disease, indicating that such impairments were *sui generis* (i.e., not secondary to domain-general dysfunctions). By the same token, our study suggests that action-semantic and motor-semantic-integration difficulties may emerge as *primary* manifestations not only following early damage to frontostriatal motor networks, but also to posterior motor hubs (in particular, the bilateral cerebellum).

Implications

Our work has theoretical and clinical implications. In the last decades, the cerebellum has been acknowledged as a key hub for adaptive control functions, including the modeling, prediction, and organization of motor, cognitive, and emotional behaviors (Schmahmann, 1991; Barton, 2012; Koziol et al., 2014; Guell et al., 2017). More particularly, sparse evidence has hinted to its role in semantic processing, through coarse-grained tasks such as word selection (Silveri and Misciagna, 2000; Murdoch, 2010) and story comprehension (Mar, 2011). However, as established in a recent consensus paper, the contributions of the cerebellum to semantic and other higher-order domains represent an "ongoing enigma" (Mariën et al., 2014). In light of our results, and considering current theoretical proposals (Barton, 2012), we propose that important theoretical breakthroughs can be made by studying cerebellar function from an embodied perspective.

Anticipatory control loops in the cerebellum have been implicated in the mental rehearsal and imagination of actions, as well as in the prediction of their distal and abstract consequences (Koziol et al., 2014). Among other things, these processes would support the simulation (Jeannerod, 2001; Hesslow, 2002) and emulation (Grush, 2004) of bodily states, as tacitly assumed by recent models characterizing the prediction and understanding of external events (Schubotz, 2007). These general findings broadly support the view that the cerebellum plays a distinct role in grounding action-specific meanings. However, no specific proposals have been advanced in such a direction, arguably because there is no consensus on the role of motor and non-motor cerebellar regions in processing action-related rules (Balsters and Ramnani, 2008; Koziol et al., 2014).

In light of our results, we propose that the cerebellum could constitute a key hub in the vast motor-preferential network supporting the embodiment of action meanings (García and Ibáñez, 2016a; García et al., 2016a). Notably, most neuroanatomical models of action semantics (Pulvermüller, 2005, 2018; Garagnani and Pulvermüller, 2016) emphasize the putative role of cortical motor regions, failing to acknowledge the contributions of subcortical and cerebellar motor hubs. This may largely be the case because several relevant studies have found cerebellar activity but failed to include it in their discussions or accompanying summary diagrams (Decety and Grèzes, 1999; Shapiro et al., 2005; Lauro et al., 2013), and because relevant lesion models of damage to subcortical motor regions have been overlooked in the field (Birba et al., 2017a). However, as shown by present results, previous evidence of action-language deficits following cerebellar atrophy (García et al., 2016a), and even some imaging studies of action semantics including results from the cerebellum (Saccuman et al., 2006; Rüschemeyer et al., 2007; Boulenger et al., 2009), the embodied foundations of action semantics may span across any and all regions subserving motor function.

This proposal also entails clinical implications. On the assumption that the contributions of the cerebellum to higher-order processes were restricted to managing novel situations, organizing responses or creating linguistic strategies (Copland et al., 2000), various authors have proposed that deficits triggered by cerebellar damage could be more accurately detected and characterized through assessments of complex domain-general processes (Murdoch, 2010). While such approaches are certainly useful, here we propose that more fine-grained examinations targeting specific semantic categories (in particular, those alluding to bodily motion) could represent a novel clinical alternative. Indeed, the very combination of tasks used in this study has revealed deficits in early (Bocanegra et al., 2015) and even preclinical (García et al., 2017b) stages of motor disorders characterized by subcortical motor-network atrophy.

Building on the notion that deficits in both action semantics and motor-language coupling could constitute sensitive biomarkers of frontostriatal motor loops (Ibáñez et al., 2013;

García and Ibáñez, 2014; Birba et al., 2017a), our findings suggest that relevant tasks could also reveal subtle and primary signatures of cerebellar damage. In this sense, embodied semantic tasks could emerge as robust transdiagnostic tools for detecting early motor-network disruptions, irrespective of lesion site or etiology. However, replication and normative studies are needed to directly test this possibility.

LIMITATIONS AND SUGGESTIONS FOR FURTHER RESEARCH

Two main limitations must be recognized in this work. First, the control sample had a modest size. However, our tests are considered robust with small control groups (∼5 subjects) (Crawford and Howell, 1998), as attested by previous single-case studies yielding robust findings with similar or even smaller control-sample sizes (Bak et al., 2006; García et al., 2016a, 2017c; Birba et al., 2017b), or even in the absence of control groups (Caramazza and Hillis, 1991; Silveri et al., 1998; Berndt and Haendiges, 2000). Second, our assessment was restricted to a single cognitive task, whereas the explored domains manifest in multiple ways. Notwithstanding, note that the KDT and the PPT test have shown good sensitivity for revealing differential and selective deficits in other pathologies (Bak and Hodges, 2004; Kargieman et al., 2014; Bocanegra et al., 2015; Tsermentseli et al., 2016; García et al., 2017b,d), which attests to their empirical relevance.

Looking forward, although single cases are crucial to determine potential links between cognitive impairments and neuroanatomical injuries (Dubois and Adolphs, 2016), future studies should test the replicability of our results in a broad population of cerebellar patients. In particular, regression models could be implemented between semantic performance and structural or functional neural correlates, with a view to identifying specific cerebellar regions implicated in action semantics. This could illuminate the controversy regarding the contributions of motor and non-motor portions of the cerebellum to processing of action-related information (Balsters and Ramnani, 2008; Koziol et al., 2014). Also, given that the cerebellum and the basal ganglia have profuse connections with classical language areas (Booth et al., 2007), assessment of structural and functional connectivity in patients with cerebellar damage could reveal the putative basis of potential embodied deficits, as revealed by relevant behavioral tasks. Finally, a comparison of action-semantic processing between cerebellar and non-cerebellar models of motor-network lesions could reveal informative dissociations and inform fine-grained models of embodied cognition.

CONCLUSION

This study offers unprecedented evidence that cerebellar damage could alter explicit processing of action-related meanings and their integration with ongoing actions. These findings illuminate the relatively unexplored semantic functions of this region while calling for extensions of motor cognition models. Moreover, as previously shown in other movement disorders, embodied semantic tasks also offer promising alternatives for detecting early motor-network disruptions upon cerebellar damage. In this sense, the study of cerebellar contributions to action-semantic processing may afford a fruitful overarching framework for future basic and applied research in cognitive neuroscience.

AUTHOR CONTRIBUTIONS

AG, AI, and LS conceived the study. SA, MMC, and GK collected the data. SC, EM, JF, and AG analyzed the data. SA and SC designed **Figure 1**. SC and AG wrote the manuscript. AI and LS provided critical revisions on the successive drafts. All authors approved the manuscript in its final form.

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REFERENCES

Abrevaya, S., Sedeño, L., Fitipaldi, S., Pineda, D., Lopera, F., Buritica, O., et al. (2017). The road less traveled: alternative pathways for action-verb processing in Parkinson's disease. *J. Alzheimers Dis.* 55, 1429–1435. doi: 10.3233/JAD-160737

Baez, S., Couto, B., Herrera, E., Bocanegra, Y., Trujillo-Orrego, N., Madrigal-Zapata, L., et al. (2013). Tracking the cognitive, social, and neuroanatomical profile in early neurodegeneration: type III Cockayne syndrome. *Front. Aging Neurosci.* 5:80. doi: 10.3389/fnagi.2013.00080

Bak, T. H., and Hodges, J. R. (2003). Kissing and dancing—a test to distinguish the lexical and conceptual contributions to noun/verb and action/object dissociation. Preliminary results in patients with frontotemporal dementia. *J. Neurolinguist.* 16, 169–181. doi: 10.1016/S0911-6044(02)00011-8

Bak, T. H., and Hodges, J. R. (2004). The effects of motor neurone disease on language: further evidence. *Brain Lang.* 89, 354–361. doi: 10.1016/S0093-934X(03)00357-2

Bak, T. H., Yancopoulou, D., Nestor, P. J., Xuereb, J. H., Spillantini, M. G., Pulvermüller, F., et al. (2006). Clinical, imaging and pathological correlates of a hereditary deficit in verb and action processing. *Brain* 129, 321–332. doi: 10.1093/brain/awh701

Balsters, J. H., and Ramnani, N. (2008). Symbolic representations of action in the human cerebellum. *Neuroimage* 43, 388–398. doi: 10.1016/j.neuroimage.2008.07.010

Barbieri, F., Buonocore, A., Volta, R. D., and Gentilucci, M. (2009). How symbolic gestures and words interact with each other. *Brain Lang.* 110, 1–11. doi: 10.1016/j.bandl.2009.01.002

Barnes, L. L., Harp, D., and Jung, W. S. (2002). Reliability generalization of scores on the Spielberger state-trait anxiety inventory. *Educ. Psychol. Meas.* 62, 603–618. doi: 10.1177/0013164402062004005

Barton, R. A. (2012). Embodied cognitive evolution and the cerebellum. *Phil. Trans. R. Soc. B* 367, 2097–2107. doi: 10.1098/rstb.2012.0112

Bernardis, P., and Gentilucci, M. (2006). Speech and gesture share the same communication system. *Neuropsychologia* 44, 178–190. doi: 10.1016/j.neuropsychologia.2005.05.007

Berndt, R. S., and Haendiges, A. N. (2000). Grammatical class in word and sentence production: evidence from an aphasic patient. *J. Mem. Lang.* 43, 249–273. doi: 10.1006/jmla.2000.2726

Birba, A., García-Cordero, I., Kozono, G., Legaz, A., Ibáñez, A., Sedeño, L., et al. (2017a). Losing ground: frontostriatal atrophy disrupts language embodiment in Parkinson's and Huntington's disease. *Neurosci. Biobehav. Rev.* 80, 673–687. doi: 10.1016/j.neubiorev.2017.07.011

Birba, A., Hesse, E., Sedeño, L., Mikulan, E., García, M., Ávalos, J., et al. (2017b). Enhanced working memory binding by direct electrical stimulation of the parietal cortex. *Front. Aging Neurosci.* 9:178. doi: 10.3389/fnagi.2017.00178

Bocanegra, Y., García, A. M., Lopera, F., Pineda, D., Baena, A., Ospina, P., et al. (2017). Unspeakable motion: selective action-verb impairments in Parkinson's disease patients without mild cognitive impairment. *Brain Lang.* 168, 37–46. doi: 10.1016/j.bandl.2017.01.005

Bocanegra, Y., García, A. M., Pineda, D., Buriticá, O., Villegas, A., Lopera, F., et al. (2015). Syntax, action verbs, action semantics, and object semantics in Parkinson's disease: dissociability, progression, and executive influences. *Cortex* 69, 237–254. doi: 10.1016/j.cortex.2015.05.022

Booth, J. R., Wood, L., Lu, D., Houk, J. C., and Bitan, T. (2007). The role of the basal ganglia and cerebellum in language processing. *Brain Res.* 1133, 136–144. doi: 10.1016/j.brainres.2006.11.074

Boulenger, V., Hauk, O., and Pulvermüller, F. (2009). Grasping ideas with the motor system: semantic somatotopy in idiom comprehension. *Cereb. Cortex* 19, 1905–1914. doi: 10.1093/cercor/bhn217

Buccino, G., Dalla Volta, R., Arabia, G., and Morelli, M. (2018). Processing graspable object images and their nouns is impaired in Parkinson's disease patients. *Cortex* 100, 32–39. doi: 10.1016/j.cortex.2017.03.009

Buccino, G., Riggio, L., Melli, G., Binkofski, F., Gallese, V., and Rizzolatti, G. (2005). Listening to action-related sentences modulates the activity of the motor system: a combined TMS and behavioral study. *Brain Res. Cogn.* 24, 355–363.

Caramazza, A., and Hillis, A. E. (1991). Lexical organization of nouns and verbs in the brain. *Nature* 349, 788–790.

Cardona, J. F., Gershanik, O., Gelormini-Lezama, C., Houck, A. L., Cardona, S., Kargieman, L., et al. (2013). Action-verb processing in Parkinson's disease: new pathways for motor-language coupling. *Brain Struct. Funct.* 218, 1355–1373. doi: 10.1007/s00429-013-0510-1

Cardona, J. F., Kargieman, L., Sinay, V., Gershanik, O., Gelormini, C., Amoruso, L., et al. (2014). How embodied is action language? Neurological evidence from motor diseases. *Cognition* 131, 311–322. doi: 10.1016/j.cognition.2014.02.001

Copland, D. A., Chenery, H. J., and Murdoch, B. E. (2000). Persistent deficits in complex language function following dominant nonthalamic subcortical lesions. *J. Med. Speech Lang. Pathol.* 8, 1–14.

Couto, B., Salles, A., Sedeño, L., Peradejordi, M., Barttfeld, P., Canales-Johnson, A., et al. (2013a). The man who feels two hearts: the different pathways of interoception. *Soc. Cogn. Affect. Neurosci.* 9, 1253–1260. doi: 10.1093/scan/nst108

Couto, B., Sedeño, L., Sposato, L. A., Sigman, M., Riccio, P. M., Salles, A., et al. (2013b). Insular networks for emotional processing and social cognition: comparison of two case reports with either cortical or subcortical involvement. *Cortex* 49, 1420–1434. doi: 10.1016/j.cortex.2012.08.006

Crawford, J. R., and Garthwaite, P. H. (2002). Investigation of the single case in neuropsychology: confidence limits on the abnormality of test scores and test score differences. *Neuropsychologia* 40, 1196–1208. doi: 10.1016/S0028-3932(01)00224-X

Crawford, J. R., and Garthwaite, P. H. (2005). Testing for suspected impairments and dissociations in single-case studies in neuropsychology: evaluation of alternatives using Monte Carlo simulations and revised tests for dissociations. *Neuropsychology* 19, 318–331. doi: 10.1037/0894-4105.19.3.318

Crawford, J. R., and Garthwaite, P. H. (2012). Single-case research in neuropsychology: a comparison of five forms of t-test for comparing a case to controls. *Cortex* 48, 1009–1016. doi: 10.1016/j.cortex.2011.06.021

Crawford, J. R., Garthwaite, P. H., and Howell, D. C. (2009). On comparing a single case with a control sample: an alternative perspective. *Neuropsychologia* 47, 2690–2695. doi: 10.1016/j.neuropsychologia.2009.04.011

Crawford, J. R., Garthwaite, P. H., and Porter, S. (2010). Point and interval estimates of effect sizes for the case-controls design in neuropsychology: rationale, methods, implementations, and proposed reporting standards. *Cogn. Neuropsychol.* 27, 245–260. doi: 10.1080/02643294.2010.513967

Crawford, J. R., Garthwaite, P. H., and Ryan, K. (2011). Comparing a single case to a control sample: testing for neuropsychological deficits and dissociations in the presence of covariates. *Cortex* 47, 1166–1178. doi: 10.1016/j.cortex.2011.02.017

Crawford, J. R., and Howell, D. C. (1998). Comparing an individual's test score against norms derived from small samples. *Clin. Neuropsychol.* 12, 482–486.

Cycowicz, Y. M., Friedman, D., Rothstein, M., and Snodgrass, J. G. (1997). Picture naming by young children: norms for name agreement, familiarity, and visual complexity. *J. Exp. Child Psychol.* 65, 171–237. doi: 10.1006/jecp.1996.2356

Dalla Volta, R., Fabbri-Destro, M., Gentilucci, M., and Avanzini, P. (2014). Spatiotemporal dynamics during processing of abstract and concrete verbs: an ERP study. *Neuropsychologia* 61, 163–174. doi: 10.1016/j.neuropsychologia.2014.06.019

De Smet, H. J., Baillieux, H., De Deyn, P. P., Mariën, P., and Paquier, P. (2007). The cerebellum and language: the story so far. *Folia Phoniatr. Logop.* 59, 165–170.

Decety, J., and Grèzes, J. (1999). Neural mechanisms subserving the perception of human actions. *Trends Cogn. Sci.* 3, 172–178. doi: 10.1016/S1364-6613(99)01312-1

Dogan, I., Tinnemann, E., Romanzetti, S., Mirzazade, S., Costa, A. S., Werner, C. J., et al. (2016). Cognition in Friedreich's ataxia: a behavioral and multimodal imaging study. *Ann. Clin. Transl. Neurol.* 3, 572–587. doi: 10.1002/acn3.315

Dubois, J., and Adolphs, R. (2016). Building a science of individual differences from fMRI. *Trends Cogn. Sci.* 20, 425–443. doi: 10.1016/j.tics.2016.03.014

Fabbro, F. (2000). Introduction to language and cerebellum. *J. Neurolinguist.* 13, 83–94. doi: 10.1016/S0911-6044(00)00005-1

Fernandino, L., Conant, L. L., Binder, J. R., Blindauer, K., Hiner, B., Spangler, K., et al. (2013a). Parkinson's disease disrupts both automatic and controlled processing of action verbs. *Brain Lang.* 127, 65–74. doi: 10.1016/j.bandl.2012.07.008

Fernandino, L., Conant, L. L., Binder, J. R., Blindauer, K., Hiner, B., Spangler, K., et al. (2013b). Where is the action? Action sentence processing in Parkinson's disease. *Neuropsychologia* 51, 1510–1517. doi: 10.1016/j.neuropsychologia.2013.04.008

Fischer, M. H., and Zwaan, R. A. (2008). Embodied language: a review of the role of the motor system in language comprehension. *Q. J. Exp. Psychol.* 61, 825–850. doi: 10.1080/17470210701623605

Garagnani, M., and Pulvermüller, F. (2016). Conceptual grounding of language in action and perception: a neurocomputational model of the emergence of category specificity and semantic hubs. *Eur. J. Neurosci.* 43, 721–737. doi: 10.1111/ejn.13145

García, A. M., Abrevaya, S., Kozono, G., Cordero, I. G., Córdoba, M., Kauffman, M. A., et al. (2016a). The cerebellum and embodied semantics: evidence from a case of genetic ataxia due to STUB1 mutations. *J. Med. Genet.* 54, 114–124. doi: 10.1136/jmedgenet-2016-104148

García, A. M., Bocanegra, Y., Herrera, E., Moreno, L., Carmona, J., Baena, A., et al. (2017a). Parkinson's disease compromises the appraisal of action meanings evoked by naturalistic texts. *Cortex* 100, 111–126. doi: 10.1016/j.cortex.2017.07.003

García, A. M., Bocanegra, Y., Herrera, E., Pino, M., Muñoz, E., Sedeño, L., et al. (2017b). Action-semantic and syntactic deficits in subjects at risk for Huntington's disease. *J. Neuropsychol.* doi: 10.1111/jnp.12120 [Epub ahead of print].

García, A. M., Carrillo, F., Orozco-Arroyave, J. R., Trujillo, N., Vargas Bonilla, J. F., Fittipaldi, S., et al. (2016b). How language flows when movements don't: an automated analysis of spontaneous discourse in Parkinson's disease. *Brain Lang.* 162, 19–28. doi: 10.1016/j.bandl.2016.07.008

García, A. M., and Ibáñez, A. (2014). Words in motion: motor-language coupling in Parkinson's disease. *Transl. Neurosci.* 5, 152–159. doi: 10.2478/s13380-014-0218-6

García, A. M., and Ibáñez, A. (2016a). A touch with words: dynamic synergies between manual actions and language. *Neurosci. Biobehav. Rev.* 68, 59–95. doi: 10.1016/j.neubiorev.2016.04.022

García, A. M., and Ibáñez, A. (2016b). Hands typing what hands do: action-semantic integration dynamics throughout written verb production. *Cognition* 149, 56–66. doi: 10.1016/j.cognition.2016.01.011

García, A. M., and Ibáñez, A. (2018). When embodiment breaks down: language deficits as novel avenues into movement disorders. *Cortex* 100, 1–7. doi: 10.1016/j.cortex.2017.12.022

García, A. M., Sedeño, L., Herrera Murcia, E., Couto, B., and Ibáñez, A. (2017c). A lesion-proof brain? Multidimensional sensorimotor, cognitive, and socio-affective preservation despite extensive damage in a stroke patient. *Front. Aging Neurosci.* 8:335. doi: 10.3389/fnagi.2016.00335

García, A. M., Sedeño, L., Trujillo, N., Bocanegra, Y., Gomez, D., Pineda, D., et al. (2017d). Language deficits as a preclinical window into Parkinson's disease: evidence from asymptomatic Parkin and Dardarin mutation carriers. *J. Int. Neuropsychol. Soc.* 23, 150–158. doi: 10.1017/S1355617716000710

García-Cordero, I., Sedeño, L., de la Fuente, L., Slachevsky, A., Forno, G., Klein, F., et al. (2016). Feeling, learning from and being aware of inner states: interoceptive dimensions in neurodegeneration and stroke. *Phil. Trans. R. Soc. B* 371:20160006. doi: 10.1098/rstb.2016.0006

García-Cordero, I., Sedeño, L., Fraiman, D., Craiem, D., de la Fuente, L. A., Salamone, P., et al. (2015). Stroke and neurodegeneration induce different connectivity aberrations in the insula. *Stroke* 46, 2673–2677. doi: 10.1161/STROKEAHA.115.009598

Gazzola, V., and Keysers, C. (2009). The observation and execution of actions share motor and somatosensory voxels in all tested subjects: single-subject analyses of unsmoothed fMRI data. *Cereb. Cortex* 19, 1239–1255. doi: 10.1093/cercor/bhn181

Glickstein, M., and Doron, K. (2008). Cerebellum: connections and functions. *Cerebellum* 7, 589–594. doi: 10.1007/s12311-008-0074-4

Gluhm, S., Goldstein, J., Brown, D., Van Liew, C., Gilbert, P. E., and Corey-Bloom, J. (2013). Usefulness of the Montreal cognitive assessment (MoCA) in Huntington's disease. *Mov. Disord.* 28, 1744–1747. doi: 10.1002/mds.25578

Grush, R. (2004). The emulation theory of representation: motor control, imagery, and perception. *Behav. Brain Sci.* 27, 377–396. doi: 10.1017/S0140525X04000093

Guell, X., Gabrieli, J. D., and Schmahmann, J. D. (2017). Embodied cognition and the cerebellum: perspectives from the dysmetria of thought and the universal cerebellar transform theories. *Cortex* 100, 140–148. doi: 10.1016/j.cortex.2017.07.005

Hesslow, G. (2002). Conscious thought as simulation of behaviour and perception. *Trends Cogn. Sci.* 6, 242–247. doi: 10.1016/S1364-6613(02)01913-7

Howard, D., and Patterson, K. E. (1992). *The Pyramids and Palm Trees Test: A Test of Semantic Access from Words and Pictures*. Bury St Edmunds: Thames Valley Test Company.

Ibáñez, A., Cardona, J. F., Dos Santos, Y. V., Blenkmann, A., Aravena, P., Roca, M., et al. (2013). Motor-language coupling: direct evidence from early Parkinson's disease and intracranial cortical recordings. *Cortex* 49, 968–984. doi: 10.1016/j.cortex.2012.02.014

Ito, M. (1993). Movement and thought: identical control mechanisms by the cerebellum. *Trends Neurosci.* 16, 448–450.

Ito, M. (2008). Control of mental activities by internal models in the cerebellum. *Nat. Rev. Neurosci.* 9, 304–313. doi: 10.1038/nrn2332

Jeannerod, M. (2001). Neural simulation of action: a unifying mechanism for motor cognition. *Neuroimage* 14, S103–S109. doi: 10.1006/nimg.2001.0832

Jirak, D., Menz, M. M., Buccino, G., Borghi, A. M., and Binkofski, F. (2010). Grasping language–a short story on embodiment. *Conscious. Cogn.* 19, 711–720. doi: 10.1016/j.concog.2010.06.020

Kargieman, L., Herrera, E., Baez, S., García, A. M., Dottori, M., Gelormini, C., et al. (2014). Motor–language coupling in Huntington's disease families. *Front. Aging Neurosci.* 6:122. doi: 10.3389/fnagi.2014.00122

Kotz, S. A., Schwartze, M., and Schmidt-Kassow, M. (2009). Non-motor basal ganglia functions: a review and proposal for a model of sensory predictability in auditory language perception. *Cortex* 45, 982–990. doi: 10.1016/j.cortex.2009.02.010

Koziol, L. F., Budding, D., Andreasen, N., D'Arrigo, S., Bulgheroni, S., Imamizu, H., et al. (2014). Consensus paper: the cerebellum's role in movement and cognition. *Cerebellum* 13, 151–177. doi: 10.1007/s12311-013-0511-x

Lauro, L. J. R., Mattavelli, G., Papagno, C., and Tettamanti, M. (2013). She runs, the road runs, my mind runs, bad blood runs between us: literal and figurative motion verbs: an fMRI study. *Neuroimage* 83, 361–371. doi: 10.1016/j.neuroimage.2013.06.050

Leritz, E., Loftis, C., Crucian, G., Friedman, W., and Bowers, D. (2004). Self-awareness of deficits in Parkinson disease. *Clin. Neuropsychol.* 18, 352–361. doi: 10.1080/1385404049052412

Manoiloff, L., Artstein, M., Canavoso, M. B., Fernandez, L., and Segui, J. (2010). Expanded norms for 400 experimental pictures in an Argentinean Spanish-speaking population. *Behav. Res. Methods* 42, 452–460. doi: 10.3758/brm.42.2.452

Manto, M., Bower, J. M., Conforto, A. B., Delgado-García, J. M., da Guarda, S. N. F., Gerwig, M., et al. (2012). Consensus paper: roles of the cerebellum in motor control—the diversity of ideas on cerebellar involvement in movement. *Cerebellum* 11, 457–487. doi: 10.1007/s12311-011-0331-9

Mar, R. A. (2011). The neural bases of social cognition and story comprehension. *Annu. Rev. Psychol.* 62, 103–134. doi: 10.1146/annurev-psych-120709-145406

Marcus, C. D., Galeon, M., Peruzzi, P., Bazin, A., Bernard, M. H., Pluot, M., et al. (1996). Lhermitte-Duclos disease associated with syringomyelia. *Neuroradiology* 38, 529–531. doi: 10.1007/BF00626089

Mariën, P., Ackermann, H., Adamaszek, M., Barwood, C. H., Beaton, A., Desmond, J., et al. (2014). Consensus paper: language and the cerebellum: an ongoing enigma. *Cerebellum* 13, 386–410. doi: 10.1007/s12311-013-0540-5

Melloni, M., Billeke, P., Baez, S., Hesse, E., De la Fuente, L., Forno, G., et al. (2016). Your perspective and my benefit: multiple lesion models of self-other integration strategies during social bargaining. *Brain* 139, 3022–3040. doi: 10.1093/brain/aww231

Melloni, M., Sedeño, L., Hesse, E., García-Cordero, I., Mikulan, E., Plastino, A., et al. (2015). Cortical dynamics and subcortical signatures of motor-language coupling in Parkinson's disease. *Sci. Rep.* 5:11899. doi: 10.1038/srep11899

Mercadillo, R. E., Galvez, V., Díaz, R., Hernández-Castillo, C. R., Campos-Romo, A., Boll, M. C., et al. (2014). Parahippocampal gray matter alterations in Spinocerebellar Ataxia Type 2 identified by voxel based morphometry. *J. Neurol. Sci.* 347, 50–58. doi: 10.1016/j.jns.2014.09.018

Murdoch, B. E. (2010). The cerebellum and language: historical perspective and review. *Cortex* 46, 858–868. doi: 10.1016/j.cortex.2009.07.018

Nasreddine, Z. S., Phillips, N. A., Bédirian, V., Charbonneau, S., Whitehead, V., Collin, I., et al. (2005). The Montreal Cognitive Assessment, MoCA: a brief screening tool for mild cognitive impairment. *J. Am. Ger. Soc.* 53, 695–699. doi: 10.1111/j.1532-5415.2005.53221.x

Neininger, B., and Pulvermüller, F. (2003). Word-category specific deficits after lesions in the right hemisphere. *Neuropsychologia* 41, 53–70. doi: 10.1016/S0028-3932(02)00126-4

Nowak, D. A., and Trost, H. A. (2002). Lhermitte–Duclos disease (dysplastic cerebellar gangliocytoma): a malformation, hamartoma or neoplasm? *Acta Neurol. Scand.* 105, 137–145. doi: 10.1034/j.1600-0404.2002.1r127.x

Orsi, L., D'Agata, F., Caroppo, P., Franco, A., Caglio, M. M., Avidano, F., et al. (2011). Neuropsychological picture of 33 spinocerebellar ataxia cases. *J. Clin. Exp. Neuropsychol.* 33, 315–325. doi: 10.1080/13803395.2010.518139

Pulvermüller, F. (2005). Brain mechanisms linking language and action. *Nat. Rev. Neurosci.* 6, 576–582. doi: 10.1038/nrn1706

Pulvermüller, F. (2018). Neural reuse of action perception circuits for language, concepts and communication. *Prog. Neurobiol.* 160, 1–44. doi: 10.1016/j.pneurobio.2017.07.001

Ramnani, N. (2006). The primate cortico-cerebellar system: anatomy and function. *Nat. Rev. Neurosci.* 7, 511–522. doi: 10.1038/nrn1953

Robinson, S., and Cohen, A. R. (2006). Cowden disease and Lhermitte–Duclos disease: an update: case report and review of the literature. *Neurosurg. focus* 20, 1–6.

Rüschemeyer, S. A., Brass, M., and Friederici, A. D. (2007). Comprehending prehending: neural correlates of processing verbs with motor stems. *J. Cogn. Neurosci.* 19, 855–865. doi: 10.1162/jocn.2007.19.5.855

Saccuman, M. C., Cappa, S. F., Bates, E. A., Arevalo, A., Della Rosa, P., Danna, M., et al. (2006). The impact of semantic reference on word class: an fMRI study of action and object naming. *Neuroimage* 32, 1865–1878. doi: 10.1016/j.neuroimage.2006.04.179

Schmahmann, J. D. (1991). An emerging concept: the cerebellar contribution to higher function. *Arch. Neurol.* 48, 1178–1187. doi: 10.1001/archneur.1991.00530230086029

Schubotz, R. I. (2007). Prediction of external events with our motor system: towards a new framework. *Trends Cogn. Sci.* 11, 211–218. doi: 10.1016/j.tics.2007.02.006

Sedeño, L., Couto, B., Melloni, M., Canales-Johnson, A., Yoris, A., Baez, S., et al. (2014). How do you feel when you can't feel your body? Interoception, functional connectivity and emotional processing in depersonalization-derealization disorder. *PLoS One* 9:e98769. doi: 10.1371/journal.pone.0098769

Shapiro, K. A., Mottaghy, F. M., Schiller, N. O., Poeppel, T. D., Flüß, M. O., Müller, H. W., et al. (2005). Dissociating neural correlates for nouns and verbs. *Neuroimage* 24, 1058–1067. doi: 10.1016/j.neuroimage.2004.10.015

Silveri, M. C., Di Betta, A. M., Filippini, V., Leggio, M. G., and Molinari, M. (1998). Verbal short-term store-rehearsal system and the cerebellum. Evidence from a patient with a right cerebellar lesion. *Brain* 121, 2175–2187. doi: 10.1093/brain/121.11.2175

Silveri, M. C., and Misciagna, S. (2000). Language, memory, and the cerebellum. *J. Neurolinguist.* 13, 129–143. doi: 10.1016/S0911-6044(00)00008-7

Spielberger, C. D., Gorsuch, R. L., and Lushene, R. E. (1970). *Manual for the Stait-Trait Anxiety Inventory*. Palo Alto, CA: Consulting Psychological Press.

Spielberger, C. D., Vagg, P. R., Barker, L. R., Donham, G. W., and Westberry, L. G. (1980). The factor structure of the state-trait anxiety inventory. *Stress Anxiety* 7, 95–109.

Tinaz, S., Courtney, M. G., and Stern, C. E. (2011). Focal cortical and subcortical atrophy in early Parkinson's disease. *Mov. Disord.* 26, 436–441. doi: 10.1002/mds.23453

Torralva, T., Roca, M., Gleichgerrcht, E., LOPez, P., and Manes, F. (2009). INECO Frontal Screening (IFS): a brief, sensitive, and specific tool to assess executive functions in dementia–CORRECTED VERSION. *J. Int. Neuropsychol. Soc.* 15, 777–786. doi: 10.1017/S1355617709990415

Tsermentseli, S., Leigh, P. N., Taylor, L. J., Radunovic, A., Catani, M., and Goldstein, L. H. (2016). Syntactic processing as a marker for cognitive impairment in amyotrophic lateral sclerosis. *Amyotroph. Lateral Scler. Frontotemporal Degener.* 17, 69–76. doi: 10.3109/21678421.2015.1071397

Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., et al. (2002). Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. *Neuroimage* 15, 273–289.

Vigliocco, G., Vinson, D. P., Druks, J., Barber, H., and Cappa, S. F. (2011). Nouns and verbs in the brain: a review of behavioural, electrophysiological, neuropsychological and imaging studies. *Neurosci. Biobehav. Rev.* 35, 407–426. doi: 10.1016/j.neubiorev.2010.04.007

Vukovic, N., Feurra, M., Shpektor, A., Myachykov, A., and Shtyrov, Y. (2017). Primary motor cortex functionally contributes to language comprehension: an online rTMS study. *Neuropsychologia* 96, 222–229. doi: 10.1016/j.neuropsychologia.2017.01.025

Zawacki, T. M., Grace, J., Friedman, J. H., and Sudarsky, L. (2002). Executive and emotional dysfunction in Machado-Joseph disease. *Mov. Disord.* 17, 1004–1010. doi: 10.1002/mds.10033

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The Neural Blending of Words and Movement: Event-Related Potential Signatures of Semantic and Action Processes during Motor–Language Coupling

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Abstract

■ Behavioral embodied research shows that words evoking limb-specific meanings can affect responses performed with the corresponding body part. However, no study has explored this phenomenon's neural dynamics under implicit processing conditions, let alone by disentangling its conceptual and motoric stages. Here, we examined whether the blending of hand actions and manual action verbs, relative to nonmanual action verbs and nonaction verbs, modulates electrophysiological markers of semantic integration (N400) and motor-related cortical potentials during a lexical decision task. Relative to both other categories, manual action verbs involved reduced posterior N400 amplitude and greater modulations of frontal motor-related cortical potentials. Such effects overlapped in a window of ~380–440 msec after word presentation and ~180 msec before response execution, revealing the possible time span in which both semantic and action-related stages reach maximal convergence. These results allow refining current models of motor–language coupling while affording new insights on embodied dynamics at large. ■

INTRODUCTION

One leading contribution of the embodied cognition framework (Moguilner et al., 2021; Pulvermüller, 2013a, 2018; de Vega, Moreno, & Castillo, 2013; Glenberg & Gallese, 2012; Barsalou, 2008) is the demonstration that language can variously affect overt behavior (Kogan, Muñoz, Ibáñez, & García, 2020; García & Ibáñez, 2016a; de Vega et al., 2013; Glenberg & Gallese, 2012). In particular, motor–language coupling paradigms show that action verbs can modulate movement-related mechanisms in an effector-specific fashion (Kogan et al., 2020; García & Ibáñez, 2016b). For example, in tasks requiring explicit semantic access, processing of manual action verbs (MaVs), compared to non-MaVs (nMaVs) and nonaction verbs (nAVs), can facilitate or delay diverse hand actions, such as keyboard typing (García & Ibáñez, 2016b) and object reaching (Dalla Volta, Gianelli, Campione, & Gentilucci, 2009). Yet, little is known about the neural dynamics underlying such limb-selective interactions, and no study has explored their emergence under implicit processing conditions—let alone by considering time-locked signatures of their conceptual and motoric subprocesses. To bridge this gap, we assessed whether the blending of hand actions and MaVs, relative to nMaVs and nAVs, can modulate electrophysiological markers of semantic integration and motor preparation in a shallow processing task, while examining the temporal overlap of both subprocesses.

Motor–language coupling is a bidirectional phenomenon whereby action–language processes affect motor dynamics, and vice versa (Afonso et al., 2019; Melloni et al., 2015; Ibáñez et al., 2013; Aravena et al., 2010). Behavioral experiments show that MaVs can increase grip force in both unimanual and bimanual tasks (Da Silva, Labrecque, Caromano, Higgins, & Frak, 2018; Nazir et al., 2017; Frak, Nazir, Goyette, Cohen, & Jeannerod, 2010),

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whereas neuroimaging studies show that these verbs differentially increase activation along partly somatotopic (hand-specific) cortical motor regions (Pulvermüller, 2013a, 2018). Yet, only limited research has examined the neurofunctional unfolding of motor–language coupling, mainly using overtly semantic tasks. In particular, manual responses to MaVs have been linked to early engagement of motor and premotor regions (Mollo, Pulvermüller, & Hauk, 2016; Klepp, Niccolai, Buccino, Schnitzler, & Biermann-Ruben, 2015; Pulvermüller, Härle, & Hummel, 2001), fast modulation of motor-evoked potentials (Gianelli & Dalla Volta, 2015; Papeo, Vallesi, Isaja, & Rumiati, 2009; Buccino et al., 2005), and reduced synchronization of movement-sensitive beta oscillations (Klepp et al., 2015). Moreover, during explicit semantic access, this functional synergy is typified by canonical neural signatures of both semantic integration (Ibáñez et al., 2013; Aravena et al., 2010) and action initiation (Melloni et al., 2015; Ibáñez et al., 2013; Aravena et al., 2010), irrespective of task accomplishment (Dalla Volta, Avanzini, De Marco, Gentilucci, & Fabbri-Destro, 2018). Thus, the dynamic neural signatures of motor–language coupling are fairly well established for tasks that overtly direct attention to word meanings.

However, this empirical corpus faces two critical shortcomings. First, none of these studies examined whether such effects also emerge under shallow-processing conditions, thus overlooking a key requisite to reveal primary embodied effects (García et al., 2019; Mollo et al., 2016; Kiefer, Sim, Herrnberger, Grothe, & Hoenig, 2008; Hauk, Johnsrude, & Pulvermüller, 2004). Second, relevant EEG research (Dalla Volta et al., 2018; Melloni et al., 2015; Ibáñez et al., 2013; Aravena et al., 2010) has failed to assess whether canonical markers of semantic integration and action planning during effector-specific (e.g., manual) movements are differentially sensitive to effector-congruent meanings (e.g., by contrasting MaVs with nMaVs). Promisingly, these shortcomings can be overcome by comparing how implicit semantic processing of different action-verb types during motor–language coupling modulates functionally critical event-related potentials (ERPs), such as the N400 and motor-related cortical potentials (MRCPs).

The N400 is a negative deflection peaking at approximately 400 msec after word presentation, with a centro-parietal scalp distribution (Lau, Phillips, & Poeppel, 2008). N400 modulations are a gold-standard signature of conceptual integration demands during processing of sentences, paired words, or even single words (Kutas & Federmeier, 2000, 2011; Lau et al., 2008). For their part, MRCPs comprise two primary (premovement) components (Castro, Díaz, & van Boxtel, 2005; Kutas & Donchin, 1980; Deecke, Scheid, & Kornhuber, 1969), which are typically maximal in central/fronto-central sites (Nguyen, Breakspear, & Cunnington, 2014; Smith & Staines, 2006) with sources in sensorimotor regions (Shibasaki & Hallett, 2006; Toma et al., 2002; Yazawa et al., 2000), namely, the readiness potential (RP), a slow-rising negativity that precedes movement onset by 100–400 msec in forced-choice tasks (Travers, Khalighinejad, Schurger, & Haggard, 2020; Haggard, 2008; Kutas & Donchin, 1980), and the motor potential (MP), a subsequent sharply negative peak occurring immediately before (−100 to −10 msec) the response (Shibasaki & Hallett, 2006; Deecke et al., 1969). Both these components are canonical indexes of increased sensorimotor cortical excitability during motor preparation (Shibasaki & Hallett, 2006; Toma et al., 2002; Yazawa et al., 2000; Deecke et al., 1969). Importantly, reduced N400 amplitude (Ibáñez et al., 2013; Aravena et al., 2010) and increased MRCP modulations (Melloni et al., 2015; Ibáñez et al., 2013; Aravena et al., 2010) have been shown to index compatibility between MaVs and (compatible) manual responses during explicit semantic tasks. Therefore, these ERPs emerge as suitable candidates to track movement-related and conceptual dimensions of implicit motor–language coupling.

Against this background, we employed high-density EEG (HD-EEG) to identify core neural signatures of semantic and motoric dynamics during motor–language coupling under implicit semantic processing conditions. We designed a lexical decision task requiring manual responses to MaVs, nMaVs, and nAVs. Building on previous findings (Ibáñez et al., 2013; Aravena et al., 2010), we predicted that MaVs would involve reduced N400 modulations relative to response-incongruent verb types (nMaVs and nAVs). Moreover, considering relevant evidence (Melloni et al., 2015; Ibáñez et al., 2013; Aravena et al., 2010), we predicted that MaVs would enhance the amplitude of MRCPs during manual response preparation. In addition, to ascertain the period of maximal semantic–motoric integration, we aimed to identify the temporal overlap between effector-specific modulations in both ERPs. Furthermore, on the basis of emergent results in the motor–language coupling literature (Klepp et al., 2015), we performed an exploratory analysis of stimulus- and response-locked time–frequency modulations over the beta band. Briefly, with this novel approach, the present work seeks to illuminate the functional underpinnings of semantic and action dimensions in implicit motor–language coupling.

METHODS

Participants

The study was composed of 22 participants (13 women), a sample size that reaches a power of 0.93. All participants were adult native Spanish speakers who were enrolled in or had completed higher education programs. The sample had a mean age of 25.9 (*SD* = 4.7) years and an average of 17.1 years of education (*SD* = 3.5 years). All but two participants were exclusively right-handed. None of the participants reported a history of neuropsychiatric diseases or substance abuse, and all had normal or corrected-to-normal vision. Each participant read and signed an informed consent form before entering the study. All experiments and procedures were performed in accordance with relevant guidelines and regulations of the Declaration of Helsinki. The study's protocols were approved by the institutional ethics committee.

Stimuli

This study used 75 verbal stimuli belonging to four categories. Sixty items were real Spanish words, including 20 MaVs, denoting actions performed with the hands (e.g., *cut* [*cortar*]); 20 nMaVs, denoting actions performed with body parts other than the hands (e.g., *walk* [*caminar*]); and 20 nAVs, denoting cognitive or affective processes that do not involve bodily motion (e.g., *improve* [*mejorar*]). All these items appeared in infinitive form (most of them ending in *-ar*), which forced their interpretation as verbs. Finally, the task included 15 pseudoverbs (PsVs). These were created by choosing five real words from each list and replacing only one letter such that the resulting letter string, although phonotactically and graphotactically legal, did not represent a Spanish word (e.g., *coltar*, *capinar*, *meborar*).

Psycholinguistic data for all stimuli were extracted from B-Pal (Davis & Perea, 2005), except for age-of-acquisition data, which were taken from a survey used in previous motor–language coupling research (Kogan et al., 2020; García & Ibáñez, 2016b). One-way ANOVA tests showed that all categories were similar in log frequency, $F(2, 57) = 0.39$, $p = .68$, familiarity, $F(2, 57) = 0.21$, $p = .82$, orthographic length, $F(2, 57) = 0.58$, $p = .56$, imageability, $F(2, 57) = 1.2823$, $p = .28$, and age of acquisition, $F(2, 57) = 1.01$, $p = .37$. As in previous motor–language coupling experiments, all items had four to eight letters; this guaranteed that all of them could be visualized in a single fixation, so that the time needed for their recognition would remain constant across categories (Lavidor & Ellis, 2002; Weekes, 1997). As expected, an additional test revealed significant differences in concreteness, $F(2, 57) = 18.974$, $p < .001$, among categories. A post hoc analysis (Tukey's honestly significant difference test, $MSE = 0.30156$, $df = 57$) corroborated that nAVs were less concrete than both MaVs ($p < .001$) and nMaVs ($p < .001$), as expected; crucially, however, no significant differences were observed between the latter two categories ($p = .36$).

Procedure

Participants were tested individually in a dimly illuminated room. They sat comfortably at a desk, facing a laptop equipped with a 15.6-in. 16:9 HD (1366 × 768) LED backlight. As the HD-EEG electrodes were being placed on their scalps, they received oral instructions on the lexical decision task (instructions were then recapped on-screen before the start of the experiment).

The task was composed of three blocks of 75 trials. Each trial consisted of the presentation of a single stimulus belonging to one of the four categories (MaVs, nMaVs, nAVs, or PsVs). As in previous studies (García et al., 2019), PsVs were irrelevant for brain-signal analyses, but they served to ensure task compliance and attentional engagement by forcing linguistic decisional processes item after item. Each block included the same stimuli but in different pseudorandomized sequences (no more than three stimuli from the same category appeared in succession, and real words linked by meaning or form were separated by at least three trials). As in previous research (García et al., 2020), this allowed maximizing signal-to-noise ratio while retaining a strict control of psycholinguistic variables across conditions. Participants had to decide, as quickly and accurately as possible, whether the string constituted a real Spanish word or not by pressing the left arrow with the index finger or the right arrow with the middle finger of their right hand, respectively.

Each trial began with a fixation cross shown for a random period between 700 and 1000 msec at the center of the screen. Immediately afterward, the target item (verb or PsV) was shown until response and for a maximum of 2300 msec, with responses being allowed after the first 300 msec. A new trial was triggered upon the participant's button press or if the trial's overall duration elapsed without a response (Figure 1A). The use of a random period for the fixation cross minimized the chances of responses being driven by rhythmic motor habituation, with no biases for any lexical category. The fixation cross and the targets (font: Microsoft Sans Serif; color: white; size: 48; style: regular) were presented at the center of the screen against a black background. A custom-made script written in MATLAB's (The MathWorks) Psychtoolbox was used to run the task and record behavioral responses (see below for details about simultaneous HD-EEG data acquisition). Before the actual task, 10 practice trials were presented with stimuli not included in the experimental blocks. The complete session for each participant lasted roughly 30 min.

Behavioral Data Analysis

Accuracy and RT data were analyzed via a linear mixed model, with Category as a fixed factor and Participant as a random factor. As in previous EEG studies on action-verb processing (Mollo et al., 2016; Pulvermüller et al., 2001), trials with RTs falling 2 *SD*s away from each participant's mean were considered outliers and removed from analysis. All analyses were performed on MATLAB (R2015a) software.

HD-EEG Data Acquisition and Processing

HD-EEG data were acquired with a Biosemi ActiveTwo 128-channel system at 2048 Hz, resampled offline at 256 Hz. The EEGLAB (13.4.4b) toolbox (Delorme & Makeig, 2004) was used for offline processing and analysis. Three participants were excluded from analysis because of data acquisition problems. For all remaining participants, data were band-pass filtered during recording (0.1–100 Hz) and offline (0.5–40 Hz) to remove undesired frequency components. The latter

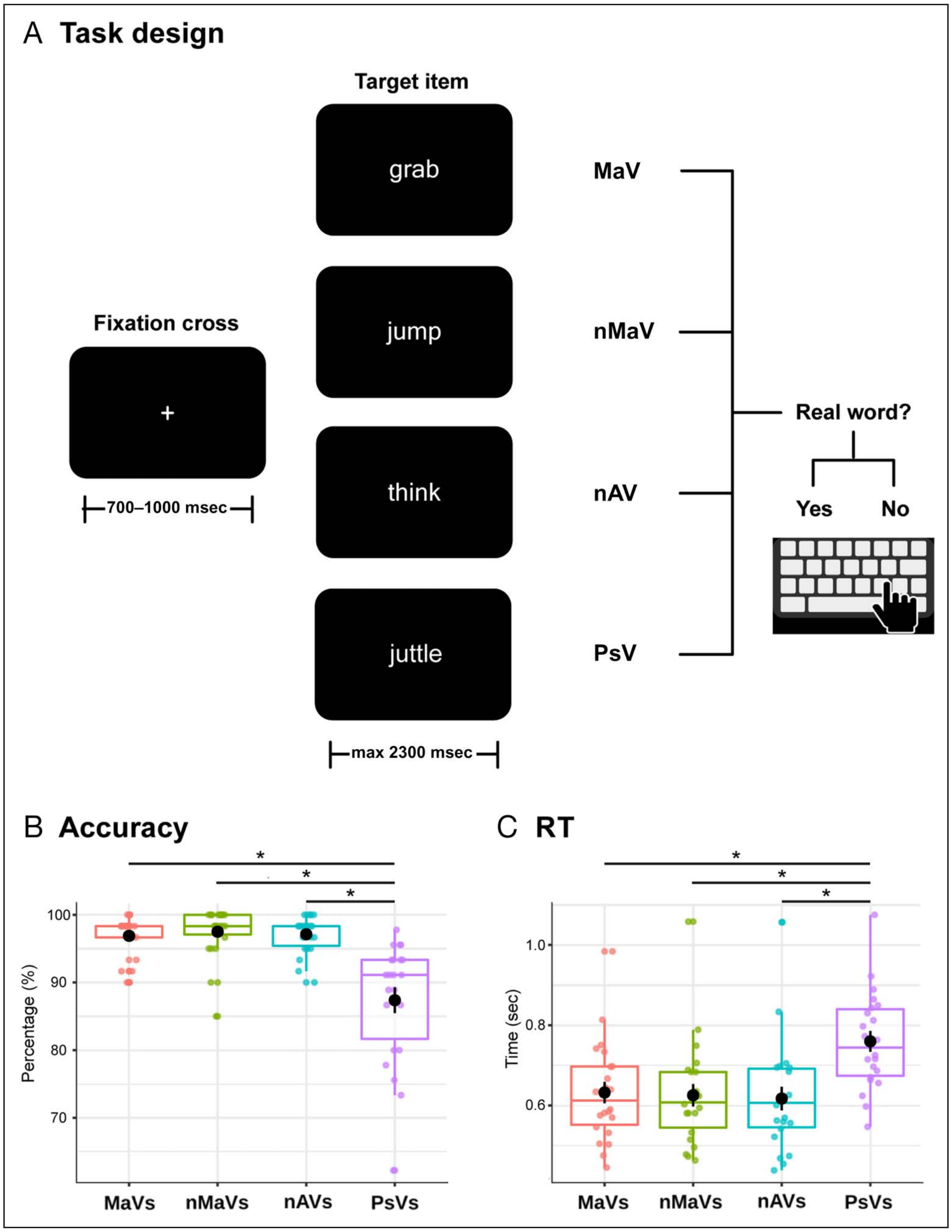

Figure 1. Lexical decision task and behavioral results. (A) Participants viewed a fixation cross, followed by a target item belonging to any of four categories: MaVs, non-MaVs, nAVs, and PsVs. In each trial, participants had to decide whether the target item was a real word or not. Verbs from each category have been translated into English for illustrative purposes. (B and C) Accuracy and RT outcomes. Circles represent each participant's score per category. The large black dot represents the mean of each condition. Asterisks indicate significant differences. Participants were significantly less accurate and slower responding to PsVs than to all real-verb categories, there being no differences among the latter.

cutoff (40 Hz) was based on gold-standard recommendations to maximize data quality and temporal precision (Cohen, 2014) and to favor comparability with ERP studies on motor responses (Gentili et al., 2018; Fabi & Leuthold, 2017; Kadosh et al., 2007), action-verb processing (Sokoliuk, Calzolari, & Cruse, 2019; Casado et al., 2018), and other embodied language categories (García et al., 2020; Daly et al., 2019; Gentsch, Sel, Marshall, & Schütz-Bosbach, 2019).

References for N400 and MRCP analyses were selected based on gold-standard recommendations (Luck, 2014) to maximize comparability with key studies in the field. N400 analyses were referenced to link mastoids and then rereferenced offline to the average of all electrodes, as done in previous studies on motor–language coupling (Aravena et al., 2010) and semantic effects at large (Kutas & Donchin, 1980; Lim et al., 2009). In addition, given the posterior topography of canonical N400 modulations (Kutas & Federmeier, 2011) and the location of our ROIs, especially in a dense-array setting like ours, this procedure guarantees a reference-independent estimation of scalp voltage for this ERP (Nunez & Srinivasan, 2006). Instead, signals for MRCP analyses were referenced to link mastoids, a common choice across embodied cognition studies targeting MRCPs and other response-locked ERPs (Wang et al., 2019; Melloni et al., 2015; Guan, Meng, Yao, & Glenberg, 2013; Santana & de Vega, 2013; Senderecka, Grabowska, Szewczyk, Gerc, & Chmylak, 2012; Aravena et al., 2010; Smith & Staines, 2006; Falkenstein, Hoormann, & Hohnsbein, 1999), including those which also tap on N400 effects by common average reference

(Aravena et al., 2010). Importantly, mastoid reference also meets other gold-standard requisites (Luck, 2014) for MRCP analyses, as they offer a low electrical activity site away from the frontal ROIs capturing maximal effects (Nguyen et al., 2014; Smith & Staines, 2006) while avoiding hemispheric bias and reducing noise (e.g., Nguyen et al., 2014; Kutas & Donchin, 1980). All subsequent processing steps were identical for both components.

In line with reported procedures (Dottori et al., 2020; Fittipaldi et al., 2020; García et al., 2020; Vilas et al., 2019; Salamone et al., 2018), eye movements or blink artifacts were corrected with independent component analysis, and remaining artifacts were rejected offline from trials that contained voltage fluctuations exceeding ±200 μV. Bad channels were identified via visual inspection by two experts (S. C. and A. P.) following the exact same approach used by our team in previous EEG studies on semantic and motoric processes (Dottori et al., 2017, 2020; Vilas et al., 2019; Yoris et al., 2017; García-Cordero et al., 2016; Melloni et al., 2015; Ibáñez et al., 2010, 2013; Aravena et al., 2010). Once identified, such channels were replaced with statistically weighted spherical interpolation (based on all sensors), and then the variance of the signal across trials was calculated to guarantee stability of the averaged waveform (Courellis, Iversen, Poizner, & Cauwenberghs, 2016). HD-EEG data were then segmented offline into 1.5-sec epochs extending from 500 msec prestimulus to 1000 msec poststimulus for stimulus-locked segments in N400 analyses (where Time 0 corresponds to stimulus onset) and for hand response-locked segments in MRCP analyses (where Time 0 corresponds to motor response execution). The epochs were baseline-corrected, using a baseline of −300 to 0 msec for the N400 component and −600 to −300 msec for motor responses. Noisy epochs were rejected from the analysis using a visual inspection procedure as in previous studies (García-Cordero et al., 2016).

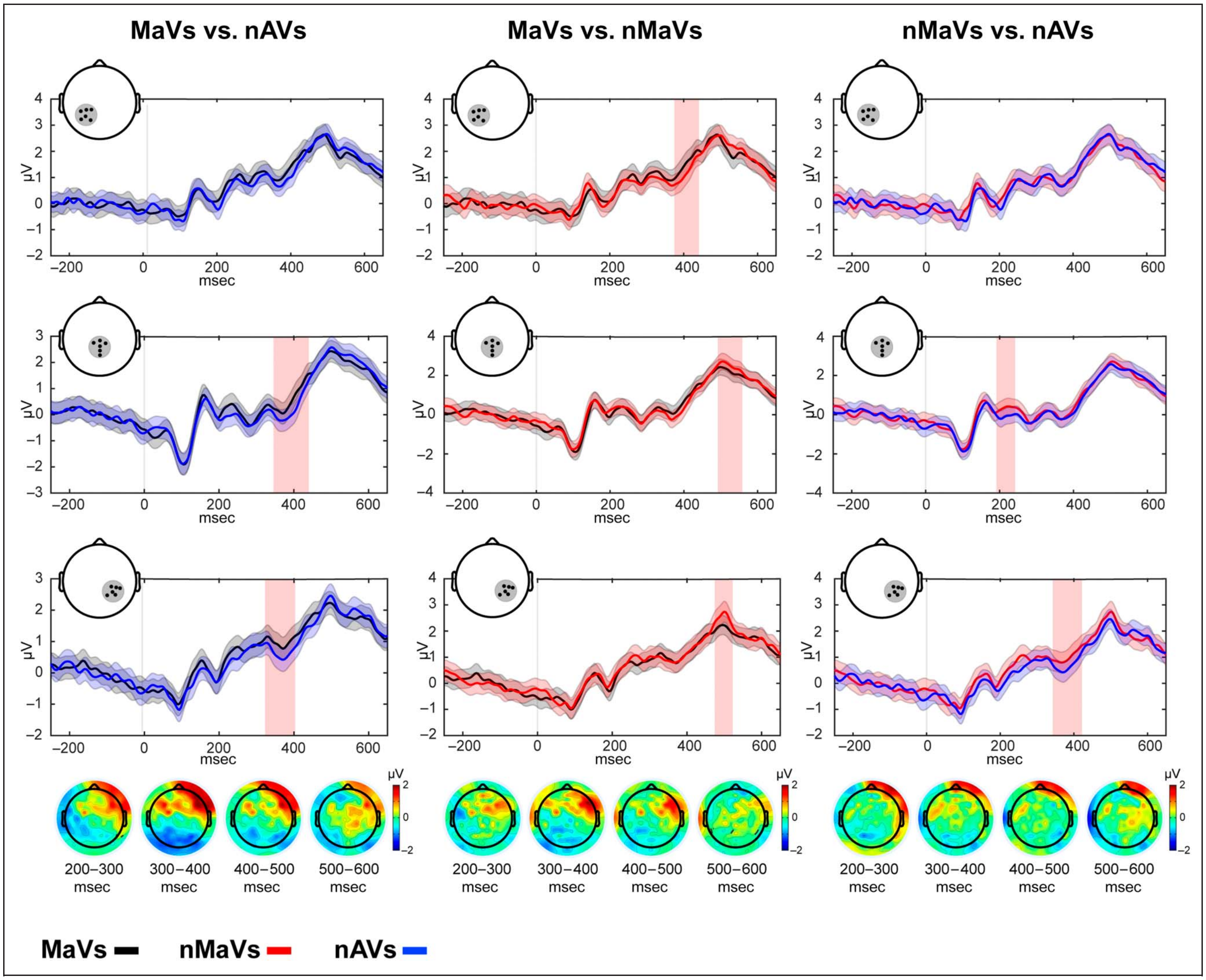

Figure 2. Electrophysiological markers of semantic integration (N400) effects during motor–language coupling. The topoplots show average modulations, locked to stimulus onset, within a canonical 350- to 450-msec window over the left (A), medial (B), and right (C) centro-posterior ROIs for MaVs (black line), nMaVs (red line), and nAVs (blue line). The baseline ranged from −300 to 0 msec before stimulus onset. Shadowed bars around the lines indicate standard errors. Vertical pink bars indicate significant differences at $p < .05$ (with a threshold of at least 10 contiguous points).

ERP Data Analysis

Analyses of N400 and MRCP modulations were performed considering only correct trials. As regards N400 analysis, upon removal of incorrect or artifactual trials, the number of remaining epochs averaged across participants was 47.4 (78.9%) for MaVs, 47 (78.3%) for nMaVs, and 49.6 (82.6%) for nAVs, $F(2, 54) = 0.74$, $p = .48$. In addition, after removal of incorrect trials and faulty segments, the number of MRCP-related epochs, averaged across participants, was 51.6 (86%) for MaVs, 52.3 (87.2%) for nMaVs, 53.5 (89.1%) for nAVs, and 35.5 (78.9%) for PsVs. The number of epochs analyzed did not differ significantly between categories, $F(2, 54) = 1.06$, $p = .35$.

N400 analyses were conducted over three canonical six-electrode ROIs, as reported in previous studies (Manfredi, Cohn, & Kutas, 2017; Schmidt-Snoek, Drew, Barile, & Agauas, 2015; Lim et al., 2009; Wu & Coulson, 2005), namely, a centro-posterior ROI (Channels A2, A3, A4, A19, D16, and B2), a left posterior ROI (Channels A5, A6, A7, D16, D17, and D28), and a right posterior ROI (Channels A32, B3, B4, B16, B18, and B19; Figure 2). Of note, these regions have proven sensitive to various semantic manipulations in action–language research, for example, expectancy or congruency between words, gestures, symbols, and images (Ibáñez et al., 2010; Lau et al., 2008). As regards MRCPs, given their typical markedly frontal distribution (Nguyen et al., 2014), these were examined in two symmetrical frontal ROIs, composed of six electrodes each: a right frontal ROI (Channels C4, C9, C10, C12, C13, and C14) and a left frontal ROI (Channels D4, C25, C26, C27, C31, and C32; Figure 3).

Point-by-point comparisons along the whole ERP signal were made via Monte Carlo permutation tests combined with bootstrapping, as done in previous works (Salamone et al., 2018; Yoris et al., 2017, 2018). This method circumvents the multiple-comparison problem and does not depend on multiple comparison corrections or Gaussian distribution assumptions (Nichols & Holmes, 2002). In addition, it avoids the selection of narrow a-priori windows for analysis, preventing circularity biases. The number of randomly simulations partitioning the data (permutations) was set to 5000. A p value was thus obtained for each distance, but only those below .05 were considered significant. Then, a minimum extension of 10 consecutive points was used as the criterion to capture reliably significant effects (Mueller, Swainson, & Jackson, 2009). In line with standard practice for permutation test results in ERP research, results of significant windows are presented by reporting the limits of the corresponding time interval, the mean difference between condition, the associated p value, and the effect size.

Exploratory Time–Frequency Analysis

In light of emerging research (Klepp et al., 2015), we explored stimulus- and response-locked oscillatory

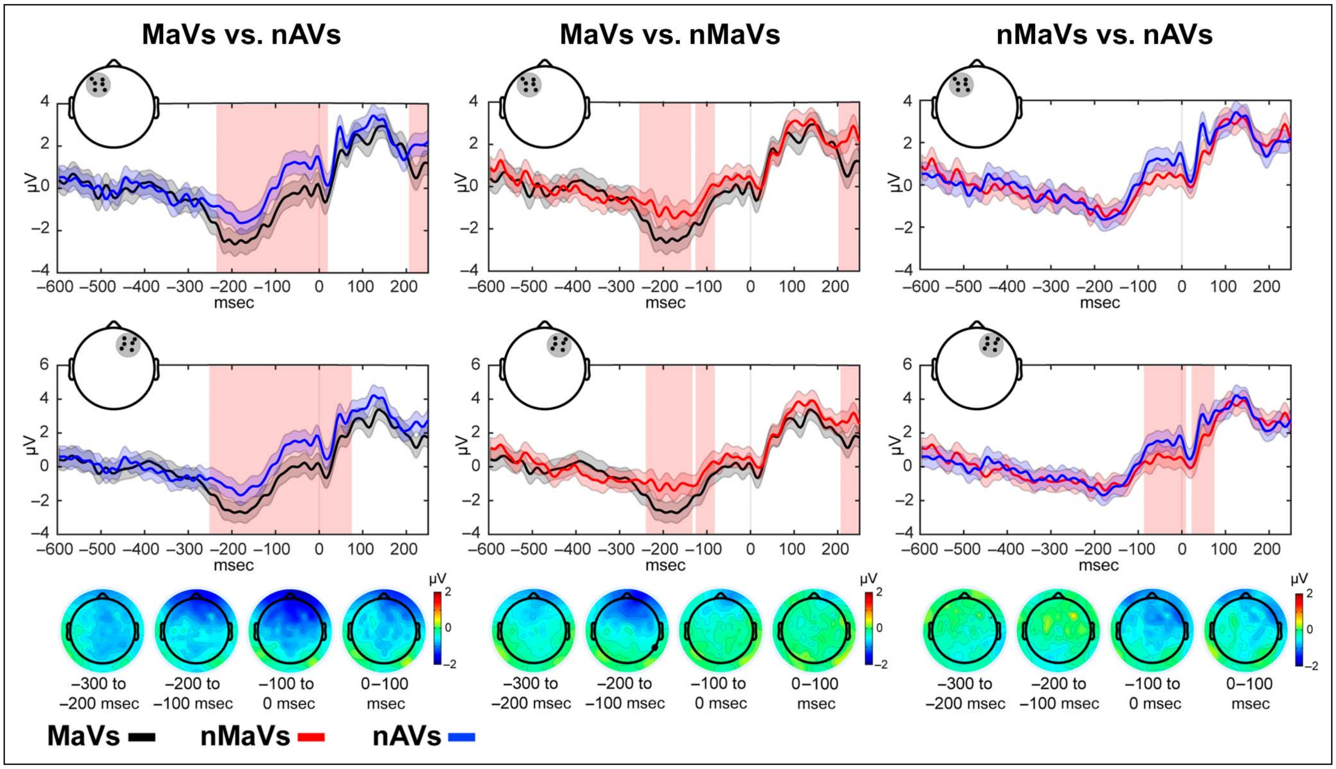

Figure 3. Electrophysiological markers of motor dynamics (MRCP) effects during motor–language coupling. The topoplots show average response-locked modulations within a canonical window (from −250 to −85 msec) over the left (A) and right (B) frontal ROIs for MaVs (black line), nMaVs (red line), and nAVs (blue line). The baseline ranged from −600 to −300 msec before response execution. Shadowed bars around the lines indicate standard errors. Vertical pink bars indicate significant differences at $p < .05$ (with a threshold of at least 10 contiguous points).

modulations in the beta band (12–30 Hz) within the same ROIs used for N400 and MRCP analyses, respectively. In line with this antecedent, we computed the time–frequency representation (TFR) on the targeted spectral power by convolving four-cycle complex Morlet wavelets with steps of 2 Hz for each single-trial epoch. Each stimulus-locked epoch ranged from −500 to 950 msec, whereas response-locked epochs ranged from −600 to 950 msec. A baseline subtraction was performed in every time point, and the ensuing difference was divided by the mean power of the baseline (set to −500 to −200 msec for stimulus-locked analyses and −600 to −300 msec for response-locked analyses). The single-trial TFRs were averaged for each condition (MaVs, nMaVs, and nAVs). The averaged TFRs were compared between each condition pair through a random pairwise permutation test across time over the same ROIs used for ERP analyses. The statistical significance threshold was set to $p = .05$.

RESULTS

Behavioral Results

Accuracy outcomes were high across all categories (MaVs = 96.9%, nMaVs = 97.1%, nAVs = 97.5%, PsVs = 87.3%). Statistical analysis revealed a main effect of Category. PsVs ($\beta = 87.34$, $SE = 1.13$, $df = 66.39$) elicited more errors than all real-word categories (MaVs: $\beta = 9.52$, $SE = 1.34$, $df = 63$; nMaVs: $\beta = 9.74$, $SE = 1.34$, $df = 63$; nAVs: $\beta = 10.12$, $SE = 1.34$, $df = 63$; all ps $< .001$), showing a canonical lexicality effect. However, there was no significant difference among the three categories of real verbs (all ps $> .90$; Figure 1B).

After removing outliers for RT analyses, the mean of remaining trials across participants was 19.4 (96%) for MaVs, 19 (94.6%) for nMaVs, 19 (95%) for nAVs, and 14.1 (96.1%) for PsVs. No trials were lost because of recording issues. RT results also revealed a main effect of category. PsVs (mean = 760 msec, $\beta = 0.75$, $SE = 0.02$, $df = 66.39$) yielded slower responses than all real-word categories (MaVs: mean = 632 msec, $\beta = -0.13$, $SE = 0.008$, $df = 63$; nMaVs: mean = 617 msec, $\beta = -0.14$, $SE = 0.008$, $df = 63$; nAVs: mean = 626 msec, $\beta = -0.13$, $SE = 0.008$, $df = 63$; all ps $< .001$), again showing a canonical lexicality effect. However, mean RTs did not differ between the real-verb categories (all ps $> .30$; Figure 1C).

N400 Results

Permutation analyses showed that N400 amplitudes were smaller for MaVs than nAVs in the right posterior ROI (from 328.1 to 410.2 msec, $M_{\text{diff}} = 0.34$, $p < .05$, $d = 2.08$) and in the centro-posterior ROI (from 347.6 to 437.5 msec, $M_{\text{diff}} = 0.39$, $p < .05$, $d = 0.79$). MaVs also elicited significantly smaller N400 amplitudes than nMaVs in a left posterior ROI (from 383.7 to 437.9 msec, $M_{\text{diff}} = 0.34$, $p < .05$, $d = 0.99$). Significant differences between nMaVs and nAVs were found only in the right posterior ROI (from 347.7 to 418 msec, $M_{\text{diff}} = 0.35$, $p < .05$, $d = 1.68$). For details, see Figure 2.

MRCP Results

As revealed by permutation analyses, MaVs elicited significantly more negative amplitudes than nAVs over the left frontal ROI (from −232.8 to 17.2 msec, $M_{\text{diff}} = 1.18$, $p < .05$, $d = 1.10$) and over the right frontal ROI (from −248.4 to 71.9 msec, $M_{\text{diff}} = 1.23$, $p < .05$, $d = 0.86$). Furthermore, MaVs elicited greater negative modulations than nMaVs before the onset of motor action, in both the left (from −252.3 to −139.1 msec, $M_{\text{diff}} = 1.16$, $p < .05$, $d = 3.59$; and from −123.4 to −84.4 msec, $M_{\text{diff}} = 0.83$, $p < .05$, $d = 1.82$) and right (from −236.7 to −135.2 msec, $M_{\text{diff}} = 1.35$, $p < .05$, $d = 5.52$; and from −123.4 to −84.4 msec, $M_{\text{diff}} = 0.84$, $p < .05$, $d = 1.71$) frontal ROIs. Differences between nMaVs and nAVs were solely observed over the right frontal ROI (from −84.4 to 5.5 msec, $M_{\text{diff}} = 0.95$, $p < .05$, $d = 5.21$; and from 25.0 to 75.8 msec, $M_{\text{diff}} = 0.97$, $p < .05$, $d = 1.17$). For details, see Figure 3.

Exploratory Time–Frequency Results

Exploratory time–frequency analyses over the beta band revealed significant effects ($p < .05$) over specific time segments. For stimulus-locked analyses, significant differences between MaVs and nAVs were observed only in the left posterior ROI, from 50 to 90 msec. The contrast between MaVs and nMaVs yielded significant differences only in the centro-posterior ROI (from 680 to 770 msec). Finally, differential modulations between nMaVs and nAVs were observed in both the centro-posterior (80–750 msec) and right posterior (120–760 msec) ROIs. For response-locked analyses, MaVs and nAVs yielded significantly different modulations over the left frontal ROI (in segments between −260 and 110 msec) and in the right frontal ROI (between −270 and 100 msec). Differences between MaVs and nMaVs reached significance over the left frontal ROI (in time segments comprised between −270 and 0 msec) and over the right frontal ROI (between −270 and 120 msec). Finally, differences between nMaVs and nAVs reached significance in the left frontal ROI (across successive time segments between −190 and 150 msec) and in the right frontal ROI (between −200 and 120 msec).

DISCUSSION

This study examined neural signatures of semantic and motoric dynamics during motor–language coupling in a shallow processing task. Relative to both nAVs and nMaVs, MaVs involved (a) reduced posterior N400 effects locked to stimulus onset and (b) greater modulations of frontal MRCPs locked to response execution. Moreover, only the former ERP discriminated between nMaVs and nAVs. Suggestively, effector-specific modulations for both components overlapped in a window of ~380–440 msec after word presentation and ~180 msec before response execution. Such results provide new insights to understand the neural co-determinations of lexical and motoric processes, as discussed below.

N400 Modulations: Semantic Dynamics during Motor–Language Coupling

N400 results revealed two informative patterns. First, both MaVs and nMaVs elicited smaller N400 amplitude than nAVs. This resembles previous research (Dalla Volta, Fabbri-Destro, Gentilucci, & Avanzini, 2014) showing that ERP modulations for MaVs and nMaVs differed from those of nAVs in windows from roughly 220 to 400 msec. Given that N400 amplitude indexes semantic integration of linguistic material with active contextual signals (Lau et al., 2008), even during lexical access (Penolazzi, Hauk, & Pulvermüller, 2007), increased modulations for nAVs than for both action-verb categories probably signal the former's greater incongruity with an ongoing physical response. In fact, as amply shown by speech/co-speech gesture paradigms, N400 amplitude is greater for incongruent than congruent pairings of word meaning and manual movement (Ibáñez et al., 2010, 2012, 2013; Kelly, Creigh, & Bartolotti, 2010; Cornejo et al., 2009; Holle & Gunter, 2007; Kelly, Ward, Creigh, & Bartolotti, 2007; Özyürek, Willems, Kita, & Hagoort, 2007; Wu & Coulson, 2005; Kelly, Kravitz, & Hopkins, 2004; for a review, see Amoruso et al., 2013).

More particularly, the N400 modulations yielded by MaVs were smaller than those of nMaVs. Comparable effects were reported in manual-response tasks showing enhanced beta suppression for MaVs relative to nMaVs (foot verbs) around 350 and 750 msec (Klepp et al., 2015), although the effect may also occur in later time windows (Klepp, Van Dijk, Niccolai, Schnitzler, & Biermann-Ruben, 2019). In addition, mismatch negativity effects around ~300 msec can be modulated over frontocentral electrodes when a preceding action sound (e.g., footsteps) is incompatible with an effector-specific action word (e.g., *kiss*; Grisoni, Dreyer, & Pulvermüller, 2016). This suggests that, during motor–language coupling, N400 modulations are sensitive not only to general motor resonance but also to effector-specific dynamics.

This interpretation fits with evidence that N400 modulations capture compatibility between the hand positions evoked by words and those used for ongoing actions (Ibáñez et al., 2013; Aravena et al., 2010) and with hemodynamic (Kemmerer, Castillo, Talavage, Patterson, & Wiley, 2008; Assmus, Giessing, Weiss, & Fink, 2007; Buxbaum, Kyle, Tang, & Detre, 2006; Hamzei et al., 2003) and electromagnetic (Mollo et al., 2016; Pulvermüller, Shtyrov, & Ilmoniemi, 2005) studies showing that motor–language coupling is indexed by modulation changes in different hubs of core semantic networks (e.g., posterior superior temporal cortex). In line with these antecedents, our results suggest that semantic components of motor–language coupling are sensitive to fine-grained (limb-specific) features and not only to coarse (limb-neutral) integrations of movement and meaning (Pulvermüller, 2013a, 2013b).

MRCP Modulations: Action Dynamics during Motor–Language Coupling

MRCP results also revealed two key patterns. First, compared with nAVs, MaVs yielded greater frontal modulations since 250 msec before until 75 msec after response execution, with nMaVs yielding similar effects in the latter part of that segment (from −85 until 75 msec). This extended pattern encompasses two critical ERPs, namely, the RP and the MP (Haggard, 2008; Shibasaki, Barrett, Halliday, & Halliday, 1980), even extending onto postmovement MRCPs (Shibasaki & Hallett, 2006; Deecke et al., 1969). Crucially, modulation of these components indexes heightened motor-system recruitment not only during action preparation and execution (Siemionow, Yue, Ranganathan, Liu, & Sahgal, 2000), respectively, but also during relevant higher-order processes, such as action imagery (Moran, Campbell, Holmes, & MacIntyre, 2012; Niazi et al., 2011; Sharma, Pomeroy, & Baron, 2006) and observation (Bozzacchi, Spinelli, Pitzalis, Giusti, & Di Russo, 2015). More particularly, RP amplitude discriminates between nAVs and diverse (mouth, leg, and hand related) action verbs, with additional modulations for each category around the MP window (Dalla Volta et al., 2018). In line with this evidence, our results suggest that verbs that evoke bodily motion, relative to those that do not, prime successive action-related cortical mechanisms.

Yet, when compared with nMaVs, MaVs elicited a greater negative deflection only between −250 and −85 msec, thus being mainly restricted to the canonical window of the RP (Haggard, 2008; Libet, Wright, & Gleason, 1993). Interestingly, previous motor–language coupling studies assessing response-locked activity (Melloni et al., 2015; Ibáñez et al., 2013; Aravena et al., 2010) reported MP effects without RP modulations. However, because these studies compared different subtypes of MaVs (denoting open and closed manual actions) following congruent hand shapes (i.e., open or closed), they were blind to the integration of same- and different-effector information. Accordingly, our findings suggest that RP modulations during motor–language coupling are particularly sensitive to effector-specific effects. In other words, this ERP seems to index the match between the limb implied by a verb and the one set in motion—a synergy that is also captured in hemodynamic (Kemmerer et al., 2008; Assmus et al., 2007; Buxbaum et al., 2006; Hamzei et al., 2003) and electromagnetic (Mollo et al., 2016; Pulvermüller et al., 2005) dimensions.

It is worth noting that such effector specificity was traced by the RP, as opposed to the MP. Unfortunately, the only previous EEG study on response-locked modulations during processing of mouth-, leg-, and hand-related action verbs did not compare among these categories, as it exclusively contrasted them with nAVs (Dalla Volta et al., 2018). Still, this dissociation between MRCPs does echo previous findings. Indeed, the RP has proven sensitive to action dynamics that escape the MP and other MRCPs, such as the contrast between executed and nonexecuted movements (Castro et al., 2005). Compatibly, then, our results indicate that MRCPs would have a graded sensitivity in the unfolding of motor–language coupling, with the RP capturing both coarse-grained (general motor resonance) and fine-grained (effector-specific) embodied dynamics and the MP tracking only the former effects. Note, incidentally, that this pattern was corroborated even when considering a much longer window.

Theoretical Implications

The results above have a number of theoretical implications. First, they indicate that both the semantic and action dimensions of motor–language coupling are typified by effector-sensitive neural modulations. In other words, both the conceptual integration and movement-related stages of the phenomenon are influenced by fine-grained (limb-specific) features of the word's meaning and the to-be-executed action. Note that previous studies have reached similar conclusions by comparing different categories of action verbs relative to nAVs (but not with each other) in manual-response tasks (Dalla Volta et al., 2018) or by examining compatibility effects between subsets of MaVs and different hand responses (Melloni et al., 2015; Ibáñez et al., 2013; Aravena et al., 2010). Therefore, all this previous evidence proves blind to limb-specific effects. Conversely, in line with recent works (Klepp et al., 2015, 2019), our study indicates that motor–language coupling is characterized by not only gross motor resonance and effector-position effects but also the overlap between the body part denoted by the verbal material and the one used to perform an action.

In addition, to our knowledge, our study is the first to dissociate specific MRCPs underlying these two embodied phenomena. General motor resonance effects seem to cut across the RP (Travers et al., 2020; Haggard, 2008; Kutas & Donchin, 1980) and the MP (Shibasaki & Hallett, 2006; Deecke et al., 1969), suggesting that coarse-grained embodied dynamics extend from distal stages of motor preparation until motor execution proper. Conversely, effector-specific effects were indexed only by the RP, indicating that fine-grained embodied dynamics are shorter-lived and vanish as motor execution becomes imminent. This suggests that semantic specificity might influence which motor-processing stages are engaged in motor–language coupling, opening new avenues for research.

Such findings allow extending the Hand-Action-Network Dynamic Language Embodiment model (García & Ibáñez, 2016a), the most systematic account of motor–language coupling phenomena to date. Succinctly, this framework posits that ongoing manual action processes can be modulated in predictable ways if accompanied by verbal materials evoking hand-specific meanings. In particular, the model posits that the temporal lag between word onset and action execution can determine whether the latter will be facilitated (Afonso et al., 2019; Kelly et al., 2010; Springer & Prinz, 2010; Masson, Bub, & Warren, 2008; Lindemann, Stenneken, Van Schie, & Bekkering, 2006; Tucker & Ellis, 2004) or delayed (García & Ibáñez, 2016b; Spadacenta, Gallese, Fragola, & Mirabella, 2014; Mirabella, Iaconelli, Spadacenta, Federico, & Gallese, 2012; Bergen, Lau, Narayan, Stojanovic, & Wheeler, 2010; Sato, Mengarelli, Riggio, Gallese, & Buccino, 2008). However, the model is exclusively rooted in behavioral evidence, and it fails to disentangle the time course of motoric and semantic dynamics underlying its target phenomenon. In this sense, the Hand-Action-Network Dynamic Language Embodiment model can be refined by incorporating core findings of our study: Effector-specific motor–language coupling modulates electrophysiological signatures of both action-related and semantic integration processes, and these feature their own, partially overlapping, temporal and functional dynamics (Figure 4).

On the basis of present results, the diagram in Figure 4 maps the temporal span in which semantic and motoric processes coalesce during motor–language coupling. First, effector-specific N400 modulations, signaling semantic integration, were observed ~380–440 msec after stimulus onset. Second, considering that response latencies fell in the order of ~620 msec and that response-locked MRCPs yielded effector-specific effects starting ~250 msec before action execution, motoric stages of the phenomenon began almost in synchrony with semantic ones and extended for ~200 msec thereon. Accordingly, both stages seem to co-occur over a window of ~380–440 msec after stimulus presentation. This time span, we propose, might signal the moment of convergence between the two contributing streams shaping effector-specific motor–language coupling—a conclusion that simply cannot be derived from previous ERP studies comparing MaVs and nMaVs with nAVs, but not with each other (e.g., Dalla Volta et al., 2018). Together with research on the time course of MaV-induced muscular activity (Da Silva et al., 2018; Frak et al., 2010), such a finding further illuminates the complex embodied dynamics linking meanings and actions.

Moreover, previous motor–language coupling studies relied on explicit processing tasks, as they required participants to semantically categorize stimuli (Dalla Volta et al., 2018) or indicate when they were understood (Melloni et al., 2015; Ibáñez et al., 2013; Aravena et al., 2010). Therefore, they overlooked a key requisite to detect primary embodied effects: their emergence under implicit semantic conditions (García et al., 2019; Mollo et al., 2016; Hauk, Shtyrov, & Pulvermüller, 2008; Kiefer et al., 2008; Pulvermüller et al., 2001). Unlike those studies, our experiment was based on a lexical decision task, so that no explicit attention to meaning was required. As proposed for other embodied phenomena (García et al.,

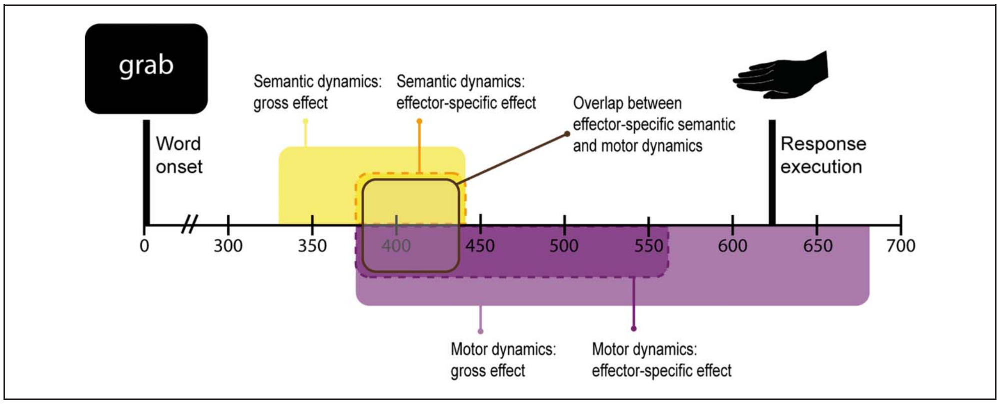

Figure 4. Schematic representation of the temporal integration of semantic and motor processes during motor–language coupling. The upper part of the figure shows N400 effects, indexing semantic integration dynamics during motor–language coupling. Whereas limb-neutral semantic integration during MaV processing (relative to nAVs) covers a ~330- to 440-msec window (light yellow), effector-specific N400 effects (relative to nMaVs) extend from ~380 to ~440 msec (dark yellow). The lower part of the figure shows MRCP effects, indexing motor dynamics during motor–language coupling. Limb-neutral motor dynamics during MaV processing (relative to nAVs) extend roughly from −250 to 75 msec relative to response execution (light purple). Instead, effector-specific MRCP modulations (relative to nMaVs) extend from approximately −250 to −85 msec (dark purple). Accordingly, the overlap between both effector-specific modulations occurs in a 380- to 440-msec window (brown), signaling the convergence of semantic and motoric stages during hand-specific motor–language coupling.

2019), this suggests that motor–language coupling dynamics are sufficiently pervasive to operate even when language is processed at a shallow level.

Finally, the observed neural patterns emerged without accompanying effects on accuracy or RT. Whereas behavioral experiments show that MaVs can induce involuntary grip force modulations shortly after presentation (Da Silva et al., 2018; Frak et al., 2010), these two variables typically yield null motor–language coupling effects in shallow-processing paradigms (García & Ibáñez, 2016a). However, several neuroscientific studies have shown that significant neural effects can be traced in embodied paradigms yielding no behavioral differences between conditions (García et al., 2020; Mollo et al., 2016; Klepp et al., 2014; Sato et al., 2008; Pulvermüller et al., 2001). As argued for other neurolinguistic phenomena (Dottori et al., 2020), this reminds us that a null effect on one dependent variable must not be taken to reflect a null effect of the independent variable at large. Indeed, as shown in this study, motor–language phenomena may be indexed by neural indices of motoric and semantic integration, despite yielding no significant effects on overt behavior.

The same might be true of different neurophysiological dimensions. As mentioned above, previous motor–language coupling research found effector-specific beta-band effects in both stimulus- and response-locked analyses (Klepp et al., 2015). Our preliminary exploration of stimulus-locked time–frequency modulations over this band yielded late (670–770 msec) coarse-grained and effector-specific effects, partly overlapping with the time window (350–750 msec) capturing comparable effects in Klepp et al.'s (2015) study. This aligns with previous works showing different temporal dynamics between N400 effects and beta oscillations in linguistic tasks (Wang et al., 2012), some of which are actually tracked by only one of these measures (Dottori et al., 2020; Vilas et al., 2019). Moreover, response-locked analyses yielded effects that broadly echoed the time windows capturing our main ERP results. Reduced beta oscillations were observed for all three contrasts starting at roughly the same time as MRCP effects and covering the entirety of their duration. However, they also extended beyond the window capturing such ERP effects. This might speak to the different temporal dynamics of motor–language coupling in each analytical dimension, a possibility that should be explored in new studies designed to compare both approaches.

Limitations and Avenues for Further Research

Notwithstanding its contributions, our study presents some limitations. First, our sample size was modest. Although the present number of participants provided good statistical power and although most previous EEG studies on motor–language coupling have employed similar or even smaller *N*s (Dalla Volta et al., 2018; Mollo et al., 2016; Melloni et al., 2015), replications with a larger group would be desirable. In addition, although recent works with comparable experimental designs (Dalla Volta et al., 2018) have used similar numbers of stimuli, it would be ideal to extend this study with more items per category. Moreover, it would be useful to assess whether the modulations observed during our present shallow-level task manifest similarly when explicit semantic processing is required—as observed in behavioral motor–language coupling experiments (Afonso et al., 2019). Finally, although the question addressed in this study pertained to the temporal dimension, future studies should aim to complement our approach with high-spatial-resolution methods, as done in recent magnetoencephalography (García et al., 2019; Klepp et al., 2014, 2015, 2019) and intracranial (García et al., 2020; Ibáñez et al., 2013) EEG experiments.

Conclusion

This is the first ERP study assessing the semantic and action stages of motor–language coupling during a shallow-processing task. Our core finding is that the execution of a manual response after processing of MaVs (as compared with nMaVs) involves reduced N400 modulations and increased MRCP effects, signaling semantic and motoric dynamics, respectively. Such modulations overlapped in a window of ~380–440 msec after word presentation and ~180 msec before response execution, a pattern that motivates new insights on when both stages reach maximal convergence during effector-specific motor–language coupling. Moreover, we showed that the RP is sensitive to both coarse-grained and effector-specific dynamics, whereas the MP only captures the former modulations, suggesting different functional roles for each ERP. Further work in this direction can hone our understanding of how language and movement coalesce in neural time.

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Author Contributions

Sabrina Cervetto: Data curation; Formal analysis; Investigation; Software; Writing – original draft. Mariano Díaz-Rivera: Investigation; Writing – original draft. Agustín Petroni: Data curation; Formal analysis. Agustina Birba: Formal analysis; Writing – review & editing. Miguel Martorell Caro: Data curation. Lucas Sedeño: Writing – review & editing. Agustín Ibáñez: Funding acquisition; Writing – review & editing. Adolfo M. García: Conceptualization; Investigation; Methodology; Project administration; Resources; Validation; Writing – original draft; Writing – review & editing.

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Diversity in Citation Practices

A retrospective analysis of the citations in every article published in this journal from 2010 to 2020 has revealed a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience* (*JoCN*) during this period were M(an)/M = .408, W(oman)/M = .335, M/W = .108, and W/W = .149, the comparable proportions for the articles that these authorship teams cited were M/M = .579, W/M = .243, M/W = .102, and W/W = .076 (Fulvio et al., *JoCN*, 33:1, pp. 3–7). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance.

Data and Code Availability Statement

All experimental data and the scripts used for their collection and analysis are available online (García, 2020).

REFERENCES

Afonso, O., Suárez-Coalla, P., Cuetos, F., Ibáñez, A., Sedeño, L., & García, A. M. (2019). The embodied Penman: Effector-specific motor–language integration during handwriting. *Cognitive Science*, *43*, e12767. https://doi.org/10.1111/cogs.12767, PubMed: 31310023

Amoruso, L., Gelormini, C., Aboitiz, F. A., González, A., Manes, F., Cardona, J., et al. (2013). N400 ERPs for actions: Building meaning in context. *Frontiers in Human Neuroscience*, *7*, 57. https://doi.org/10.3389/fnhum.2013.00057, PubMed: 23459873

Aravena, P., Hurtado, E., Riveros, R., Cardona, J. F., Manes, F., & Ibáñez, A. (2010). Applauding with closed hands: Neural signature of action–sentence compatibility effects. *PLoS One*, *5*, e11751. https://doi.org/10.1371/journal.pone.0011751, PubMed: 20676367

Assmus, A., Giessing, C., Weiss, P. H., & Fink, G. R. (2007). Functional interactions during the retrieval of conceptual action knowledge: An fMRI study. *Journal of Cognitive Neuroscience*, *19*, 1004–1012. https://doi.org/10.1162/jocn.2007.19.6.1004, PubMed: 17536970

Barsalou, L. W. (2008). Grounded cognition. *Annual Review of Psychology*, *59*, 617–645. https://doi.org/10.1146/annurev.psych.59.103006.093639, PubMed: 17705682

Bergen, B., Lau, T.-T. C., Narayan, S., Stojanovic, D., & Wheeler, K. (2010). Body part representations in verbal semantics. *Memory & Cognition*, *38*, 969–981. https://doi.org/10.3758/MC.38.7.969, PubMed: 20921109

Bozzacchi, C., Spinelli, D., Pitzalis, S., Giusti, M. A., & Di Russo, F. (2015). I know what I will see: Action-specific motor preparation activity in a passive observation task. *Social Cognitive and Affective Neuroscience*, *10*, 783–789. https://doi.org/10.1093/scan/nsu115, PubMed: 25261822

Buccino, G., Riggio, L., Melli, G., Binkofski, F., Gallese, V., & Rizzolatti, G. (2005). Listening to action-related sentences modulates the activity of the motor system: A combined TMS and behavioral study. *Cognitive Brain Research*, *24*, 355–363. https://doi.org/10.1016/j.cogbrainres.2005.02.020, PubMed: 16099349

Buxbaum, L. J., Kyle, K. M., Tang, K., & Detre, J. A. (2006). Neural substrates of knowledge of hand postures for object grasping and functional object use: Evidence from fMRI. *Brain Research*, *1117*, 175–185. https://doi.org/10.1016/j.brainres.2006.08.010, PubMed: 16962075

Casado, P., Martín-Loeches, M., León, I., Hernández-Gutiérrez, D., Espuny, J., Munoz, F., et al. (2018). When syntax meets action: Brain potential evidence of overlapping between language and motor sequencing. *Cortex*, *100*, 40–51. https://doi.org/10.1016/j.cortex.2017.11.002, PubMed: 29212607

Castro, A., Díaz, F., & van Boxtel, G. J. (2005). What happens to the readiness potential when the movement is not executed? *NeuroReport*, *16*, 1609–1613. https://doi.org/10.1097/01.wnr.0000183331.51736.7f, PubMed: 16189464

Cohen, M. X. (2014). *Analyzing neural time series data: Theory and practice*. Cambridge, MA: MIT Press. https://doi.org/10.7551/mitpress/9609.001.0001

Cornejo, C., Simonetti, F., Ibáñez, A., Aldunate, N., Ceric, F., López, V., et al. (2009). Gesture and metaphor comprehension: Electrophysiological evidence of cross-modal coordination by audiovisual stimulation. *Brain and Cognition*, *70*, 42–52. https://doi.org/10.1016/j.bandc.2008.12.005, PubMed: 19200632

Courellis, H. S., Iversen, J. R., Poizner, H., & Cauwenberghs, G. (2016). EEG channel interpolation using ellipsoid geodesic length. Paper presented at the 2016 IEEE Biomedical Circuits and Systems Conference (BioCAS). https://doi.org/10.1109/BioCAS.2016.7833851

Da Silva, R. L., Labrecque, D., Caromano, F. A., Higgins, J., & Frak, V. (2018). Manual action verbs modulate the grip force of each hand in unimanual or symmetrical bimanual tasks. *PLoS One*, *13*, e0192320. https://doi.org/10.1371/journal.pone.0192320, PubMed: 29401468

Dalla Volta, R., Avanzini, P., De Marco, D., Gentilucci, M., & Fabbri-Destro, M. (2018). From meaning to categorization: The hierarchical recruitment of brain circuits selective for action verbs. *Cortex*, *100*, 95–110. https://doi.org/10.1016/j.cortex.2017.09.012, PubMed: 29079343

Dalla Volta, R., Fabbri-Destro, M., Gentilucci, M., & Avanzini, P. (2014). Spatiotemporal dynamics during processing of abstract and concrete verbs: An ERP study. *Neuropsychologia*, *61*, 163–174. https://doi.org/10.1016/j.neuropsychologia.2014.06.019, PubMed: 24956569

Dalla Volta, R., Gianelli, C., Campione, G. C., & Gentilucci, M. (2009). Action word understanding and overt motor behavior. *Experimental Brain Research*, *196*, 403–412. https://doi.org/10.1007/s00221-009-1864-8, PubMed: 19484464

Daly, I., Williams, D., Hwang, F., Kirke, A., Miranda, E. R., & Nasuto, S. J. (2019). Electroencephalography reflects the activity of sub-cortical brain regions during approach–withdrawal behaviour while listening to music. *Scientific Reports*, *9*, 1–22. https://doi.org/10.1038/s41598-019-45105-2, PubMed: 31263113

Davis, C. J., & Perea, M. (2005). BuscaPalabras: A program for deriving orthographic and phonological neighborhood statistics and other psycholinguistic indices in Spanish. *Behavior Research Methods*, *37*, 665–671. https://doi.org/10.3758/BF03192738, PubMed: 16629300

Deecke, L., Scheid, P., & Kornhuber, H. H. (1969). Distribution of readiness potential, pre-motion positivity, and motor potential of the human cerebral cortex preceding voluntary finger movements. *Experimental Brain Research*, *7*, 158–168. https://doi.org/10.1007/BF00235441, PubMed: 5799432

Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, *134*, 9–21. https://doi.org/10.1016/j.jneumeth.2003.10.009, PubMed: 15102499

de Vega, M., Moreno, V., & Castillo, D. (2013). The comprehension of action-related sentences may cause interference rather than facilitation on matching actions. *Psychological Research*, *77*, 20–30. https://doi.org/10.1007/s00426-011-0356-1, PubMed: 21755368

Dottori, M., Hesse, E., Santilli, M., Vilas, M. G., Caro, M. M., Fraiman, D., et al. (2020). Task-specific signatures in the expert brain: Differential correlates of translation and reading in professional interpreters. *Neuroimage*, *209*, 116519. https://doi.org/10.1016/j.neuroimage.2020.116519, PubMed: 31923603

Dottori, M., Sedeño, L., Caro, M. M., Alifano, F., Hesse, E., Mikulan, E., et al. (2017). Towards affordable biomarkers of frontotemporal dementia: A classification study via network's information sharing. *Scientific Reports*, *7*, 1–12. https://doi.org/10.1038/s41598-017-04204-8, PubMed: 28630492

Fabi, S., & Leuthold, H. (2017). Empathy for pain influences perceptual and motor processing: Evidence from response force, ERPs, and EEG oscillations. *Social Neuroscience*, *12*, 701–716. https://doi.org/10.1080/17470919.2016.1238009, PubMed: 27643572

Falkenstein, M., Hoormann, J., & Hohnsbein, J. (1999). ERP components in Go/Nogo tasks and their relation to inhibition. *Acta psychologica*, *101*, 267–291. https://doi.org/10.1016/S0001-6918(99)00008-6, PubMed: 10344188

Fittipaldi, S., Abrevaya, S., de la Fuente, A., Pascariello, G. O., Hesse, E., Birba, A., et al. (2020). A multidimensional and multi-feature framework for cardiac interoception. *Neuroimage*, *212*, 116677. https://doi.org/10.1016/j.neuroimage.2020.116677, PubMed: 32101777

Frak, V., Nazir, T., Goyette, M., Cohen, H., & Jeannerod, M. (2010). Grip force is part of the semantic representation of manual action verbs. *PLoS One*, *5*, e9728. https://doi.org/10.1371/journal.pone.0009728, PubMed: 20300535

García, A. M. (2020). *Data from "ERP signatures of semantic and motoric processes during action–language coupling"*. Open Science Framework. https://osf.io/ep7f8/?view_only=74273abfa0b9470cacecb144f28ef40f

García, A. M., Hesse, E., Birba, A., Adolfi, F., Mikulan, E., Caro, M. M., et al. (2020). Time to face language: Embodied mechanisms underpin the inception of face-related meanings in the human brain. *Cerebral Cortex*, *30*, 6051–6068. https://doi.org/10.1093/cercor/bhaa178, PubMed: 32577713

García, A. M., & Ibáñez, A. (2016a). A touch with words: Dynamic synergies between manual actions and language. *Neuroscience & Biobehavioral Reviews*, *68*, 59–95. https://doi.org/10.1016/j.neubiorev.2016.04.022, PubMed: 27189784

García, A. M., & Ibáñez, A. (2016b). Hands typing what hands do: Action–semantic integration dynamics throughout written verb production. *Cognition*, *149*, 56–66. https://doi.org/10.1016/j.cognition.2016.01.011, PubMed: 26803393

García, A. M., Moguilner, S., Torquati, K., García-Marco, E., Herrera, E., Muñoz, E., et al. (2019). How meaning unfolds in neural time: Embodied reactivations can precede multimodal semantic effects during language processing. *Neuroimage*, *197*, 439–449. https://doi.org/10.1016/j.neuroimage.2019.05.002, PubMed: 31059796

García-Cordero, I., Sedeño, L., De La Fuente, L., Slachevsky, A., Forno, G., Klein, F., et al. (2016). Feeling, learning from and being aware of inner states: Interoceptive dimensions in neurodegeneration and stroke. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, *371*, 20160006. https://doi.org/10.1098/rstb.2016.0006, PubMed: 28080965

Gentili, R. J., Jaquess, K. J., Shuggi, I. M., Shaw, E. P., Oh, H., Lo, L. C., et al. (2018). Combined assessment of attentional reserve and cognitive–motor effort under various levels of challenge with a dry EEG system. *Psychophysiology*, *55*, e13059. https://doi.org/10.1111/psyp.13059, PubMed: 29424021

Gentsch, A., Sel, A., Marshall, A. C., & Schütz-Bosbach, S. (2019). Affective interoceptive inference: Evidence from heart-beat evoked brain potentials. *Human Brain Mapping*, *40*, 20–33. https://doi.org/10.1002/hbm.24352, PubMed: 30159945

Gianelli, C., & Dalla Volta, R. (2015). Does listening to action-related sentences modulate the activity of the motor system? Replication of a combined TMS and behavioral study. *Frontiers in Psychology*, *5*, 1511. https://doi.org/10.3389/fpsyg.2014.01511, PubMed: 25601845

Glenberg, A. M., & Gallese, V. (2012). Action-based language: A theory of language acquisition, comprehension, and production. *Cortex*, *48*, 905–922. https://doi.org/10.1016/j.cortex.2011.04.010, PubMed: 21601842

Grisoni, L., Dreyer, F. R., & Pulvermüller, F. (2016). Somatotopic semantic priming and prediction in the motor system. *Cerebral Cortex*, *26*, 2353–2366. https://doi.org/10.1093/cercor/bhw026, PubMed: 26908635

Guan, C. Q., Meng, W., Yao, R., & Glenberg, A. M. (2013). The motor system contributes to comprehension of abstract language. *PLoS One*, *8*, e75183. https://doi.org/10.1371/journal.pone.0075183, PubMed: 24086463

Haggard, P. (2008). Human volition: Towards a neuroscience of will. *Nature Reviews Neuroscience*, *9*, 934–946. https://doi.org/10.1038/nrn2497, PubMed: 19020512

Hamzei, F., Rijntjes, M., Dettmers, C., Glauche, V., Weiller, C., & Büchel, C. (2003). The human action recognition system and its relationship to Broca's area: An fMRI study. *Neuroimage*, *19*, 637–644. https://doi.org/10.1016/S1053-8119(03)00087-9, PubMed: 12880794

Hauk, O., Johnsrude, I., & Pulvermüller, F. (2004). Somatotopic representation of action words in human motor and premotor cortex. *Neuron*, *41*, 301–307. https://doi.org/10.1016/S0896-6273(03)00838-9, PubMed: 14741110

Hauk, O., Shtyrov, Y., & Pulvermüller, F. (2008). The time course of action and action-word comprehension in the human brain as revealed by neurophysiology. *Journal of Physiology-Paris*, *102*, 50–58. https://doi.org/10.1016/j.jphysparis.2008.03.013, PubMed: 18485679

Holle, H., & Gunter, T. C. (2007). The role of iconic gestures in speech disambiguation: ERP evidence. *Journal of Cognitive Neuroscience*, *19*, 1175–1192. https://doi.org/10.1162/jocn.2007.19.7.1175, PubMed: 17583993

Ibáñez, A., Cardona, J. F., Dos Santos, Y. V., Blenkmann, A., Aravena, P., Roca, M., et al. (2013). Motor–language coupling: Direct evidence from early Parkinson's disease and intracranial cortical recordings. *Cortex*, *49*, 968–984. https://doi.org/10.1016/j.cortex.2012.02.014, PubMed: 22482695

Ibáñez, A., Manes, F., Escobar, J., Trujillo, N., Andreucci, P., & Hurtado, E. (2010). Gesture influences the processing of figurative language in non-native speakers: ERP evidence. *Neuroscience Letters*, *471*, 48–52. https://doi.org/10.1016/j.neulet.2010.01.009, PubMed: 20079804

Ibáñez, A., Melloni, M., Huepe, D., Helgiu, E., Rivera-Rei, A., Canales-Johnson, A., et al. (2012). What event-related potentials (ERPs) bring to social neuroscience? *Social Neuroscience*, *7*, 632–649. https://doi.org/10.1080/17470919.2012.691078, PubMed: 22642412

Kadosh, R. C., Kadosh, K. C., Linden, D. E., Gevers, W., Berger, A., & Henik, A. (2007). The brain locus of interaction between number and size: A combined functional magnetic resonance imaging and event-related potential study. *Journal of Cognitive Neuroscience*, *19*, 957–970. https://doi.org/10.1162/jocn.2007.19.6.957, PubMed: 17536966

Kelly, S. D., Creigh, P., & Bartolotti, J. (2010). Integrating speech and iconic gestures in a Stroop-like task: Evidence for automatic processing. *Journal of Cognitive Neuroscience*, *22*, 683–694. https://doi.org/10.1162/jocn.2009.21254, PubMed: 19413483

Kelly, S. D., Kravitz, C., & Hopkins, M. (2004). Neural correlates of bimodal speech and gesture comprehension. *Brain and Language*, *89*, 253–260. https://doi.org/10.1016/S0093-934X(03)00335-3, PubMed: 15010257

Kelly, S. D., Ward, S., Creigh, P., & Bartolotti, J. (2007). An intentional stance modulates the integration of gesture and speech during comprehension. *Brain and Language*, *101*, 222–233. https://doi.org/10.1016/j.bandl.2006.07.008, PubMed: 16997367

Kemmerer, D., Castillo, J. G., Talavage, T., Patterson, S., & Wiley, C. (2008). Neuroanatomical distribution of five semantic components of verbs: Evidence from fMRI. *Brain and Language*, *107*, 16–43. https://doi.org/10.1016/j.bandl.2007.09.003, PubMed: 17977592

Kiefer, M., Sim, E.-J., Herrnberger, B., Grothe, J., & Hoenig, K. (2008). The sound of concepts: Four markers for a link between auditory and conceptual brain systems. *Journal of Neuroscience*, *28*, 12224–12230. https://doi.org/10.1523/JNEUROSCI.3579-08.2008, PubMed: 19020016

Klepp, A., Niccolai, V., Buccino, G., Schnitzler, A., & Biermann-Ruben, K. (2015). Language–motor interference reflected in MEG beta oscillations. *Neuroimage*, *109*, 438–448. https://doi.org/10.1016/j.neuroimage.2014.12.077, PubMed: 25576646

Klepp, A., Van Dijk, H., Niccolai, V., Schnitzler, A., & Biermann-Ruben, K. (2019). Action verb processing specifically modulates motor behaviour and sensorimotor neuronal oscillations. *Scientific Reports*, *9*, 1–11. https://doi.org/10.1038/s41598-019-52426-9, PubMed: 31690784

Klepp, A., Weissler, H., Niccolai, V., Terhalle, A., Geisler, H., Schnitzler, A., et al. (2014). Neuromagnetic hand and foot motor sources recruited during action verb processing. *Brain and Language*, *128*, 41–52. https://doi.org/10.1016/j.bandl.2013.12.001, PubMed: 24412808

Kogan, B., Muñoz, E., Ibáñez, A., & García, A. M. (2020). Too late to be grounded? Motor resonance for action words acquired after middle childhood. *Brain and Cognition*, *138*, 105509. https://doi.org/10.1016/j.bandc.2019.105509, PubMed: 31855702

Kutas, M., & Donchin, E. (1980). Preparation to respond as manifested by movement-related brain potentials. *Brain Research*, *202*, 95–115. https://doi.org/10.1016/S0006-8993(80)80037-0, PubMed: 7427748

Kutas, M., & Federmeier, K. D. (2000). Electrophysiology reveals semantic memory use in language comprehension. *Trends in Cognitive Sciences*, *4*, 463–470. https://doi.org/10.1016/S1364-6613(00)01560-6, PubMed: 11115760

Kutas, M., & Federmeier, K. D. (2011). Thirty years and counting: Finding meaning in the N400 component of the event-related brain potential (ERP). *Annual Review of Psychology*, *62*, 621–647. https://doi.org/10.1146/annurev.psych.093008.131123, PubMed: 20809790

Lau, E. F., Phillips, C., & Poeppel, D. (2008). A cortical network for semantics:(de) constructing the N400. *Nature Reviews Neuroscience*, *9*, 920–933. https://doi.org/10.1038/nrn2532, PubMed: 19020511

Lavidor, M., & Ellis, A. W. (2002). Word length and orthographic neighborhood size effects in the left and right cerebral hemispheres. *Brain and Language*, *80*, 45–62. https://doi.org/10.1006/brln.2001.2583, PubMed: 11817889

Libet, B., Wright, E. W., & Gleason, C. A. (1993). Readiness-potentials preceding unrestricted 'spontaneous' vs.

pre-planned voluntary acts. In B. Libet (Ed.), *Neurophysiology of consciousness* (pp. 229–242). Heidelberg: Springer. https://doi.org/10.1007/978-1-4612-0355-1_13

Lim, V. K., Wilson, A. J., Hamm, J. P., Phillips, N., Iwabuchi, S. J., Corballis, M. C., et al. (2009). Semantic processing of mathematical gestures. *Brain and Cognition*, *71*, 306–312. https://doi.org/10.1016/j.bandc.2009.07.004, PubMed: 19665831

Lindemann, O., Stenneken, P., Van Schie, H. T., & Bekkering, H. (2006). Semantic activation in action planning. *Journal of Experimental Psychology: Human Perception and Performance*, *32*, 633–643. https://doi.org/10.1037/0096-1523.32.3.633, PubMed: 16822129

Luck, S. J. (2014). *An introduction to the event-related potential technique*. Cambridge, MA: MIT Press.

Manfredi, M., Cohn, N., & Kutas, M. (2017). When a hit sounds like a kiss: An electrophysiological exploration of semantic processing in visual narrative. *Brain and Language*, *169*, 28–38. https://doi.org/10.1016/j.bandl.2017.02.001, PubMed: 28242517

Masson, M. E., Bub, D. N., & Warren, C. M. (2008). Kicking calculators: Contribution of embodied representations to sentence comprehension. *Journal of Memory and Language*, *59*, 256–265. https://doi.org/10.1016/j.jml.2008.05.003

Melloni, M., Sedeno, L., Hesse, E., García-Cordero, I., Mikulan, E., Plastino, A., et al. (2015). Cortical dynamics and subcortical signatures of motor–language coupling in Parkinson's disease. *Scientific Reports*, *5*, 11899. https://doi.org/10.1038/srep11899, PubMed: 26152329

Mirabella, G., Iaconelli, S., Spadacenta, S., Federico, P., & Gallese, V. (2012). Processing of hand-related verbs specifically affects the planning and execution of arm reaching movements. *PLoS One*, *7*, e35403. https://doi.org/10.1371/journal.pone.0035403, PubMed: 22536380

Moguilner, S., Birba, A., Fino, D., Isoardi, R., Huetagoyena, C., Otoya, R., et al. (2021). Multimodal neurocognitive markers of frontal lobe epilepsy: Insights from ecological text processing. *Neuroimage*, *235*, 117998. https://doi.org/10.1016/j.neuroimage.2021.117998, PubMed: 33789131

Mollo, G., Pulvermüller, F., & Hauk, O. (2016). Movement priming of EEG/MEG brain responses for action-words characterizes the link between language and action. *Cortex*, *74*, 262–276. https://doi.org/10.1016/j.cortex.2015.10.021, PubMed: 26706997

Moran, A., Campbell, M., Holmes, P., & MacIntyre, T. (2012). Mental imagery, action observation and skill learning. *Skill Acquisition in Sport: Research, Theory and Practice*, *94*.

Mueller, S. C., Swainson, R., & Jackson, G. M. (2009). ERP indices of persisting and current inhibitory control: A study of saccadic task switching. *Neuroimage*, *45*, 191–197. https://doi.org/10.1016/j.neuroimage.2008.11.019, PubMed: 19100841

Nazir, T. A., Hrycyk, L., Moreau, Q., Frak, V., Cheylus, A., Ott, L., et al. (2017). A simple technique to study embodied language processes: The grip force sensor. *Behavior Research Methods*, *49*, 61–73. https://doi.org/10.3758/s13428-015-0696-7, PubMed: 26705116

Nguyen, V. T., Breakspear, M., & Cunnington, R. (2014). Fusing concurrent EEG–fMRI with dynamic causal modeling: Application to effective connectivity during face perception. *Neuroimage*, *102*, 60–70. https://doi.org/10.1016/j.neuroimage.2013.06.083, PubMed: 23850464

Niazi, I. K., Jiang, N., Tiberghien, O., Nielsen, J. F., Dremstrup, K., & Farina, D. (2011). Detection of movement intention from single-trial movement-related cortical potentials. *Journal of Neural Engineering*, *8*, 066009. https://doi.org/10.1088/1741-2560/8/6/066009, PubMed: 22027549

Nichols, T. E., & Holmes, A. P. (2002). Nonparametric permutation tests for functional neuroimaging: A primer with examples. *Human Brain Mapping*, *15*, 1–25. https://doi.org/10.1002/hbm.1058, PubMed: 11747097

Nunez, P. L., & Srinivasan, R. (2006). *Electric fields of the brain: The neurophysics of EEG*. Oxford: Oxford University Press. https://doi.org/10.1093/acprof:oso/9780195050387.001.0001

Özyürek, A., Willems, R. M., Kita, S., & Hagoort, P. (2007). On-line integration of semantic information from speech and gesture: Insights from event-related brain potentials. *Journal of Cognitive Neuroscience*, *19*, 605–616. https://doi.org/10.1162/jocn.2007.19.4.605, PubMed: 17381252

Papeo, L., Vallesi, A., Isaja, A., & Rumiati, R. I. (2009). Effects of TMS on different stages of motor and non-motor verb processing in the primary motor cortex. *PLoS One*, *4*, e4508. https://doi.org/10.1371/journal.pone.0004508, PubMed: 19240793

Penolazzi, B., Hauk, O., & Pulvermüller, F. (2007). Early semantic context integration and lexical access as revealed by event-related brain potentials. *Biological Psychology*, *74*, 374–388. https://doi.org/10.1016/j.biopsycho.2006.09.008, PubMed: 17150298

Pulvermüller, F. (2013a). How neurons make meaning: Brain mechanisms for embodied and abstract-symbolic semantics. *Trends in Cognitive Sciences*, *17*, 458–470. https://doi.org/10.1016/j.tics.2013.06.004, PubMed: 23932069

Pulvermüller, F. (2013b). Semantic embodiment, disembodiment or misembodiment? In search of meaning in modules and neuron circuits. *Brain and Language*, *127*, 86–103. https://doi.org/10.1016/j.bandl.2013.05.015, PubMed: 23932167

Pulvermüller, F. (2018). Neural reuse of action perception circuits for language, concepts and communication. *Progress in Neurobiology*, *160*, 1–44. https://doi.org/10.1016/j.pneurobio.2017.07.001, PubMed: 28734837

Pulvermüller, F., Härle, M., & Hummel, F. (2001). Walking or talking?: Behavioral and neurophysiological correlates of action verb processing. *Brain and Language*, *78*, 143–168. https://doi.org/10.1006/brln.2000.2390, PubMed: 11500067

Pulvermüller, F., Shtyrov, Y., & Ilmoniemi, R. (2005). Brain signatures of meaning access in action word recognition. *Journal of Cognitive Neuroscience*, *17*, 884–892. https://doi.org/10.1162/0898929054021111, PubMed: 15969907

Salamone, P. C., Esteves, S., Sinay, V. J., García-Cordero, I., Abrevaya, S., Couto, B., et al. (2018). Altered neural signatures of interoception in multiple sclerosis. *Human Brain Mapping*, *39*, 4743–4754. https://doi.org/10.1002/hbm.24319, PubMed: 30076770

Santana, E. J., & de Vega, M. (2013). An ERP study of motor compatibility effects in action language. *Brain Research*, *1526*, 71–83. https://doi.org/10.1016/j.brainres.2013.06.020, PubMed: 23796780

Sato, M., Mengarelli, M., Riggio, L., Gallese, V., & Buccino, G. (2008). Task related modulation of the motor system during language processing. *Brain and Language*, *105*, 83–90. https://doi.org/10.1016/j.bandl.2007.10.001, PubMed: 18054379

Schmidt-Snoek, G. L., Drew, A. R., Barile, E. C., & Agauas, S. J. (2015). Auditory and motion metaphors have different scalp distributions: An ERP study. *Frontiers in Human Neuroscience*, *9*, 126. https://doi.org/10.3389/fnhum.2015.00126, PubMed: 25821433

Senderecka, M., Grabowska, A., Szewczyk, J., Gerc, K., & Chmylak, R. (2012). Response inhibition of children with ADHD in the stop-signal task: An event-related potential study. *International Journal of Psychophysiology*, *85*, 93–105. https://doi.org/10.1016/j.ijpsycho.2011.05.007, PubMed: 21641941

Sharma, N., Pomeroy, V. M., & Baron, J.-C. (2006). Motor imagery: A backdoor to the motor system after stroke? *Stroke*, *37*, 1941–1952. https://doi.org/10.1161/01.STR.0000226902.43357.fc, PubMed: 16741183

Shibasaki, H., & Hallett, M. (2006). What is the Bereitschaftspotential? *Clinical Neurophysiology*, *117*, 2341–2356. https://doi.org/10.1016/j.clinph.2006.04.025, PubMed: 16876476

Shibasaki, H., Barrett, G., Halliday, E., & Halliday, A. (1980). Components of the movement-related cortical potential and their scalp topography. *Electroencephalography and Clinical Neurophysiology*, *49*, 213–226. https://doi.org/10.1016/0013-4694(80)90216-3, PubMed: 6158398

Siemionow, V., Yue, G. H., Ranganathan, V. K., Liu, J. Z., & Sahgal, V. (2000). Relationship between motor activity-related cortical potential and voluntary muscle activation. *Experimental Brain Research*, *133*, 303–311. https://doi.org/10.1007/s002210000382, PubMed: 10958520

Smith, A. L., & Staines, W. R. (2006). Cortical adaptations and motor performance improvements associated with short-term bimanual training. *Brain Research*, *1071*, 165–174. https://doi.org/10.1016/j.brainres.2005.11.084, PubMed: 16405871

Sokoliuk, R., Calzolari, S., & Cruse, D. (2019). Dissociable electrophysiological correlates of semantic access of motor and non-motor concepts. *Scientific Reports*, *9*, 1–14. https://doi.org/10.1038/s41598-019-47835-9, PubMed: 31391537

Spadacenta, S., Gallese, V., Fragola, M., & Mirabella, G. (2014). Modulation of arm reaching movements during processing of arm/hand-related action verbs with and without emotional connotation. *PLoS One*, *9*, e104349. https://doi.org/10.1371/journal.pone.0104349, PubMed: 25093410

Springer, A., & Prinz, W. (2010). Action semantics modulate action prediction. *Quarterly Journal of Experimental Psychology*, *63*, 2141–2158. https://doi.org/10.1080/17470211003721659, PubMed: 20526978

Toma, K., Matsuoka, T., Immisch, I., Mima, T., Waldvogel, D., Koshy, B., et al. (2002). Generators of movement-related cortical potentials: fMRI-constrained EEG dipole source analysis. *Neuroimage*, *17*, 161–173. https://doi.org/10.1006/nimg.2002.1165, PubMed: 12482074

Travers, E., Khalighinejad, N., Schurger, A., & Haggard, P. (2020). Do readiness potentials happen all the time? *Neuroimage*, *206*, 116286. https://doi.org/10.1016/j.neuroimage.2019.116286, PubMed: 31629833

Tucker, M., & Ellis, R. (2004). Action priming by briefly presented objects. *Acta Psychologica*, *116*, 185–203. https://doi.org/10.1016/j.actpsy.2004.01.004, PubMed: 15158182

Vilas, M. G., Santilli, M., Mikulan, E., Adolfi, F., Caro, M. M., Manes, F., et al. (2019). Reading Shakespearean tropes in a foreign tongue: Age of L2 acquisition modulates neural responses to functional shifts. *Neuropsychologia*, *124*, 79–86. https://doi.org/10.1016/j.neuropsychologia.2019.01.007, PubMed: 30664853

Wang, L., Jensen, O., Van den Brink, D., Weder, N., Schoffelen, J. M., Magyari, L., et al. (2012). Beta oscillations relate to the N400m during language comprehension. *Human Brain Mapping*, *33*, 2898–2912. https://doi.org/10.1002/hbm.21410, PubMed: 22488914

Wang, H., Li, J., Wang, X., Jiang, M., Cong, F., & de Vega, M. (2019). Embodiment effect on the comprehension of Mandarin manual action language: An ERP study. *Journal of Psycholinguistic Research*, *48*, 713–728. https://doi.org/10.1007/s10936-018-09627-6, PubMed: 30656462

Weekes, B. S. (1997). Differential effects of number of letters on word and nonword naming latency. *Quarterly Journal of Experimental Psychology*, *50*, 439–456. https://doi.org/10.1080/713755710

Wu, Y. C., & Coulson, S. (2005). Meaningful gestures: Electrophysiological indices of iconic gesture comprehension. *Psychophysiology*, *42*, 654–667. https://doi.org/10.1111/j.1469-8986.2005.00356.x, PubMed: 16364061

Yazawa, S., Ikeda, A., Kunieda, T., Ohara, S., Mima, T., Nagamine, T., et al. (2000). Human presupplementary motor area is active before voluntary movement: Subdural recording of Bereitschaftspotential from medial frontal cortex. *Experimental Brain Research*, *131*, 165–177. https://doi.org/10.1007/s002219900311, PubMed: 10766269

Yoris, A., Abrevaya, S., Esteves, S., Salamone, P., Lori, N., Martorell, M., et al. (2018). Multilevel convergence of interoceptive impairments in hypertension: New evidence of disrupted body–brain interactions. *Human Brain Mapping*, *39*, 1563–1581. https://doi.org/10.1002/hbm.23933, PubMed: 29271093

Yoris, A., García, A. M., Traiber, L., Santamaría-García, H., Martorell, M., Alifano, F., et al. (2017). The inner world of overactive monitoring: Neural markers of interoception in obsessive–compulsive disorder. *Psychological Medicine*, *47*, 1957–1970. https://doi.org/10.1017/S0033291717000368, PubMed: 28374658

NEUROSCIENCE

RESEARCH ARTICLE

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Body into Narrative: Behavioral and Neurophysiological Signatures of Action Text Processing After Ecological Motor Training

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Abstract—Embodied cognition research indicates that sensorimotor training can influence action concept processing. Yet, most studies employ isolated (pseudo)randomized stimuli and require repetitive single-effector responses, thus lacking ecological validity. Moreover, the neural signatures of these effects remain poorly understood. Here, we examined whether immersive bodily training can modulate behavioral and functional connectivity correlates of action-verb processing in naturalistic narratives. The study involved three phases. First, in the Pre-training phase, 32 healthy persons listened to an action text (rich in movement descriptions) and a non-action text (focused on its characters' perceptual and mental processes), completed comprehension questionnaires, and underwent resting-state electroencephalogram (EEG) recordings. Second, in the four-day Training phase, half the participants completed an exergaming intervention (eliciting full-body movements for 60 min a day) while the remaining half played static videogames (requiring no bodily engagement other than button presses). Finally, in the Post-training phase, all participants repeated the Pre-training protocol with different action and non-action texts and a new EEG session. We found that exergaming selectively reduced action-verb outcomes and fronto-posterior functional connectivity in the motor-sensitive $\sim$ 10–20 Hz range, both patterns being positively correlated. Conversely, static videogame playing yielded no specific effect on any linguistic category and did not modulate functional connectivity. Together, these findings suggest that action-verb processing and key neural correlates can be focally influenced by full-body motor training in a highly ecological setting. Our study illuminates the role of situated experience and sensorimotor circuits in action-concept processing, addressing calls for naturalistic insights on language embodiment.

Key words: Embodied cognition, Action concepts, Exergaming, Naturalistic texts, Functional connectivity.

INTRODUCTION

Emerging findings suggest that action concept processing may be influenced by sensorimotor training (Yang, 2014). However, no study has combined naturalistic texts with real-life physical activity and relevant neural measures, creating a gap between embodiment research and ecological approaches to neurocognition. To tackle the issue, we investigated behavioral and functional connectivity (FC) signatures of action text (AT) and non-action text (nAT) processing before and after (i) an exergaming intervention and (ii) a static gaming intervention.

In healthy persons, processing of action concepts (linguistic units denoting physical movements) distinctly hinges on motor brain mechanisms (Pulvermüller, 2018; García et al., 2019; Birba et al., 2021; Moguilner et al., 2021a, 2021b) and proves sensitive to individual bodily experience (Yang, 2014; Bidet-Ildei et al., 2017; Beauprez et al., 2020). For example, professional athletes outperform novices in processing sport-specific (as opposed to general) action sentences (Beilock et al., 2008), especially when motorically feasible movements are described (Tomasino et al., 2012, 2013). Similarly, sentence-picture congruency judgments are facilitated

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Abbreviations: AT, action text; EEG, electroencephalogram; FC, functional connectivity; nAT, non-action text; Post-T, post-training; Pre-T, pre-training; T, training; WBB, Wii balance board; wSMI, weighted symbolic mutual information.

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upon three weeks of complex manual action training (Locatelli et al., 2012). Yet, opposite effects have been documented following shorter motor stimulation periods. For instance, upon 20 min of displacing objects toward or away from one's body, semantic decisions on directionally congruent sentences become significantly slower (Glenberg et al., 2008). Compatibly, short-lived upregulation of the primary motor cortex selectively reduces action-verb outcomes during lexical decision (Gijssels et al., 2018). Thus, action concept processing can be distinctly modulated by changes induced in the sensorimotor system, with briefer engagement periods seemingly involving interference effects. Yet, this evidence fails to tackle two outstanding questions for embodied language models: do similar effects emerge under ecologically valid conditions, involving naturalistic texts and real-life bodily activities? And, if so, what are their underlying neural mechanisms?

As regards the first question, emerging research shows that the motor system critically supports comprehension of actions described in naturalistic ATs, relative to nATs (Garcia et al., 2018; Birba et al., 2020a, 2020b, 2021; Moguilner et al., 2021b). Evidence from dyslexic children shows that a sustained exergaming protocol (playing full-body-immersion videogames over nine days, 90 min a day) selectively enhanced comprehension of AT verbs relative to nAT verbs and circumstantial information, there being no effects for static videogames (Trevisan et al., 2017). Yet, shorter modulations of the sensorimotor system may trigger opposite results, especially in neurotypicals. Indeed, hyper-excitation of the primary motor cortex via direct current stimulation selectively reduces comprehension of AT verbs – again, relative to nAT verbs and circumstantial information (Birba et al., 2020a, 2020b). Potentially, then, a short exergaming protocol in healthy persons may also selectively interfere with AT verb processing, as previously observed for action sentences following short-term manual training (Glenberg et al., 2008).

Concerning the second question, indirect evidence points to potential neural underpinnings of such effects. Motor training may either boost (Tan et al., 2016) or decrease (Di et al., 2012; Wang et al., 2016) FC between fronto-parietal regions subserving sensorimotor functions. Importantly, lower fronto-parietal connectivity has been associated to reduced AT verb outcomes (Moguilner et al., 2021b), highlighting the relevance of brain coupling measures to establish signatures of the domain. A critical metric is afforded by electroencephalogram (EEG)-derived FC, a method that captures (de)coupling patterns across relevant oscillatory networks (Palva and Palva, 2012). Crucially, these include frontal and fronto-posterior FC modulations in low frequency bands (below 20 Hz) sensitive to motor activity/training (Orgs et al., 2008; Denis et al., 2017) as well as naturalistic AT reading (Birba et al., 2020a) and AT verb comprehension (Birba et al., 2021). Accordingly, the impact of bodily training on AT verb outcomes might be mediated by specific fronto-posterior FC patterns below 20 Hz.

Against this background, we investigated whether short-term bodily training modulates behavioral and neural signatures of AT and nAT processing. We quantified comprehension of action, non-action, and circumstantial information before and after a four-day exergaming protocol and evaluated associated EEG-derived FC patterns with the weighted symbolic mutual information (wSMI) metric (shown to capture non-linear information sharing associated with action concept processing) (Melloni et al., 2015; Birba et al., 2020a, 2021). To test for specificity, as a control condition, we replicated the experiment with a second group of participants who played static videogames (requiring no full body movement).

We raised three hypotheses. First, we predicted that exergaming would selectively affect AT verb outcomes. Second, we anticipated that no such effects would be observed in the non-motor videogame group. Third, we hypothesized that exergaming would modulate fronto-posterior FC in the $\sim$ 10–20 Hz range. Finally, we predicted that AT verb outcomes following exergaming would correlate with training-induced FC changes. With this design, we aimed to bridge the gap between embodied and ecological neurolinguistic models.

EXPERIMENTAL PROCEDURES

We report how we determined our sample size, all data exclusions (if any), all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

Participants

The study comprised 38 healthy Spanish speakers (27 female) complying with the following inclusion criteria: (i) no history of psychiatric or neurological disease, (ii) normal or corrected-to-normal vision and hearing, (iii) minimal exposure to videogames at large (less than three hours per week), (iv) null exposure to exergames in the last three months, (v) low levels of physical activity (less than three hours of regular exercising per week in the last three months, upon exclusion of high-level athletes and persons with high exposure to sports practice in childhood and adolescence), and (vi) commitment not to play videogames at home or doing extra physical activity during the course of the study. Participants were randomly allocated to the exergaming (EG) group and the static gaming (SG) group. Upon exclusion of six subjects due to extremely low performance in the naturalistic text task ($\leq$30 % accuracy on any condition from any text before the gaming protocol), the final sample comprised 16 participants in the EG group and 16 in the SG group. All these participants completed the full protocol. Both samples were matched for sex, age, years of education, handedness, physical activity profile, vocabulary knowledge, and working memory skills (Table 1). A power estimation analysis showed that this sample size conferred sufficient statistical power to reach reliable effects (see Supplementary material 1). All participants read and signed an informed consent form in

Table 1. Participants' demographic, physical, and cognitive profile.

	EG group $n = 16$	**SG group** $n = 16$	**EG group vs SG group** *p*-value[a]	Cohen's *d*
Demographic data				
Sex (F:M)	9:7	13:3	0.25	–
Handedness (R:L)[b]	12:4	13:3	1	–
Years of age	22.06 (2.87)	23.69 (3.77)	0.18	0.49
Years of education	14.75 (3.02)	16.13 (3.56)	0.25	0.42
Physical activity profile				
Physical activity load at present	1.03 (1.44)	0.97 (1.6)	0.91	0.49
Sports practice load in childhood and adolescence	3.47 (2.06)	4.3 (3.43)	0.42	0.29
Years of sports practice in childhood and adolescence	5.25 (3.84)	5.8 (4.26)	0.71	0.12
Cognitive profile				
Vocabulary knowledge[c]	151.5 (12.3)	150.9 (18.3)	0.91	0.04
Working memory skills[d]	36.6 (2.26)	36.13 (2.36)	0.57	0.2

Data presented as mean (*SD*), except for sex and handedness. a. Based on unpaired two-tailed *t*-tests (except for sex and handedness), based on a chi-squared test); b. Based on a Spanish version of Edinburgh Handedness Inventory (Oldfield, 1971, Bryden, 1977); c. Based on the Peabody Picture Vocabulary Test III (Dunn and Dunn, 1997); d. Based on a Spanish version (Rodrigo et al., 2014) of Siegel and Ryan's sentence-based working memory test (Siegel and Ryan, 1989). EG: exergaming; SG: static gaming.

accordance with the Declaration of Helsinki. The study was approved by institutional ethics committee.

Main condition: Exergaming group

Our main condition involved all 16 participants from the EG group. The protocol comprised three phases over a six-day period: a pre-training (Pre-T) phase, a training (T) phase, and a post-training (Post-T) phase (Fig. 1). In the Pre-T phase (day 1), participants completed a naturalistic text task alongside sociodemographic and neuropsychological measures. The T phase (days 2–5) consisted of four sessions (one per day, in consecutive days) of motor training via exergames. Finally, in the Post-T phase (day 6), participants performed a new run of the naturalistic text task with materials different from those of the Pre-T phase.

Pre-training phase. Naturalistic text task. *Narratives*. The study involved four short narratives (two ATs,

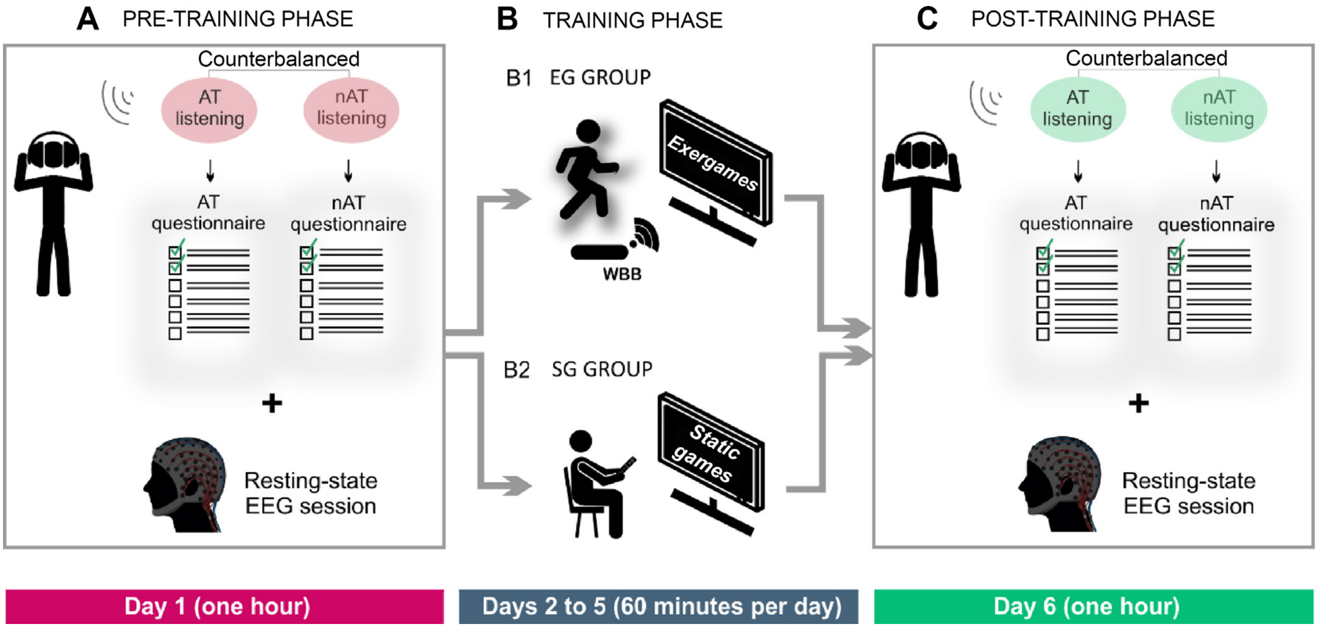

Fig. 1. Study design. **(A)** Pre-training phase: on day 1, subjects first listened to an action text and a non-action text, and answered their corresponding multiple-choice questionnaires (read by the experimenter) after each recording. Then, they sat with eyes closed while EEG activity was recorded at rest. **(B)** Training phase: from days 2 to 5, subjects completed the videogame intervention using the Nintendo® console. **(B1)** Subjects in the EG group performed an exergaming protocol based on Wii Fit Plus software. Multiple bodily movements were required and captured via a Wiimote and a nunchuck while standing on a balance board. **(B2)** Subjects in the SG group played videogames that required minimal body movements, based on Wii Party software, totally controlled via button presses on the wiimote. **(C)** Post-training phase: on day 6, subjects first listened to a different pair of action and non-action texts, and answered their respective multiple-choice questionnaires after each recording. Then they completed the same resting-state EEG protocol administered on day 1. EG: exergaming; SG: static gaming.

two nATs). These were composed through a validated procedure (Trevisan and García, 2019) capturing embodied effects in diverse settings (Garcia et al., 2018; Birba et al., 2020b, 2021; Moguilner et al., 2021b), including longitudinal (i.e., post vs pre training) exergaming research (Trevisan et al., 2017). The ATs described multiple bodily movements of their characters, including physical interactions with people and objects (e.g., *Peter took his brother's hand and both ran towards the sea*). Conversely, the nATs focused on non-motoric events, such as the characters' feelings, thoughts, and perceptions (e.g., *Albert heard his favorite song and felt uplifted*). Each narrative abounded in details regarding the story's location, elements, and other setting details (collectively termed 'circumstances' in the present paradigm). The full texts and their approximate English translations are transcribed in Supplementary material 2.

All four narratives were built on the same set of 22 grammatical patterns, pseudo-randomly sequenced for each text and filled with strategic lexical items. Each text contained critical verbs manifesting the action versus non-action contrast, following semantic, syntactic, and distributional criteria (Halliday and Matthiessen, 2014). The texts were matched for (i) character count; (ii) and content-word-type counts; (iii) mean content-word frequency, familiarity, syllabic length, number of letters, and imageability; (iv) sentence and sentence-type counts; (v) reading difficulty; (vi) readability ratings; (vii) overall emotional content; and (viii) arousal level. Furthermore, the specific verbs targeted by each verb-related question in the questionnaires were matched for frequency, familiarity, syllabic length, number of letters, and imageability. See Table 2 for statistical details.

The texts were audio-recorded by a male native speaker of *rioplatense* Spanish, the participants' native dialect. A smooth narration pace was used in all cases. The files were recorded in.mp3 format with stereo output, and each of them lasted roughly 100 s (all audio files and their scripts are available upon request). Analyses performed with Neuro-Speech (Orozco-Arroyave et al., 2018) confirmed that the four narratives did not differ significantly in terms of voiced segments, silence segments, average fundamental frequency, and average energy (Table 2).

Questionnaires. Each text was accompanied with a 20-item multiple-choice questionnaire, previously used with healthy adults (Birba et al., 2020b). In each questionnaire, 10 questions referred to verb-related information while the other 10 pointed to circumstantial (locative, causal, temporal or modal) information, realized by adverbial or prepositional phrases. All verb-related questions in the AT questionnaires referred to action verbs, and those in the nAT questionnaires pointed to non-action verbs. Questions were presented following the sequence of the corresponding events in the texts, alternating between verb-related and circumstantial items. Five answer options accompanied each question: one correct option, three subtly incorrect options, and an 'I don't remember' option. Sequencing of the options was randomized, except for the 'I don't remember' option, which always appeared last. Correct responses were given one point. Incorrect answers and the 'I don't remember' option were given zero points. Therefore, each questionnaire had a maximum score of 20 points (10 for verb-related questions and 10 for circumstantial questions).

Procedure. The assessment was carried out in a noiseless, dimly lit room. First, participants were informed about the study's protocol and materials. They were then asked to listen attentively to each text (AT, nAT) with their eyes closed. The recordings were presented through professional, high-definition headphones (Sony MDR-XB950B1). At the end of each recording, an experimenter (the same for all participants) read each questionnaire item and its corresponding options. No time limit was established for participants to choose their option, and they could ask for one repetition (items for which more than one repetition was requested obtained zero points). The examiner marked the selected option on a scoring sheet. After a short break, this procedure was repeated with the next audio. The AT and the nAT were counterbalanced across participants considering which text of each type was used and the order in which they were presented.

Training phase. All training sessions were conducted in a separate customized room under supervision of an examiner. Participants were invited to play energetically, aiming to achieve the highest scores possible. Each session totaled 60 min of actual exergaming, with an optional ten-minute break after the first half. Participants played all games on their feet, standing at about 2 m from a 50-inch ultra HD smart TV. Game audio was delivered through wireless professional headphones (Sony MDR-XB950B1). We used the Nintendo Wii Fit Plus gaming software, used to modulate sensorimotor-system activity in neuro-rehabilitation (Goble et al., 2014), sport rehabilitation (Baltaci et al., 2013), and training of healthy elderly persons (Toulotte et al., 2012). The system involves two haptic sensor-based manual controllers (Wiimote and Nanchuck) and a force platform (Wii balance board, WBB).

The exergaming protocol encompassed 14 games from Wii Fit Plus, chosen by a physiotherapist to maximize neuromuscular engagement through a combination of mobility, coordination, and balance demands. All games required moving an avatar that reflects the participant's three-dimensional movements, via accelerations of the controllers and displacement of the center or pressure over the WBB. The games were classified into three categories, namely: aerobic games (e.g., 'Obstacle Course,' which involves running, jumping, and dodging obstacles), high-precision balance games (e.g., 'Table Tilt Plus,' which requires shifting the body weight to tilt a moving platform and insert balls into holes), and fast-reaction games (e.g., 'Snowball Fight,' which involves quick movements for throwing snowballs while avoiding incoming ones). Two games from Wii Party software, taxing oculo-manual coordination skills, were added to complement the motor training.

Table 2. Linguistic features of the texts.

	AT 1	**AT 2**	**nAT 1**	**nAT 2**	***p*-values**
Characters	941	908	976	934	0.47$^{\#}$
Words	207	203	204	199	0.98$^{\#}$
Nouns	48	48	44	43	0.93$^{\#}$
Adjectives	7	8	9	10	0.90$^{\#}$
Adverbs	6	8	8	8	0.94$^{\#}$
Verbs	32	32	32	32	1$^{\#}$
Action verbs	24	28	1	2	$X^2 = 9.94$, $p < .001$. Tukey's HSD tests showed that each NT differed from both ATs (*ps* < 0.001), with no differences between NTs or ATs (all *ps* > 0.58)
Non-action verbs	8	4	31	30	
Content word frequency	1.64 (0.08)	1.67 (0.08)	1.79 (0.08)	1.79 (0.08)	0.38*
Content word familiarity	6.17 (0.08)	6.00 (0.09)	6.28 (0.08)	6.23 (0.09)	0.11*
Content word syllabic length	2.50 (0.08)	2.50 (0.09)	2.44 (0.09)	2.52 (0.09)	0.88*
Content word imageability	5.17 (0.16)	5.27 (0.17)	4.96 (0.16)	4.89 (0.17)	0.33*
Target verb frequency	1.08 (0.16)	1.48 (0.17)	1.10 (0.18)	1.43 (0.17)	0.22*
Target verb familiarity	5.61 (0.36)	6.20 (0.28)	6.23 (0.34)	6.09 (0.30)	0.58*
Target verb syllabic length	2.63 (0.19)	2.4 (0.18)	2.88 (0.19)	2.66 (0.17)	0.35*
Mean target verb imageability	6.45 (0.42)	6.70 (0.44)	7.55 (0.46)	6.55 (0.46)	0.31*
Complex sentences	7	7	8	8	0.99$^{\#}$
Comprehensibility	4.5 (0.20)	4.10 (0.19)	4.38 (0.19)	4.18 (0.19)	0.44*
Coherence	4.0 (0.22)	3.52 (0.21)	4.00 (0.21)	3.73 (0.21)	0.32*
Grammatical Correctness	4.45 (0.18)	4.14 (0.17)	4.24 (0.17)	4.36 (0.17)	0.28*
Reading difficulty[a]	79.38	79.93	77.9	75.09	0.98
Readability[b]	Fairly Easy	Fairly easy	Fairly Easy	Fairly easy	-
Emotional valence[c] **(main effect of text)**	33.38 (1.40)	33.54 (1.40)	33.33 (1.40)	33.23 (1.40)	0.99*
Arousal[d] **(main effect of text)**	2.02 (0.12)	2.40 (0.12)	2.14 (0.12)	2.44 (0.12)	*F* (240,3) = 2.82, *p* = .04. Tukey's HSD test (MSE = 0.43 *df* = 240) showed no differences among texts (all *ps* > 0.05)
Number of voiced segments	184	202	177	228	0.21$^{\#}$
Number of silence segments	61	61	60	64	0.23$^{\#}$
Fundamental frequency (Hz)	115.05 (27.24)	111.6 (27.09)	112.6 (26.1)	115.83 (26.36)	0.3871*
Energy (dB)	10.29 (12.29)	11.61 (13.48)	9.5 (12.02)	10.03 (12.19)	0.3893*

a. Measured through the Szigriszt-Pazos Index; b. Measured through the Inflesz scale; c. Overall emotional content was established by 31 Spanish-speaking readers who rated each sentence in each text as positive, neutral, or negative; d. Arousal level was established by the same panel of raters as the intensity of the chosen emotion on a scale from 1 (null arousal) to 7 (high arousal). The hashtag (#) denotes *p*-values calculated with chi-squared test. The asterisk (*) denotes *p*-values calculated with independent measures ANOVA, considering text as a factor.

We created four game sets of five different games each, aiming for maximal within-session variability and between-session homogeneity (see videogame list in Supplementary material 3). A different game set was administered randomly in each of the four sessions. Each game was played for 10 min and then the participant could choose which game to replay in order to complete the 60 min of training.

Post-training phase. The post-T phase consisted in the very same naturalistic text protocol used in the pre-T phase, except that the texts employed here were those not employed in the pre-T phase. The order of the texts in this phase was counterbalanced across participants.

Control condition: Static gaming group

To assess whether potential effects in the EG group were due to video-gaming at large, as opposed to exergaming in particular, we included a control condition involving all 16 participants from the SG group. The protocol was identical to that of the main condition, except that the games used during the T phase were characterized by a low degree of dynamic bodily engagement.

Specifically, we selected 16 games from the Wii Party software that induced amusement while minimizing movement demands (Supplementary material 3). All of them were played using only the Wiimote. Three games involved mental prediction tasks (e.g., in 'Walk-off,' the player keeps a button pressed to keep an avatar running, at a given speed, and must release it when she estimates a predefined distance has been reached). In five games, the player had to aim at the target (the avatar or an object) with the Wiimote's infrared sensor in order to select it or move it (e.g., in 'Garden Gridlock,' the player must place the avatar on the right point of a maze to reach the goal). In the other eight games, the player had to control a character by pressing buttons (e.g., in 'Zombie Tag,' correct button presses are required to elude zombies). All these games were played in sitting position. Most of them required solely-two-finger movements to press buttons, and some required aiming the Wiimote at the screen to select an option. None of the games required movements of the arms, legs, trunk or head.

Behavioral data analysis

Following a previous report of this paradigm (Trevisan et al., 2017), questionnaire scores from each condition (main condition: EG group; control condition: SG group) were analyzed with a 2 × 2 × 2 factorial ANOVA including the factors Text type (AT, nAT), Information type (verb-related, circumstantial), and Time point (Pre-T, Post-T). Given our moderate sample sizes and the highly specific nature of our hypotheses (i.e., selective Post-T modulations for AT verbs but not for nAT verbs or circumstances from either text), significant main and interaction effects were further analyzed via planned pairwise comparisons through paired two-tailed *t*-tests. Effect sizes were calculated through partial eta square (η_p^2) for ANOVA results and Cohen's *d* for pairwise comparisons (Cohen, 1988). All analyses were performed on R 4.0.3.

Electroencephalogram (EEG) data acquisition and preprocessing

Resting-state EEG data were recorded for 10 consecutive minutes while participants sat comfortably on a reclining chair in a Faraday cage with a Biosemi Active Two 64-channel system (Amsterdam, NLD). Participants were instructed to keep their eyes closed and to think about nothing in particular (Dottori et al., 2017; Birba et al., 2021). Signals were originally sampled at 1024 Hz and then down-sampled to 512 Hz. During recording, the reference was set as default to link mastoids and re-referenced offline to the average of all electrodes. Signals were band-pass filtered offline between 0.1 and 100 Hz. We also applied a digital bandpass filter between 0.5 and 40 Hz offline to remove unwanted frequency components. Bad channels were replaced via means of the statistically weighted spherical interpolation (based on neighboring sensors) method (Courellis et al., 2016). Clean resting-state recordings were then segmented into 4-second trials (Amoruso et al., 2022). A two-tailed paired *t*-test showed that the number of trials for the EG group did not significantly differ [$t(14) = -0.82$, $p = .43$] between Post-T (mean = 248.67, *SD* = 41.06) and Pre-T (mean = 256.73, *SD* = 21.97) sessions. The same analysis revealed non-significant differences in the SG group [$t(15) = -0.89$, $p = .39$] between the Post-T (mean = 235.75, *SD* = 22.57) and Pre-T (mean = 243.44, *SD* = 22.68) sessions. Preprocessing was performed with the EEGLAB toolbox (Delorme and Makeig, 2004) and custom-made scripts.

Electroencephalogram resting-state functional connectivity analysis

Electroencephalogram (EEG) resting-state FC analyses were performed for the EG and SG groups separately (one participant from the EG group was excluded as he lacked EEG recordings in the Pre-T phase). We employed the weighted Symbolic Mutual Information (wSMI) metric (King et al., 2013), which proves robust against artefactual coupling and has been used to examine specific lexico-semantic categories in different tasks (Hesse et al., 2019; García et al., 2020), including AT processing (Birba et al., 2020a, 2021). This metric quantifies the amount of information shared by two signals over a given time interval (King et al., 2013). First, the signals are reduced into a set of discrete symbols, defined by a number of points ($k = 3$), separated by a fixed temporal interval τ. This τ determines the frequency bands for which the index becomes most sensitive. Here, we focused on $\tau = 16$ ms, sensitized for the motor-sensitive ~ 10–20 Hz range. Mutual information coefficients were obtained based on the entropies of each transformed signal and their joint entropy. Finally, binary weights are applied to discard pairs of symbols likely arising from common source artifacts (e.g., blink artifacts or volume conduction).

Cluster-based permutation statistics (Maris and Oostenveld, 2007) were performed on the wSMI topographical metrics (Perez et al., 2021) to test for potential training-induced FC changes in each group separately. Specifically, we ran a permutation test on the wSMI coefficient matrices obtained for each subject in each experimental condition (i.e., Pre-T vs Post-T), to obtain clusters of connections based on neighboring criteria (measured through Euclidean distance). Two connections were considered neighbors if both electrodes in one connection were neighbors of the electrodes in the other connection. For each cluster obtained in a given permutation, we quantified its size as the number of intervening connections. The largest cluster size was used as cluster-level statistic in each permutation. As in previous works on AT processing (Birba et al., 2020a), we estimated the *p*-value of each cluster ($p_{cluster}$) in the actually observed data (i.e., before the permutation test was performed) as the proportion of 2,000 random permutations of the wSMI matrices that yielded a cluster-level statistic greater than the size of the given cluster. To identify connections with significant differences between conditions, we ran two-tailed *t*-tests at $p_{connection} < 0.05$. Only those who surpassed this test would be considered part of clusters. Finally, clusters with $p_{cluster} < 0.05$ were deemed significant. This method circumvents the multiple comparisons problem, as $p_{cluster}$ thus obtained do not need to be corrected in further steps.

Brain-behavior correlations

Given the normal distribution of the data we used Pearson correlations to explore potential associations between resting-state FC and behavior. We calculated mean connectivity wSMI values for each participant across the electrodes encompassed in any significant cluster upon subtracting the Post-T and Pre-T sessions, and masked activity within those electrodes in each session separately. Mean connectivity values for each participant within the cluster were correlated with an action-verb index. As in previous work (Birba et al., 2020b), we calculated, for each participant, AT scores in each category adjusted for the corresponding nAT scores (namely, AT verbs minus nAT verbs, and AT circumstances minus nAT circumstances). To further reduced data dimensionality we adjusted performance by text type and category (namely, adjusted AT verbs minus adjusted nAT circumstances). This yielded one action-verb index value per participant, adjusted for all relevant factors in the naturalistic text task.

Data and code availability

All experimental data, as well as the scripts used for their collection and analysis, are fully available online at: https://bit.ly/3zMIBBS.

RESULTS

Main condition: Exergaming group

Results from the EG group revealed that all main effects and double interactions were not significant (all *p*-values > 0.09). Critically, however, a significant triple interaction emerged among Text type, Information type, and Time point [$F(1,105) = 4.81$, $p = .03$, $\eta_p^2 = 0.04$]. Post-hoc comparisons revealed that AT verb outcomes were significantly lower in the Post-T than in the Pre-T phase ($t = -2.8$, $p = .01$, $d = 0.71$), there being no significant differences between phases in any other condition (nAT verbs: $t = 1.8$, $p = .10$, $d = 0.44$; AT circumstances: $t = 1.5$, $p = .17$, $d = 0.36$; nAT circumstances: $t = 0.5$, $p = .64$, $d = 0.12$). Also, whereas all four conditions yielded similar scores in the Pre-T phase (all *p*-values > 0.20), Post-T scores for AT verbs were significantly lower than those of AT circumstances ($t = 2.7$, $p = .02$, $d = 0.68$) and marginally lower than those of nAT verbs ($t = -2.1$, $p = .05$, $d = 0.53$). See Fig. 2A. For full results, see Supplementary material 4.

Control condition: Static gaming group

Results from the SG group revealed a main effect of the Time point [$F(1,105) = 7.51$, $p = .007$, $\eta_p^2 = 0.07$], with better performance on the Post-T than the Pre-T phase ($p = .01$, $d = 0.77$). The main effects of Text type [$F(1,105) = 1.2$, $p = .28$] and Information type [$F(1,105) = 0.08$, $p = .78$] were not significant. A significant interaction emerged between Text type and Information type [$F(1,105) = 4.80$, $p = .031$, $\eta_p^2 = 0.04$], with lower performance for AT verbs than nAT verbs ($p = .04$, $d = 0.55$) and no differences between other condition pairs (all *p*-values > 0.14). No significant differences emerged between Text type and Time point [$F(1,105) = 1.88$, $p = .17$] nor between Information type and Time point [$F(1,105) = 1.88$, $p = .17$]. The triple interaction was not significant [$F(1,105) = 2.71$, $p = .10$]. For details, see Supplementary material 5.

Functional connectivity results

The EG group exhibited significantly lower FC after training over a cluster spanning left temporo-parietal electrodes and bilateral frontal electrodes, at $\tau = 16$ ms (~10–20 Hz) ($p_{connection} < 0.05$; $p_{cluster} = 0.03$). No significant differences were observed between time points in the SG group (all $p_{connection}$-values > 0.05). See Fig. 2B, left inset.

Correlation results

In the EG group, a significant positive correlation ($r = 0.54$, $p = .03$) emerged between the action-verb index and Post-T FC at $\tau = 16$ ms (~10–20 Hz) –i.e., the lower the connectivity, the lower the accuracy on the action-verb index. No correlations were observed between behavioral performance and Pre-T FC ($p = 0.9$). To further understand this pattern, we explored whether Pre-T connectivity levels were associated with pre-training physical activity. To this end, we performed a correlation between physical activity load (weekly hours of physical activity over the preceding three months) and the mean connectivity of the significant cluster. No significant correlation emerged ($r = -0.33$, $p = 0.22$). See Fig. 2B, middle and right insets.

DISCUSSION

We examined whether short-term motor training, via exergaming, modulates processing of action concepts evoked by naturalistic texts. This intervention selectively reduced action-verb outcomes and fronto-posterior connectivity in the ~ 10–20 Hz range, both patterns being significantly correlated. Conversely, static videogame playing yielded no specific effect on any linguistic category, nor did it change FC in the frequency

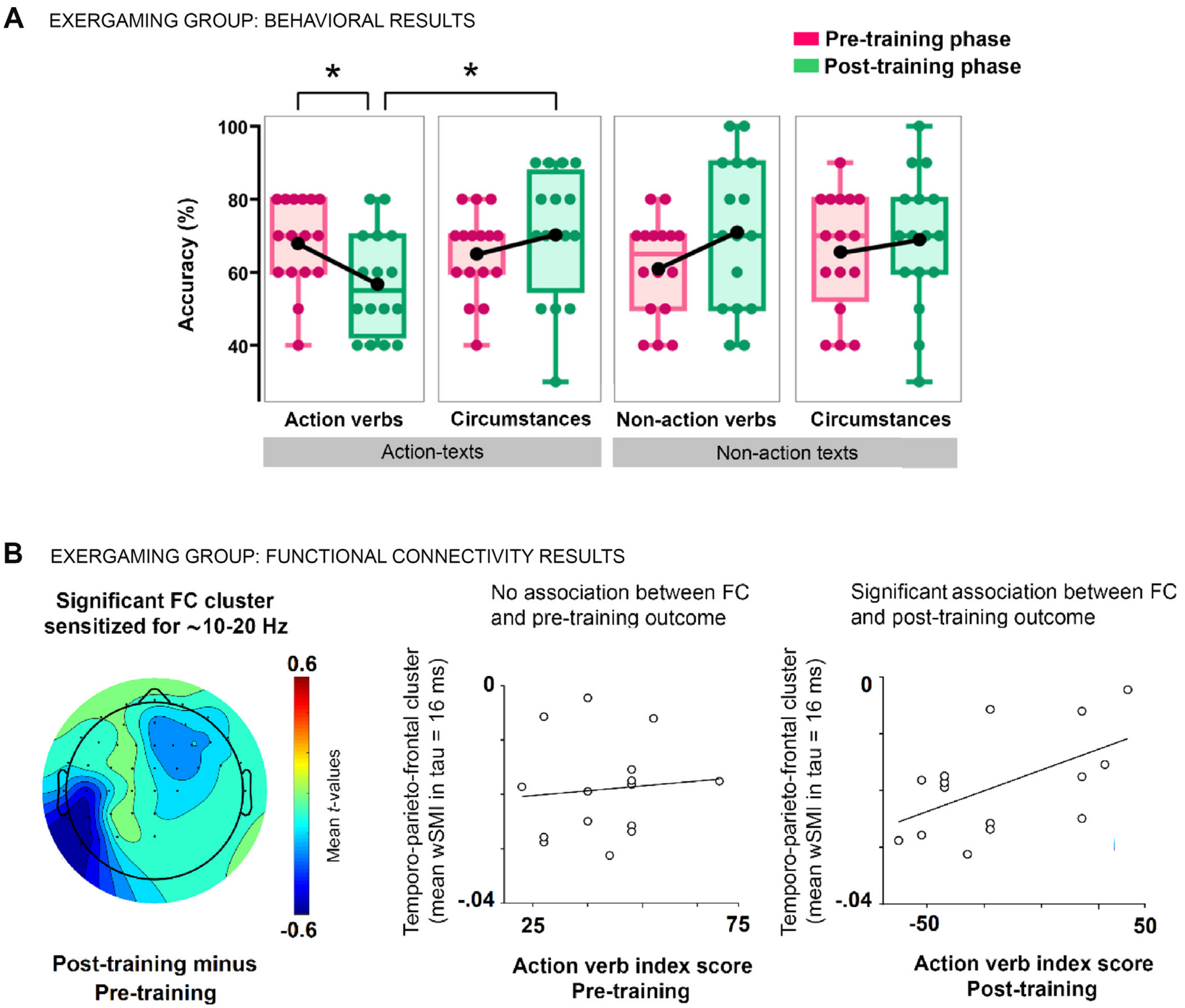

Fig. 2. Behavioral and functional connectivity results in the exergaming group. **(A)** Significant triple interaction among Text type, Information type, and Time point. Post-hoc tests revealed that, while no pairwise comparison was significant in the Pre-T session, Post-T AT verb outcomes were significantly lower than Pre-T AT verb outcomes and Post-T circumstance outcomes. No other pairwise comparison yielded significant differences. Values on the Y-axes indicate percentage of scores. Asterisks (*) indicate significant differences. AT: action text; nAT: non-action text; Pre-T: pre-training; Post-T: post-training. **(B)** Significant lower connectivity (sensitized for the ~ 10–20 Hz range) after training over a cluster spanning left temporo-parieto-frontal electrodes. Color bar indicates *t*-value scaling. Correlation results showed no significant associations between Pre-T FC in the significant cluster and the action-verb index. Conversely, Post-T FC in the significant cluster was positively correlated with the action-verb index. Color bar indicates mean wSMI. FC: functional connectivity.

range under consideration. These findings illuminate the role of bodily experience and sensorimotor circuits in action concept processing, as discussed below.

Exergaming selectively reduced AT verb outcomes, whereas raw scores for every other condition actually increased after the intervention. This category-specific effect aligns with evidence of less efficient action-verb processing following short-lived motor system modulations via physical action training (Glenberg et al., 2008) and non-invasive brain stimulation (Gijssels et al., 2018). In particular, the absence of similar effects on nAT verbs rules out an unspecific impact on processing of verbs as a broad lexical category. In this sense, differential motor-system engagement for action relative to abstract concepts has been reported in word-level (García et al., 2019; Moguilner et al., 2021a) and text-level (Moguilner et al., 2021b) tasks, reinforcing the view that semantic processing hinges on embodied reactivations of modality-specific experiences (García and Ibañez, 2016; Zwaan, 2016; Birba et al., 2017, Pulvermüller, 2018).

AT circumstances were also unaffected by exergaming, corroborating the intervention's focal effects on action concepts, rather than on ATs at large. Note that circumstantial adjuncts conveyed temporal, locative, or logical aspects that are neither semantically nor syntactically required by the regime of action verbs (Halliday and Matthiessen, 2014). It would seem, then, that training-induced simulations did not percolate beyond the semantic reenactment of movements proper. Accordingly, the effects of bodily training seem to be conceptually and grammatically specific to action-related units.

Interestingly, raw scores showed similar Pre/Post changes in the SG condition across all categories. Crucially, however, the magnitude of the difference between Post-T and Pre-T AT verbs was markedly smaller in the SG condition than in the EG condition. This raises the possibility that exergaming *amplified* proto-effects associated with action perception in videogames at large. This view is consistent with the notion that action semantics may be modulated by movement observation, as claimed in previous exergaming research (Trevisan et al., 2017), while accounting for the condition-specific effect observed in the EG group. Yet, this remains speculative. Future studies should be run with larger samples to disentangle the specific contributions of action execution and observation to the observed effects. Be that as it may, our findings reinforce models which posit direct links between situated experiences and germane conceptual domains (Barsalou, 2003; García and Ibañez, 2016).

The direction of this selective effect might seem surprising. Indeed, Trevisan et al. (2017) found that a nine-day exergaming protocol selectively *enhanced* AT verb processing (Trevisan et al., 2017). Importantly, however, such an experiment involved children with dyslexia, a population with known motor system alterations (Fawcett and Nicolson, 1995; Chaix et al., 2007; Marchand-Krynski et al., 2017) –for a meta-analysis, see Obeid et al. (2022). In such a population, we surmise, exergaming may boost *impaired* motor-system dynamics, facilitating semantic processes that hinge on such resources. Contrariwise, in healthy individuals, the same intervention may boost *normal* motor-system dynamics, reaching supra-threshold activation levels that render those circuits unavailable for concomitant processes. This view is consistent with previous findings. In fact, following anodal M1 stimulation, action-verb processing has been shown to *improve* in patients with motor-system deficits (Suárez-García et al., 2021) and to *decrease* in healthy individuals (Birba et al., 2020b). Such patterns may be interpreted in terms of the Hand-Action-Network Dynamic Language Embodiment (HANDLE) model (García and Ibañez, 2016). Indeed, building on dozens of experiments, HANDLE posits that action-verb processing can be primed if motor networks are excited following low baseline activation, but that the same category be interfered with if such excitation follows higher baseline activation.

In addition, the different directionalities of these embodied effects might also be influenced by motor training duration. Whereas the studies yielding action-concept facilitation tended to be considerably long (ranging from nine to 20 days and up to several years) (Beilock et al., 2008; Locatelli et al., 2012; Tomasino et al., 2012, 2013; Trevisan et al., 2017), those resulting in category-specific decrements were substantially briefer (ranging from minutes to only a few days) (Glenberg et al., 2008; Gijssels et al., 2018; Birba et al., 2020b) –note, however, that facilitation may also be attained following shorter practice periods if these involve familiarization with unusual actions (Beauprez et al., 2020) or sustained practice of highly specific actions (Lyons et al., 2010). Our exergaming protocol was considerably short (four 60-min sessions), especially vis-à-vis that of Trevisan et al. (nine 90-min sessions), and the texts did not focus on the specific actions elicited by the exergaming protocol. These differences might also partly account for the studies' discrepant findings. In fact, due to their distinct impact on cortical excitability, brief periods of motor training may be typified by cross-skill interference, whereas longer periods are typically associated with behavioral improvements (Luft and Buitrago, 2005; Dayan and Cohen Leonardo, 2011; Cantarero et al., 2013). Reduced action comprehension could be further promoted by the lack of effector-specific relations between the actions described by the texts and performed by participants (Lyons et al., 2010). Briefly, motor-system integrity at baseline, training duration, and the absence of limb-specific action-semantic couplings may have jointly shaped the behavioral decline observed in the EG group.

Of note, this behavioral effect was mirrored by EEG results. Whereas the SG group showed no FC changes after training, the EG group exhibited reduced temporo-parieto-frontal connectivity. Previous studies showed that specific sensorimotor networks including fronto-parietal hubs may become decoupled following brief training periods (Floyer-Lea and Matthews, 2005). Left temporal and fronto-parietal networks, indeed, become jointly recruited during initial stages of motor training, possibly indexing an early reliance on conscious verbal control (supported via temporal structures) during the acquisition of new visuo-motor patterns (Haufler et al., 2000; Kerick et al., 2001, 2004). In particular, training-dependent motor system modulations seem to be distinctly indexed by alpha and beta activity, including mu rhythms (Orgs et al., 2008; Denis et al., 2017; Amoruso et al., 2022). This evidence aligns with our finding that reduced fronto-parietal connectivity after exergaming occurred exclusively within the $\sim$ 10–20 Hz frequency range. Importantly, recruited brain mechanisms keep reverberating at rest following exposure to new experiences (Lewis et al., 2009; Jolles et al., 2013), suggesting that training-induced effects may have remained operative until the Post-T EEG recording took place.

Crucially, this post-training FC reduction was positively correlated with action-concept outcomes (controlling for other lexical categories), showing that the lower the connectivity, the lower the performance on AT verbs. Other text-level studies (on patient populations) have linked lower outcomes in this category with reduced connectivity along fronto-parietal (Moguilner et al., 2021a) and other sensorimotor (Birba et al., 2021) networks, without comparable effects in non-action categories. In line with embodied views of language (Gallese and Sinigaglia, 2011; Pulvermüller, 2013a, 2013b; Gallese and Cuccio, 2018; Cervetto et al., 2021), this association speaks to a direct link between action semantics and sensorimotor systems, as bodily training would induce proportional changes in their behavioral and FC signatures, respectively. In this sense, our study extends previous evidence on athletes, showing that the neural signatures of action verb processing are shaped by individual experience (Lyons et al., 2010).

Importantly, a complementary analysis showed that Pre-T connectivity was not associated with pre-training physical activity. This suggests that baseline connectivity and exergaming-induced changes were not primarily driven by previous physical activity, reinforcing the generalizability of our results. More particularly, the direction of the significant behavioral and FC effects indicates that connectivity changes induced by newly encoded motor behaviors either *interfered* with linguistic processes supported by this network (Bays et al., 2005; Krakauer et al., 2005; Gagne and Cohen, 2016) or rendered this network *insufficiently engaged* to optimally subserve such processes (García and Ibañez, 2016). Future studies with strategic designs could disentangle between these competing views.

Finally, it is worth stressing that present findings came from a highly ecological setting, involving naturalistic texts and real-life bodily engagement. Most action-language studies, including motor-training protocols, involve responding to (pseudo)randomized sequences of isolated words or sentences with basic and repetitive single-effector actions (Yang, 2014; García and Ibañez, 2016; Kogan et al., 2020). While such evidence is fundamental to capture embodied phenomena, it fails to inform their deployment in everyday scenarios, which often involve rich, coherent, cohesive texts alongside full-body dynamics. Our study bridges this gap with its combination of naturalistic narratives and immersive movements, extending evidence that action-concept processing in naturalistic texts can be selectively impaired due to motor-network disruptions (Garcia et al., 2018; Birba et al., 2021; Moguilner et al., 2021b), decreased upon non-invasive M1 neurostimulation (Birba et al., 2020b), and influenced by linguistic experience (Birba et al., 2020a). Further efforts in this direction are vital to address the plea for more ecological insights in neurolinguistics (Desai et al., 2016; Hasson et al., 2018).

Limitations and further research

This study is not without limitations. First, our sample size was moderate. Although power estimation results attested to its adequacy for present analyses, replication studies should be conducted with more participants. Second, behavioral measures were restricted to 20 items per questionnaire. While other works with similar materials obtained strong findings with even fewer questions (Trevisan et al., 2017; Birba et al., 2021), it would be useful to extend this research line with materials offering an even longer range of possible scores. Third, examination of neural correlates was limited to offline recordings. Despite its usefulness to capture embodied signatures in text-level paradigms (Birba et al., 2021; Moguilner et al., 2021b), such an approach fails to reveal ongoing modulations as meaning is built on-the-fly during language processing. Future works should strive to include real-time EEG measures as participants process both ATs and nATs, as done elsewhere (Birba et al., 2020a). Finally, our design cannot disentangle the relative contributions of action execution and observation to the observed effects. Granted, the SG group exhibited no category-specific effects even though their games' characters did perform bodily movements, suggesting that action observation may not be the primary driver of results in the EG group. Still, given that embodied motor mechanisms can be recruited by virtue of action imagery and visualization (Eaves et al., 2016), future studies should implement strategic designs manipulating the role of both self-initiated and visualized movements during exergaming.

Unlike static videogames, a brief exergaming protocol can selectively undermine action-verb processing in narrative texts. This effect correlates with reduced resting-state FC over left temporo-parieto-frontal electrodes in the $\sim$ 10–20 Hz range, a pattern implicated in motor activity. Jointly, such findings reveal direct neurocognitive links between situated bodily experience and germane semantic categories, while meeting the imperative of ecological validity. Further work along these lines can would be crucial to consolidate a naturalistic neurolinguistic agenda.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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CREDIT AUTHORSHIP CONTRIBUTION STATEMENT

Sabrina Cervetto: Methodology, Formal analysis, Data curation, Writing – original draft. **Agustina Birba:** Methodology, Formal analysis, Writing – original draft, Writing – review & editing. **Gonzalo Pérez:** Formal analysis, Writing – review & editing. **Lucía Amoruso:** Formal analysis, Writing – original draft, Writing – review & editing. **Adolfo M. García:** Conceptualization, Validation, Methodology, Writing – original draft, Writing – review & editing, Supervision, Funding acquisition, Project administration.

REFERENCES

Amoruso L, Pusil S, Garcia AM, Ibanez A (2022) Decoding motor expertise from fine-tuned oscillatory network organization. Hum Brain Mapp 43:2817–2832.

Baltaci G, Harput G, Haksever B, Ulusoy B, Ozer H (2013) Comparison between Nintendo Wii Fit and conventional rehabilitation on functional performance outcomes after hamstring anterior cruciate ligament reconstruction: prospective, randomized, controlled, double-blind clinical trial. Knee Surg Sports Traumatol Arthrosc 21:880–887.

Barsalou L (2003) Situated simulation in the human conceptual system. Lang Cogn Processes 18:513–562.

Bays PM, Flanagan JR, Wolpert DM (2005) Interference between velocity-dependent and position-dependent force-fields indicates that tasks depending on different kinematic parameters compete for motor working memory. Exp Brain Res 163:400–405.

Beauprez S-A, Blandin Y, Almecija Y, Bidet-Ildei C (2020) Physical and observational practices of unusual actions prime action verb processing. Brain Cogn 138 103630.

Beilock SL, Lyons IM, Mattarella-Micke A, Nusbaum HC, Small SL (2008) Sports experience changes the neural processing of action language. Proc Natl Acad Sci U S A 105:13269–13273.

Bidet-Ildei C, Meugnot A, Beauprez SA, Gimenes M, Toussaint L (2017) Short-term upper limb immobilization affects action-word understanding. J Exp Psychol Learn Mem Cogn 43:1129–1139.

Birba A, García-Cordero I, Kozono G, Legaz A, Ibáñez A, Sedeño L, García AM (2017) Losing ground: Frontostriatal atrophy disrupts language embodiment in Parkinson's and Huntington's disease. Neurosci Biobehav Rev 80:673–687.

Birba A, Beltrán D, Caro MM, Trevisan P, Kogan B, Sedeño L, Ibáñez A, García AMJN (2020a) Motor-system dynamics during naturalistic reading of action narratives in first and second language. Neuroimage 216 116820.

Birba A, Vitale F, Padrón I, Dottori M, de Vega M, Zimerman M, Sedeño L, Ibañez A, García AM (2020b) Electrifying discourse: Anodal tDCS of the primary motor cortex selectively reduces action appraisal in naturalistic narratives. Cortex 132:460–472.

Birba A, Fittipaldi S, Cediel Escobar JC, Gonzalez Campo C, Legaz A, Galiani A, Diaz Rivera MN, Martorell Caro M, Alifano F, Pina-Escudero SD, Cardona JF, Neely A, Forno G, Carpinella M, Slachevsky A, Serrano C, Sedeno L, Ibanez A, Garcia AM (2021) Multimodal Neurocognitive Markers of Naturalistic Discourse Typify Diverse Neurodegenerative Diseases. Cereb Cortex 32:3377–3391.

Bryden MP (1977). Measuring handedness with questionnaires. Neuropsy 15:617–624.

Cantarero G, Tang B, O'Malley R, Salas R, Celnik P (2013) Motor learning interference is proportional to occlusion of LTP-like plasticity. J Neurosci 33:4634–4641.

Cervetto S, Diaz-Rivera M, Petroni A, Birba A, Caro MM, Sedeno L, Ibanez A, Garcia AM (2021) The neural blending of words and movement: Event-related potential signatures of semantic and action processes during motor-language coupling. J Cogn Neurosci 33:1413–1427.

Chaix Y, Albaret JM, Brassard C, Cheuret E, de Castelnau P, Benesteau J, Karsenty C, Démonet JF (2007) Motor impairment in dyslexia: the influence of attention disorders. Eur J Paediatr Neur 11:368–374.

Cohen J (1988) Statistical Power Analysis for the Behavioral Sciences. New York, NY: Routledge Academic.

Courellis HS, Iversen JR, Poizner H, Cauwenberghs G (2016) EEG channel interpolation using ellipsoid geodesic length. 2016 IEEE Biomed Circuits Syst Conf (BioCAS):540–543, 2016.

Dayan E, Cohen Leonardo G (2011) Neuroplasticity Subserving Motor Skill Learning. Neuron 72:443–454.

Delorme A, Makeig S (2004) EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. J Neurosci Methods 134:9–21.

Denis D, Rowe R, Williams AM, Milne E (2017) The role of cortical sensorimotor oscillations in action anticipation. NeuroImage 146:1102–1114.

Desai RH, Choi W, Lai VT, Henderson JM (2016) Toward Semantics in the Wild: Activation to Manipulable Nouns in Naturalistic Reading. J Neurosci 36:4050–4055.

Di X, Zhu S, Jin H, Wang P, Ye Z, Zhou K, Zhuo Y, Rao H (2012) Altered resting brain function and structure in professional badminton players. Brain Connect 2:225–233.

Dottori M, Sedeño L, Martorell Caro M, Alifano F, Hesse E, Mikulan E, García AM, Ruiz-Tagle A, Lillo P, Slachevsky A, Serrano C, Fraiman D, Ibanez A (2017) Towards affordable biomarkers of frontotemporal dementia: a classification study via network's information sharing. Sci Rep 7:3822.

Dunn LM, Dunn LM (1997) Examiner's manual for the PPVT-III peabody picture vocabulary test: Form IIIA and Form IIIB. AGS.

Eaves DL, Riach M, Holmes PS, Wright DJ (2016) Motor Imagery during Action Observation: A Brief Review of Evidence, Theory and Future Research Opportunities. Front Neurosci 10:514.

Fawcett AJ, Nicolson RI (1995) Persistent Deficits in Motor Skill of Children with Dyslexia. J Mot Behav 27:235–240.

Floyer-Lea A, Matthews PM (2005) Distinguishable Brain Activation Networks for Short- and Long-Term Motor Skill Learning. J Neurophysiol 94:512–518.

Gagne MH, Cohen H (2016) Interference effects between manual and oral motor skills. Exp Brain Res 234:845–851.

Gallese V, Cuccio V (2018) The neural exploitation hypothesis and its implications for an embodied approach to language and cognition: Insights from the study of action verbs processing and motor disorders in Parkinson's disease. Cortex 100:215–225.

Gallese V, Sinigaglia C (2011) What is so special about embodied simulation? Trends Cogn Sci 15:512–519.

Garcia AM, Bocanegra Y, Herrera E, Moreno L, Carmona J, Baena A, Lopera F, Pineda D, Melloni M, Legaz A, Muñoz E, Sedeño L, Baez B, Ibáñez A (2018) Parkinson's disease compromises the appraisal of action meanings evoked by naturalistic texts. Cortex 100:111–126.

García AM, Ibañez A (2016) A touch with words: Dynamic synergies between manual actions and language. Neurosci Biobehav Rev 68:59–95.

García AM, Moguilner S, Torquati K, García-Marco E, Herrera E, Muñoz E (2019) How meaning unfolds in neural time: Embodied reactivations can precede multimodal semantic effects during language processing. Neuroimage 197:439–449.

García AM, Hesse E, Birba A, Adolfi F, Mikulan E, Caro MM, Petroni A, Bekinschtein TA, del Carmen GM, Silva W, Ciraolo C, Vaucheret E, Sedeño L, Ibáñez A (2020) Time to Face Language: Embodied Mechanisms Underpin the Inception of Face-Related Meanings in the Human Brain. Cereb Cortex 30:6051–6068.

Gijssels T, Ivry RB, Casasanto D (2018) tDCS to premotor cortex changes action verb understanding: Complementary effects of inhibitory and excitatory stimulation. Sci Rep 8:11452.

Glenberg AM, Sato M, Cattaneo L (2008) Use-induced motor plasticity affects the processing of abstract and concrete language. Curr Biol 18:R290–R291.

Goble DJ, Cone BL, Fling BW (2014) Using the Wii Fit as a tool for balance assessment and neurorehabilitation: the first half decade of "Wii-search". J Neuroeng Rehabil 11:1–9.

Halliday MAK, Matthiessen CM (2014) An Introduction to Functional Grammar. fourth edition. London: Routledge.

Hasson U, Egidi G, Marelli M, Willems RM (2018) Grounding the neurobiology of language in first principles: The necessity of non-language-centric explanations for language comprehension. Cogn 180:135–157.

Haufler AJ, Spalding TW, Santa Maria DL, Hatfield BD (2000) Neuro-cognitive activity during a self-paced visuospatial task: comparative EEG profiles in marksmen and novice shooters. Biol Psychol 53:131–160.

Hesse E, Mikulan E, Sitt JD, del Carmen Garcia M, Silva W, Ciraolo C, Vaucheret E, Raimondo F, Baglivo F, Adolfi FJIToNS, Engineering R (2019) Consistent gradient of performance and decoding of stimulus type and valence from local and network activity. IEEE Trans Neural Syst Rehabil Eng 27:619–629.

Jolles DD, van Buchem MA, Crone EA, Rombouts SA (2013) Functional brain connectivity at rest changes after working memory training. Hum Brain Mapp 34:396–406.

Kerick SE, McDowell K, Hung TM, Santa Maria DL, Spalding TW, Hatfield BD (2001) The role of the left temporal region under the cognitive motor demands of shooting in skilled marksmen. Biol Psychol 58:263–277.

Kerick SE, Douglass LW, Hatfield BD (2004) Cerebral cortical adaptations associated with visuomotor practice. Med Sci Sports Exerc 36:118–129.

King JR, Sitt JD, Faugeras F, Rohaut B, El Karoui I, Cohen L, Naccache L, Dehaene S (2013) Information sharing in the brain indexes consciousness in noncommunicative patients. Curr Biol 23:1914–1919.

Kogan B, Muñoz E, Ibáñez A, García AM (2020) Too late to be grounded? Motor resonance for action words acquired after middle childhood. Brain Cogn 138 105509.

Krakauer JW, Ghez C, Ghilardi MF (2005) Adaptation to visuomotor transformations: consolidation, interference, and forgetting. J Neurosci 25:473–478.

Lewis CM, Baldassarre A, Committeri G, Romani GL, Corbetta M (2009) Learning sculpts the spontaneous activity of the resting human brain. Proc Natl Acad Sci U S A 106:17558–17563.

Locatelli M, Gatti R, Tettamanti M (2012) Training of manual actions improves language understanding of semantically related action sentences. Front Psychol 3:547.

Luft AR, Buitrago MM (2005) Stages of motor skill learning. Mol Neurobiol 32:205–216.

Lyons IM, Mattarella-Micke A, Cieslak M, Nusbaum HC, Small SL, Beilock SL (2010) The role of personal experience in the neural processing of action-related language. Brain Lang 112:214–222.

Marchand-Krynski M, Morin-Moncet O, Bélanger AM, Beauchamp MH, Leonard G (2017) Shared and differentiated motor skill impairments in children with dyslexia and/or attention deficit disorder: From simple to complex sequential coordination. PLoS One 12:e0177490.

Maris E, Oostenveld R (2007) Nonparametric statistical testing of EEG- and MEG-data. J Neurosci Methods 164:177–190.

Melloni M, Sedeño L, Hesse E, García-Cordero I, Mikulan E, Plastino A, Marcotti A, López JD, Bustamante C, Lopera F, Pineda D, García AM, Manes F, Trujillo N, Ibáñez A (2015) Cortical dynamics and subcortical signatures of motor-language coupling in Parkinson's disease. Sci Rep 5:11899.

Moguilner S, Birba A, Fino D, Isoardi R, Huetagoyena C, Otoya R, Tirapu V, Cremaschi F, Sedeno L, Ibanez A, Garcia AM (2021a) Structural and functional motor-network disruptions predict selective action-concept deficits: Evidence from frontal lobe epilepsy. Cortex 144:43–55.

Moguilner S, Birba A, Fino D, Isoardi R, Huetagoyena C, Otoya R, Tirapu V, Cremaschi F, Sedeño L, Ibañez A, García AM (2021b) Multimodal neurocognitive markers of frontal lobe epilepsy: Insights from ecological text processing. NeuroImage 235 117998.

Obeid R, Messina CM, Zapparrata N, Gravelle CD, Brooks PJ (2022) Dyslexia and motor skills: A meta-analysis. Proc Annu Meet Cogn Sci Soc 44.

Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. Neuropsy 9:97–113.

Orgs G, Dombrowski JH, Heil M, Jansen-Osmann P (2008) Expertise in dance modulates alpha/beta event-related desynchronization during action observation. Eur J Neurosci 27:3380–3384.

Orozco-Arroyave JR, Vásquez-Correa JC, Vargas-Bonilla JF, Arora R, Dehak N, Nidadavolu PS, Christensen H, Rudzicz F, Yancheva M, Chinaei H, Vann A, Vogler N, Bocklet T, Cernak M, Hannink J, Nöth E (2018) NeuroSpeech: An open-source software for Parkinson's speech analysis. Digital Signal Process 77:207–221.

Palva S, Palva JM (2012) Discovering oscillatory interaction networks with M/EEG: challenges and breakthroughs. Trends Cogn Sci 16:219–230.

Perez G, Hesse E, Dottori M, Birba A, Amoruso L, Martorell Caro M, Ibanez A, Garcia AM (2021) The Bilingual Lexicon, Back and Forth: Electrophysiological Signatures of Translation Asymmetry. Neurosci 481:134–143.

Pulvermüller F (2013a) How neurons make meaning: brain mechanisms for embodied and abstract-symbolic semantics. Trends Cogn Sci 17:458–470.

Pulvermüller F (2013b) Semantic embodiment, disembodiment or misembodiment? In search of meaning in modules and neuron circuits. Brain Lang 127:86–103.

Pulvermüller F (2018) Neural reuse of action perception circuits for language, concepts and communication. Prog Neurobiol 160:1–44.

Rodrigo MJ, Padrón I, De Vega M, Ferstl EC (2014) Adolescents' risky decision-making activates neural networks related to social cognition and cognitive control processes. Front Hum Neurosci 8:60.

Siegel LS, Ryan EB (1989) The development of working memory in normally achieving and subtypes of learning disabled children. Child Dev:973–980.

Suárez-García DMA, Birba A, Zimerman M, Diazgranados JA, Lopes da Cunha P, Ibáñez A, Grisales-Cárdenas JS, Cardona JF, García AM (2021) Rekindling Action Language: A Neuromodulatory Study on Parkinson's Disease Patients. Brain Sci 11:887.

Tan XY, Pi YL, Wang J, Li XP, Zhang LL, Dai W, Zhu H, Ni Z, Zhang J, Wu Y (2016) Morphological and Functional Differences between Athletes and Novices in Cortical Neuronal Networks. Front Hum Neurosci 10:660.

Tomasino B, Guatto E, Rumiati RI, Fabbro F (2012) The role of volleyball expertise in motor simulation. Acta Psychol 139:1–6.

Tomasino B, Maieron M, Guatto E, Fabbro F, Rumiati RI (2013) How are the motor system activity and functional connectivity between the cognitive and sensorimotor systems modulated by athletic expertise? Brain Res 1540:21–41.

Toulotte C, Toursel C, Olivier N (2012) Wii Fit® training vs. Adapted Physical Activities: which one is the most appropriate to improve the balance of independent senior subjects? A randomized controlled study. Clin Rehabil 26:827–835.

Trevisan P, García AM (2019) Systemic functional grammar as a tool for experimental stimulus design: New appliable horizons in psycholinguistics and neurolinguistics. Lang Sci 75:35–46.

Trevisan P, Sedeño L, Birba A, Ibáñez A, García AM (2017) A moving story: Whole-body motor training selectively improves the appraisal of action meanings in naturalistic narratives. Sci Rep 7:12538.

Wang J, Lu M, Fan Y, Wen X, Zhang R, Wang B, Ma Q, Song Z, He Y, Wang J, Huang R (2016) Exploring brain functional plasticity in world class gymnasts: a network analysis. Brain Struct Funct 221:3503–3519.

Yang J (2014) Influences of motor contexts on the semantic processing of action-related language. Cogn Affect Behav Neurosci 14:912–922.

Zwaan RA (2016) Situation models, mental simulations, and abstract concepts in discourse comprehension. Psychon Bull Rev 23:1028–1034.

APPENDIX A. SUPPLEMENTARY MATERIAL

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5. DISCUSIÓN

5.1. Síntesis de los principales aportes

Esta tesis ofrece nuevos aportes al estudio de cómo el sistema motor y las experiencias sensoriomotoras contribuyen al procesamiento de conceptos de acción, integrando evidencia conductual y neurofisiológica en contextos progresivamente más ecológicos. A lo largo de tres estudios, se han identificado mecanismos clave de interacción entre los circuitos motores y semánticos, avanzando en la comprensión del procesamiento del lenguaje de acción desde la perspectiva corporizada.

El primer estudio exploró el papel del cerebelo en la semántica de la acción a partir del análisis de un paciente con atrofia cerebelosa, contribuyendo así a extender el foco más allá de las regiones corticales tradicionalmente estudiadas. Los resultados mostraron un déficit selectivo en el procesamiento de significados relacionados con acciones, así como una alteración en la integración entre procesos semánticos y motores, en comparación con un grupo control. Este hallazgo aporta evidencia sobre el rol del cerebelo como nodo relevante en la red semántico-motora, y permite especular con un posible rol en la integración funcional entre la comprensión de los conceptos de acción y ejecución de acciones, incluso en tareas no lingüísticas.

El segundo estudio muestra que el procesamiento de conceptos de acción modula la dinámica funcional del sistema motor, incluso en condiciones de procesamiento implícito. A partir de registros de EEG y análisis de MRCPs, se identificaron modulaciones diferenciadas en la actividad cortical durante la preparación (*readiness potencial*, RP) y ejecución motora (MP). Estas modulaciones muestran una activación selectiva del sistema motor que depende tanto del tipo de verbo procesado como del efector implicado en la acción. Los hallazgos evidencian que el sistema motor interactúa de manera situada con el contexto semántico y revela distintos niveles de resonancia motora, reflejando una integración funcional con un componente específico (resonancia fina) y generalizada (resonancia gruesa) entre lenguaje y acción.

El tercer estudio exploró cómo el entrenamiento motor en contexto naturalista puede modular el procesamiento semántico de narrativas ricas en descripciones de acción. Los resultados muestran que una exposición de cuatros días a videojuegos de inmersión corporal indujo interferencias selectivas en la comprensión y/o recuperación de información de acción, asociadas a un peor desempeño en el cuestionario de preguntas relacionadas a acciones, junto con una reducción en la conectividad funcional fronto-parietal en bandas motoras (10–20 Hz). Este hallazgo refuerza la dependencia entre la experiencia sensoriomotora y la semántica de acción, al tiempo que resalta la necesidad de investigar cómo la duración y especificidad del entrenamiento determinan estos efectos.

En conjunto, estos aportes ilustran desde distintos puntos de vista y diseños metodológicos, cómo el sistema motor participa activamente en el procesamiento semántico de acciones, desde la participación de estructuras extracorticales hasta la plasticidad inducida por experiencias motoras. Cada estudio contribuye de manera complementaria a una visión más integradora, que abarca niveles funcionales y dinámicos, así como escenarios más próximos a la vida cotidiana. Las secciones siguientes profundizan en estas contribuciones específicas, articulándolas con hallazgos previos y discutiendo sus implicancias para los modelos de cognición corporizada.

5.2. El Cerebelo en la semántica de la acción: Aportes

Tradicionalmente, la comprensión del lenguaje de acción ha sido explicada por modelos corticales que postulan la activación somatotópica de áreas motoras durante el procesamiento de conceptos relacionados con acciones. Según Pulvermüller (2005), estas activaciones reflejan una organización funcional distribuida, donde las redes sensoriomotoras intervienen en el acceso al significado de palabras y frases asociadas a acciones específicas. Evidencia de estudios de neuroimagen y ERP ha mostrado activaciones tempranas y específicas en regiones motoras corticales durante la lectura o escucha de verbos motores (Hauk et al., 2004; Tettamanti et al., 2005).

Sin embargo, enfoques más recientes han trascendido la perspectiva estrictamente cortical, incorporando estructuras extracorticales en los modelos de semántica de acción. En esta línea, Pulvermüller (2018) propuso que los circuitos sensoriomotores, desarrollados originalmente para la percepción y ejecución de acciones, han sido reutilizados evolutivamente para funciones lingüísticas y conceptuales más abstractas. Este modelo sugiere que estructuras como el cerebelo podrían desempeñar un papel activo en la integración y coordinación de redes corticales y subcorticales implicadas en el procesamiento semántico.

El primer antecedente empírico que evidenció el involucramiento del cerebelo en la semántica de la acción fue reportado por García et al. (2017). En este estudio pionero, un paciente con ataxia genética mostró déficits selectivos en tareas de decisión léxica con estímulos lingüísticos, destacando el papel del cerebelo en el acceso al significado de palabras de acción en un contexto de procesamiento implícito. Estos hallazgos desafiaron los modelos tradicionales centrados en la corteza cerebral y posicionaron al cerebelo como un nodo relevante dentro de las redes semántico-motoras.

El primer artículo de esta tesis amplía dicha evidencia al evaluar el rol del cerebelo en tareas semánticas no lingüísticas. Mediante un estudio de caso en un paciente con gangliocitoma cerebeloso, se observaron déficits específicos en tareas de integración semántica vinculadas a representaciones de acción, con estímulos no verbales a través de imágenes. Este hallazgo es relevante porque sugiere que el cerebelo participa en la organización de conceptos motores más allá del lenguaje explícito, sugiriendo un rol transmodal en la semántica de acción.

Una contribución clave de este trabajo es el aporte de evidencia empírica a favor de la propuesta de integrar al cerebelo como parte de una red funcional distribuida, en la que regiones corticales y subcorticales interactúan de manera dinámica durante el procesamiento de conceptos motores. Desde la perspectiva del modelo de reutilización neural (Pulvermüller, 2018), el cerebelo no solo podría facilitar la integración entre niveles específicos (como la codificación somática de acciones) y niveles abstractos del significado conceptual, sino que también desempeñar un papel activo en la generación de representaciones predictivas y la simulación interna de acciones. Koziol et al. (2014) proponen que la arquitectura homogénea del cerebelo le permite ejecutar operaciones computacionales en dominios motores y cognitivos, como la predicción, el aprendizaje y la integración de información multimodal. Este mecanismo podría explicar cómo el cerebelo contribuye al procesamiento semántico, no solo apoyando tareas explícitas, sino también facilitando la interacción de procesos sensoriomotores y conceptuales en escenarios más complejos.

Estos hallazgos obligan a reconsiderar las bases de los modelos actuales de semántica de acción, que han priorizado las activaciones corticales y somatotópicas (Pulvermüller, 2005). El trabajo aquí presentado promueve una visión más amplia y distribuida, en la que el cerebelo actúa como un integrador clave dentro de las redes semántico-motoras, modulando dinámicamente el procesamiento conceptual a distintos niveles.

Si bien este estudio presenta limitaciones, como la dependencia de datos conductuales de un único caso, sus resultados abren interrogantes fundamentales sobre el rol del cerebelo en la cognición corporizada. Estudios futuros que incorporen técnicas de neuroimagen funcional (fMRI, EEG) y análisis de conectividad cerebral permitirán validar y profundizar estos hallazgos, contribuyendo a una comprensión más robusta y global del papel del cerebelo en el procesamiento semántico.

En síntesis, el primer artículo de esta tesis amplía el conocimiento existente al evidenciar que el cerebelo desempeña un papel crucial en el procesamiento de conceptos motores, incluso en contextos no lingüísticos. Al incorporar al cerebelo como un componente activo y modulador dentro de la red semántico-motora, este trabajo promueve una reformulación de los modelos tradicionales y destaca la naturaleza dinámica y distribuida del procesamiento semántico en el cerebro.

5.3. Modulaciones cerebrales por el acoplamiento de procesos motores y semánticos: Aportes

Este trabajo aporta evidencia novedosa sobre la interacción funcional y bidireccional entre los procesos motores y semánticos desde una perspectiva neurofisiológica, abordando vacíos en un estado del arte dominado por estudios comportamentales. Los hallazgos del segundo artículo destacan al identificar modulaciones diferenciadas de marcadores cerebrales canónicos de procesamiento motor y semántico.

Como ya fue descrito, el RP refleja la actividad cortical que anticipa y prepara la ejecución manual realizada por los sujetos en respuesta a la tarea semántica. En este estudio, el RP mostró una mayor amplitud durante el procesamiento de verbos manuales (MaVs) en comparación con verbos no manuales (nMaVs) y verbos abstractos (nAVs). Este efecto, asociado a la resonancia de grano fino, evidencia una modulación específica del sistema motor en función de la congruencia del efector corporal implicado en la tarea semántica.

Por otro lado, el MP, característico de una ventana temporal en torno a la ejecución de la acción, presentó una modulación más generalizada o de grano grueso, asociada a una integración semántico-motora más global, independientemente de la coincidencia del efector. Este patrón jerárquico, en el que el RP refleja resonancias específicas y el MP integra resonancias más amplias, ofrece una caracterización novedosa de la participación del sistema motor en el procesamiento semántico.

De manera complementaria, el N400 mostró una sutil pero significativa disminución de su amplitud en contextos de congruencia semántico-motora. Este componente, que típicamente refleja la dificultad o facilidad de integrar información semántica (Kutas & Federmeier, 2011), aporta evidencia adicional sobre la interacción entre los dominios semántico y motor. En este caso, la reducción del N400 indica que los estímulos congruentes facilitaron la integración semántica, resaltando el impacto bidireccional de las demandas semántico-motoras en ambos dominios.

El diseño experimental de este trabajo sobresale por superar las limitaciones de investigaciones previas. Mientras que estudios anteriores se centraron en aspectos somatotópicos específicos o en dinámicas aisladas de procesamiento semántico (Grisoni et al., 2017; Dalla Volta et al., 2018), este estudio integra múltiples categorías conceptuales (MaVs, nMaVs y nAVs) y evalúa simultáneamente marcadores semánticos y motores. Este enfoque permitió evidenciar una interacción bidireccional y analizar distintos niveles de resonancia en dicha interacción.

Los hallazgos de este estudio evidencian dos niveles jerárquicos de resonancia motora en el contexto del procesamiento semántico. Por un lado, la resonancia de grano fino se caracteriza por activaciones específicas del efector corporal, como las observadas en el RP durante el procesamiento de MaVs. Este nivel de resonancia ha sido vinculado a una organización somatotópica de las áreas motoras corticales, consistente con estudios previos (Hauk et al., 2004; Tettamanti et al., 2005). Por otro lado, la resonancia de grano grueso, reflejada en el MP, representa un patrón más generalizado que trasciende la especificidad del efector, sugiriendo que las redes motoras también participan en la integración conceptual más abstracta (Pulvermüller, 2013; Kemmerer, 2015a).

Estos hallazgos plantean la necesidad de revisar y ampliar los modelos teóricos predominantes. Mientras que las investigaciones tradicionales han enfatizado las activaciones somatotópicas, los resultados de este estudio subrayan la importancia de considerar dinámicas jerárquicas que integren representaciones motoras tanto somáticas como simbólicas. Este enfoque jerárquico no solo contribuye a una mejor comprensión del acoplamiento motor-semántico, sino que también abre preguntas sobre cómo estas dinámicas pueden variar en función de factores como la experiencia motora, el contexto lingüístico o la complejidad de la tarea.

En particular, las diferencias temporales observadas entre las resonancias de grano fino y grueso arrojan luz sobre la secuencialidad del acoplamiento motor-semántico. La activación temprana de áreas motoras reportada en la literatura (~200 ms) sugiere un reclutamiento inicial somatotópico, mientras que activaciones más tardías (~400 ms) reflejan una integración semántica más global y multimodal (Pulvermüller et al., 2005; Dalla Volta et al., 2018). Estas dinámicas temporales, además, resaltan la importancia de emplear herramientas neurofisiológicas de alta resolución para desentrañar las relaciones causales entre sistemas motor y semántico.

Los resultados del segundo artículo también se alinean con las predicciones del modelo HANDLE (García & Ibáñez, 2016), el cual propone que los efectos de facilitación o inhibición motora dependen de la complejidad de las tareas y la temporalidad entre ellas. En particular, este modelo sugiere que, en tareas simples, la coincidencia entre procesos semánticos y motores puede generar facilitación cuando los tiempos de reacción superan los 450 ms. En concordancia con esta propuesta, los hallazgos del presente estudio mostraron un aumento en la amplitud de los componentes RP y MP durante el procesamiento de estímulos congruentes, lo que indica una facilitación motora y evidencia una interacción funcional entre los sistemas motor y semántico.

En síntesis, este trabajo aporta evidencia robusta sobre la interacción jerárquica entre los sistemas motor y semántico, destacando cómo diferentes niveles de resonancia motora contribuyen al procesamiento conceptual. Los hallazgos no solo refuerzan la noción de que el sistema motor desempeña un papel activo en la integración semántica, sino que también abren nuevas preguntas sobre las dinámicas temporal y funcional de esta interacción. Al integrar medidas neurofisiológicas de alta resolución y un diseño experimental que abarca múltiples categorías conceptuales, esta investigación ofreció un análisis más completo de cómo se articulan los procesos motores y semánticos. Estos avances no solo enriquecen el entendimiento teórico del acoplamiento motor-lenguaje, sino que también establecen una base sólida para futuras investigaciones que exploren estas interacciones en escenarios más ecológicos y aplicados.

5.4. Cambios en el procesamiento semántico por adquisición de nuevas experiencias sensoriomotoras: Aportes

El tercer artículo de esta tesis explora cómo las experiencias sensoriomotoras adquiridas en contextos ecológicos pueden reorganizar las dinámicas de las redes semántico-motoras, aportando evidencia clave sobre la plasticidad de estas interacciones. A diferencia de estudios previos que emplearon estímulos lingüísticos aislados y acciones motoras artificiales (Glenberg et al., 2008; Locatelli et al., 2012), este trabajo integra narrativas naturalistas con un protocolo de entrenamiento motor funcional, proporcionando una aproximación más cercana a la vida cotidiana y con mayor validez ecológica. Los resultados destacan que las redes semántico-motoras son flexibles y pueden operar en distintos niveles de granularidad, adaptándose a las demandas específicas y generales del contexto.

El protocolo de cuatro días de entrenamiento utilizado en este estudio incluyó movimientos corporales funcionales realizados sobre una plataforma de equilibrio que requerían una rápida coordinación visuomotora para efectuar cambios posturales. Los textos narrativos asociados abordaban acciones más amplias y diversas, como lanzar, nadar o patear, lo que permitió evaluar el impacto de un entrenamiento motor inespecífico en la recuperación de información relacionada con acciones. Los resultados mostraron que el grupo de *Exergaming* experimentó una reducción significativa en la precisión de respuesta, específicamente en las preguntas sobre acciones realizadas por los personajes del relato, mientras que otras categorías conceptuales permanecieron inalteradas. Este efecto no se observó en el grupo de control que participó en videojuegos estáticos, lo que refuerza la selectividad del efecto del entrenamiento sobre la información de acción.

A nivel neurofisiológico, se identificó una disminución en la conectividad funcional entre regiones fronto-parietales en el rango de 10-20 Hz, espectro que ha sido previamente asociado con la actividad sensoriomotora y su modulación por el entrenamiento motor (Orgs et al., 2008). Además, una menor conectividad funcional se correlacionó con una reducción en la precisión de respuesta en las preguntas sobre acciones, sugiriendo un vínculo directo entre las dinámicas funcionales de las redes motoras y el procesamiento semántico. Estudios previos han demostrado que las modulaciones en esta banda de frecuencia están implicadas en la coordinación funcional entre regiones sensoriomotoras y frontoparietales, lo cual podría jugar un papel clave en la integración de información motora y semántica (Rosanova et al., 2009; Thut & Miniussi, 2009). Los resultados hallados coinciden con investigaciones como la de Birba et al. (2020), quienes observaron que una mayor conectividad entre áreas motoras y semánticas predice un mejor desempeño en tareas lingüísticas relacionadas con conceptos de acción, mientras que déficits en esta conectividad se asocian con deterioro en el desempeño.

Desde una perspectiva temporal, la reducción de conectividad funcional observada tras el protocolo de entrenamiento podría relacionarse con los efectos de entrenamientos de corta duración. Glenberg et al. (2008) sugieren que protocolos breves tenderían a generar interferencia debido a una sobrecarga en los recursos cognitivos y motores, afectando la disponibilidad de estas redes para tareas semánticas. En contraste, entrenamientos más prolongados, como los utilizados por Locatelli et al. (2012), podrían promover la estabilización de adaptaciones funcionales, lo que se traduce en un mejor rendimiento semántico. El protocolo utilizado en este trabajo, aunque de mayor duración que el de Glenberg et al. (2008) pero menor que el utilizado por Locatelli et al. (2012), indujo un efecto de interferencia, el cual podría ser explicado por una reorganización funcional transitoria. Esta reorganización podría comprometer temporalmente su disponibilidad para sostener procesos semánticos, lo que explica cómo la duración del entrenamiento, junto con las demandas específicas del contexto, puede influir de manera crítica en el procesamiento y el desempeño semántico.

Estos resultados también se pueden poner en diálogo con modelos teóricos como el HANDLE (García & Ibáñez, 2016), que como ya se mencionó, postula que los estados funcionales de las redes motoras, modulados por su excitabilidad basal, influyen directamente en la eficacia del procesamiento semántico. Aunque este estudio no evaluó directamente la excitabilidad cortical, se podría especular que la alteración de los estados funcionales de las redes motoras (reflejada por la modulación en bandas de 10-20 Hz) puede influir en el desempeño semántico, interfiriendo o facilitando según una serie variables como por ejemplo la ventana de intervención.

Por otro lado, los resultados de este artículo dialogan con los hallazgos del segundo artículo, donde se identificó resonancia motora de grano grueso en condiciones de no coincidencia entre el efector corporal del verbo y la acción motora realizada. Mientras que estos datos destacaron la flexibilidad de las redes semántico-motoras en procesar conceptos no estrictamente coincidentes, el tercer artículo amplía este conocimiento al mostrar que un entrenamiento motor inespecífico puede reorganizar estas redes y generar efectos en el procesamiento conceptual en un nivel más general. Este resultado encuentra apoyo en estudios como el de Locatelli et al. (2012), que observaron efectos de entrenamiento en condiciones tanto congruentes como no congruentes con los conceptos evaluados, sugiriendo que un solapamiento parcial en las representaciones motoras es suficiente para inducir cambios en el procesamiento semántico.

Desde un enfoque teórico, estos hallazgos refuerzan la idea de que las redes semántico-motoras operan en diferentes niveles de granularidad, desde representaciones motoras específicas hasta patrones más abstractos activados según las demandas contextuales. Este análisis plantea preguntas relevantes para futuras investigaciones, como el impacto del grado de congruencia entre acción entrenada y concepto semántico, o el rol de las características individuales, como la experiencia motora previa, en la modulación del procesamiento conceptual.

En conjunto, estos resultados subrayan la flexibilidad y plasticidad de las redes semántico-motoras, destacando su capacidad para adaptarse a contextos diversos y entrenamientos inespecíficos. Futuros estudios podrían manipular sistemáticamente el grado de congruencia entre entrenamiento y tareas semánticas, utilizando herramientas neurofisiológicas para evaluar las dinámicas funcionales subyacentes. Este enfoque permitirá avanzar hacia una comprensión más integral de cómo las experiencias motoras influyen en la organización conceptual y en las interacciones entre lenguaje y acción.

6. IMPLICANCIAS TEÓRICAS

Los hallazgos de esta tesis, interpretados a la luz del marco teórico de la cognición corporizada y desde una perspectiva evolutiva, destacan cómo los mecanismos cognitivos y neurales están profundamente arraigados en los esquemas sensoriomotores. La evidencia presentada refuerza la noción de que el procesamiento del lenguaje y, en particular, la semántica de la acción, no son fenómenos aislados ni abstractos, sino que se originan y se estructuran a partir de las dinámicas corporales y la interacción con el entorno.

Desde la perspectiva de la cognición corporizada, se reconoce que los procesos cognitivos están íntimamente vinculados con las experiencias físicas y las interacciones motoras. Los resultados aquí obtenidos reflejan cómo las redes neurales implicadas en la semántica de la acción se solapan con las responsables de la planificación y ejecución de movimientos, evidenciando una continuidad funcional entre el lenguaje y la acción. Este solapamiento funcional no solo apoya la teoría de la simulación motora en el lenguaje, sino que también apunta a un aprovechamiento evolutivo de los sistemas existentes para responder a nuevas demandas cognitivas.

En un contexto evolutivo, los circuitos neurales originales desarrollados para gestionar las necesidades básicas de los organismos multicelulares —como el movimiento, la navegación y la interacción con el entorno— fueron cooptados y reciclados para cumplir funciones más complejas en especies con cerebros progresivamente más sofisticados. La evidencia presentada en esta tesis permite hipotetizar que, en el caso del lenguaje, las redes sensoriomotoras fueron aprovechadas para integrar representaciones simbólicas y conceptuales, dando lugar a estructuras emergentes que habilitaron nuevas formas de comunicación y abstracción.

Este fenómeno de cooptación y reciclaje neuronal refleja un principio económico en la evolución del cerebro, donde las estructuras preexistentes son reorganizadas para cumplir con las demandas funcionales de nuevas capacidades. En este marco, el lenguaje puede entenderse no como una facultad separada, sino como una extensión natural de los sistemas motores y perceptivos que fueron adaptados para codificar y comunicar significados.

La tesis también sugiere que este proceso de cooptación neuronal no es estático, sino dinámico y sensible al entorno y la experiencia. La plasticidad observada en los circuitos sensoriomotores y su capacidad para integrar funciones lingüísticas reflejan cómo los sistemas cognitivos actuales siguen siendo moldeados por los desafíos y oportunidades del aprendizaje y el entrenamiento. Esta interacción constante entre estructura, función y contexto evolutivo pone de relieve la importancia de considerar la cognición no solo como un fenómeno individual, sino como una propiedad emergente de sistemas corporales en interacción con su entorno.

En conclusión, los hallazgos aquí presentados refuerzan la visión de la cognición como un fenómeno situado, corporizado y dinámico, donde los esquemas sensoriomotores no solo proporcionan la base para las habilidades cognitivas, sino que también actúan como catalizadores de estructuras emergentes, como el lenguaje. Este enfoque integrador, que une la cognición corporizada con una perspectiva evolutiva, abre nuevas posibilidades para explorar cómo los sistemas neurales contemporáneos reflejan y responden a las demandas de un mundo cada vez más complejo y simbólico. La investigación futura deberá profundizar en estas conexiones, explorando cómo los principios de cooptación y reciclaje neuronal continúan moldeando nuestra capacidad de comprender, aprender y comunicarnos.

7. CONCLUSIONES

Esta tesis se abocó a explorar cómo los circuitos motores y semánticos interactúan en el procesamiento de conceptos relacionados con acciones, abordando vacíos críticos en la literatura desde tres perspectivas complementarias: el papel de estructuras extracorticales, la interacción funcional semántico-motora y los efectos de la experiencia sensoriomotora.

A través de un estudio de caso, se demostró que el cerebelo desempeña un rol clave en la integración léxico-semántica de conceptos de acción, destacando su relevancia más allá de las funciones motoras básicas. Este hallazgo amplía los modelos corporizados al incluir estructuras extracorticales en la dinámica semántica, sugiriendo que el cerebelo podría actuar como un modulador esencial en escenarios que requieren integración sensoriomotora.

El segundo estudio mostró una interacción jerárquica entre los sistemas semántico y motor, identificando resonancias de grano fino y grueso en función de la congruencia semántico-motora. Estos resultados enfatizan que las redes semántico-motoras operan en múltiples niveles, desde la especificidad somatotópica hasta integraciones más generales, aportando una base para futuros modelos teóricos sobre la organización jerárquica de estos sistemas.

El tercer artículo evidenció cómo experiencias motoras recientes pueden modular la recuperación de información de acción y reorganizar transitoriamente la conectividad funcional entre regiones motoras y semánticas. Estos hallazgos destacan la plasticidad del circuito semántico-motor y abren nuevas líneas de investigación sobre cómo la duración, congruencia y diversidad de los entrenamientos sensoriomotores influyen en los procesos semánticos.

En conjunto, los resultados de esta tesis no solo subrayan la flexibilidad y plasticidad del circuito semántico-motor, sino que también aportan implicancias teóricas significativas para el marco de la cognición corporizada. Al evidenciar cómo las experiencias sensoriomotoras recientes y las dinámicas funcionales del sistema motor contribuyen a la integración conceptual, este trabajo plantea un modelo más dinámico y jerárquico, en el que los circuitos sensoriomotores no son únicamente un reflejo pasivo de la experiencia, sino actores activos en la reorganización conceptual. Estas contribuciones invitan a repensar cómo se construyen y modifican las representaciones semánticas en función de factores tanto contextuales como individuales, estableciendo un puente entre la plasticidad neural y los procesos cognitivos complejos.

Referencias bibliográficas

Abrevaya, S., Sedeño, L., Fitipaldi, S., Pineda, D., Lopera, F., Buritica, O., ... & García, A. M. (2016). The road less traveled: alternative pathways for action-verb processing in Parkinson's disease. *Journal of Alzheimer's Disease, 55(4),* 1429-1435.

Aravena, P., Hurtado, E., Riveros, R., Cardona, J. F., Manes, F., & Ibáñez, A. (2010). Applauding with closed hands: neural signature of action-sentence compatibility effects. *PloS one*, *5*(7), e11751.

Calvo-Merino, B., Glaser, D. E., Grèzes, J., Passingham, R. E., & Haggard, P. (2005). Action observation and acquired motor skills: an FMRI study with expert dancers. *Cerebral cortex*, *15*(8), 1243-1249.

Barsalou, L. W. (2005). Continuity of the conceptual system across species. *Trends in cognitive sciences*, *9*(7), 309-311.

Barsalou, L. W. (2008). Grounded cognition. *Annu. Rev. Psychol.*, *59*(1), 617-645.

Beilock, S. L., Lyons, I. M., Mattarella-Micke, A., Nusbaum, H. C., & Small, S. L. (2008). Sports experience changes the neural processing of action language. *Proceedings of the national Academy of Sciences*, *105*(36), 13269-13273.

Bertella, L., Albani, G., Greco, E., Priano, L., Mauro, A., Marchi, S., ... & Semenza, C. (2002). Noun verb dissociation in Parkinson's disease. *Brain and cognition*, *48*, 277-280.

Binder, J. R., & Desai, R. H. (2011). The neurobiology of semantic memory. *Trends in cognitive sciences*, *15*(11), 527-536.

Birba, A., García-Cordero, I., Kozono, G., Legaz, A., Ibáñez, A., Sedeño, L., & García, A. M. (2017). Losing ground: Frontostriatal atrophy disrupts language embodiment in Parkinson's and Huntington's disease. *Neuroscience & Biobehavioral Reviews*, *80*, 673-687.

Birba, A., Beltrán, D., Caro, M. M., Trevisan, P., Kogan, B., Sedeño, L., ... & García, A. M. (2020). Motor-system dynamics during naturalistic reading of action narratives in first and second language. *NeuroImage*, *216*, 116820.

Bocanegra, Y., García, A. M., Lopera, F., Pineda, D., Baena, A., Ospina, P., ... & Cuetos, F. (2017). Unspeakable motion: Selective action-verb impairments in Parkinson's disease patients without mild cognitive impairment. *Brain and language*, *168*, 37-46.

Bogdan, D., Christian, G., Volker, B., Gerhard, S., Ulrich, B., & Arne, M. (2004). Neuroplasticity: Changes in grey matter induced by training. *Nature*, *427*(6972), 311-31.

Buccino, G., Riggio, L., Melli, G., Binkofski, F., Gallese, V., & Rizzolatti, G. (2005). Listening to action-related sentences modulates the activity of the motor system: a combined TMS and behavioral study. *Cognitive Brain Research*, *24*(3), 355-363.

Capitani, E., Laiacona, M., Mahon, B., & Caramazza, A. (2003). What are the facts of semantic category-specific deficits? A critical review of the clinical evidence. *Cognitive Neuropsychology*, *20*(3-6), 213-261.

Chersi, F., Thill, S., Ziemke, T., & Borghi, A. M. (2010). Sentence processing: linking language to motor chains. *Frontiers in neurorobotics*, *4*, 1255.

Conca, F., & Tettamanti, M. (2018). Conceptual semantics as grounded in personal experience. *Phenomenology and Mind*, *14*, 98-116.

Cotelli, M., Borroni, B., Manenti, R., Alberici, A., Calabria, M., Agosti, C., ... & Cappa, S. F. (2006). Action and object naming in frontotemporal dementia, progressive supranuclear palsy, and corticobasal degeneration. *Neuropsychology*, *20*(5), 558.

Cree, G. S., & McRae, K. (2003). Analyzing the factors underlying the structure and computation of the meaning of chipmunk, cherry, chisel, cheese, and cello (and many other such concrete nouns). *Journal of experimental psychology: general*, *132*(2), 163.

Dalla Volta, R., Avanzini, P., De Marco, D., Gentilucci, M., & Fabbri-Destro, M. (2018). From meaning to categorization: the hierarchical recruitment of brain circuits selective for action verbs. *Cortex*, *100*, 95-110.

de Vega, M., Moreno, V., & Castillo, D. (2013). The comprehension of action-related sentences may cause interference rather than facilitation on matching actions. *Psychological research*, *77*, 20-30.

Fernandino, L., Conant, L. L., Binder, J. R., Blindauer, K., Hiner, B., Spangler, K., & Desai, R. H. (2013a). Parkinson's disease disrupts both automatic and controlled processing of action verbs. *Brain and language*, *127*(1), 65-74.

Fernandino, L., Conant, L. L., Binder, J. R., Blindauer, K., Hiner, B., Spangler, K., & Desai, R. H. (2013b). Where is the action? Action sentence processing in Parkinson's disease. *Neuropsychologia*, *51*(8), 1510-1517.

Gallese, V., & Cuccio, V. (2018). The neural exploitation hypothesis and its implications for an embodied approach to language and cognition: insights from the study of action verbs processing and motor disorders in Parkinson's disease. *Cortex*, *100*, 215-225.

Gallese, V., & Lakoff, G. (2005). The brain's concepts: The role of the sensory-motor system in conceptual knowledge. *Cognitive neuropsychology*, *22*(3-4), 455-479.

García, A. M., & Ibáñez, A. (2014). Words in motion: Motor-language coupling in Parkinson's disease. *Translational Neuroscience*, *5*, 152-159.

García, A. M., & Ibáñez, A. (2016). A touch with words: Dynamic synergies between manual actions and language. *Neuroscience & Biobehavioral Reviews*, *68*, 59-95.

García, A. M., Abrevaya, S., Kozono, G., Cordero, I. G., Córdoba, M., Kauffman, M. A., ... & Ibáñez, A. (2017). The cerebellum and embodied semantics: evidence from a case of genetic ataxia due to STUB1 mutations. *Journal of Medical Genetics*, *54*(2), 114-124.

García, A. M., Bocanegra, Y., Herrera, E., Moreno, L., Carmona, J., Baena, A., ... & Ibáñez, A. (2018). Parkinson's disease compromises the appraisal of action meanings evoked by naturalistic texts. *Cortex*, *100*, 111-126.

Glenberg, A. M., Sato, M., & Cattaneo, L. (2008). Use-induced motor plasticity affects the processing of abstract and concrete language. *Current biology*, *18*(7), R290-R291.

Glenberg, A. M., & Kaschak, M. P. (2002). Grounding language in action. *Psychonomic bulletin & review*, *9*(3), 558-565.

Grisoni, L., Miller, T. M., & Pulvermüller, F. (2017). Neural correlates of semantic prediction and resolution in sentence processing. *Journal of Neuroscience*, *37*(18), 4848-4858.

González, J., Barros-Loscertales, A., Pulvermüller, F., Meseguer, V., Sanjuán, A., Belloch, V., & Ávila, C. (2006). Reading cinnamon activates olfactory brain regions. *Neuroimage*, *32*(2), 906-912.

Hauk, O., Johnsrude, I., & Pulvermüller, F. (2004). Somatotopic representation of action words in human motor and premotor cortex. *Neuron*, *41*(2), 301-307.

Hommel, B., Müsseler, J., Aschersleben, G., & Prinz, W. (2001). The theory of event coding (TEC): A framework for perception and action planning. *Behavioral and brain sciences*, *24*(5), 849-878.

Ibáñez, A., Cardona, J. F., Dos Santos, Y. V., Blenkmann, A., Aravena, P., Roca, M., ... & Bekinschtein, T. (2013). Motor-language coupling: direct evidence from early Parkinson’s disease and intracranial cortical recordings. *cortex*, *49*(4), 968-984.

Jäncke, L., Koeneke, S., Hoppe, A., Rominger, C., & Hänggi, J. (2009). The architecture of the golfer's brain. *PloS one*, *4*(3), e4785.

Kemmerer, D. (2015a). Visual and motor features of the meanings of action verbs: A cognitive neuroscience perspective. *Cognitive science perspectives on verb representation and processing*, 189-212.

Kemmerer, D. (2015b). Are the motor features of verb meanings represented in the precentral motor cortices? Yes, but within the context of a flexible, multilevel architecture for conceptual knowledge. *Psychonomic Bulletin & Review*, *22*, 1068-1075.

Klepp, A., Niccolai, V., Buccino, G., Schnitzler, A., & Biermann-Ruben, K. (2015). Language–motor interference reflected in MEG beta oscillations. *NeuroImage*, *109*, 438-448.

Koziol, L. F., Budding, D., Andreasen, N., D’Arrigo, S., Bulgheroni, S., Imamizu, H., ... & Yamazaki, T. (2014). Consensus paper: the cerebellum's role in movement and cognition. *The Cerebellum*, *13*, 151-177.

Kutas, M., & Federmeier, K. D. (2011). Thirty years and counting: finding meaning in the N400 component of the event-related brain potential (ERP). *Annual review of psychology*, *62*(1), 621-647.

Locatelli, M., Gatti, R., & Tettamanti, M. (2012). Training of manual actions improves language understanding of semantically related action sentences. *Frontiers in Psychology*, *3*, 547.

Mahon, B. Z. (2015). What is embodied about cognition?. *Language, cognition and neuroscience*, *30*(4), 420-429.

Mahon, B. Z. (2015b). The burden of embodied cognition. *Canadian Journal of Experimental Psychology/Revue canadienne de psychologie expérimentale*, *69*(2), 172.

Markie, P., (2021). Rationalism vs. Empiricism, The Stanford Encyclopedia of Philosophy, Edward N. Zalta (ed.).

Melloni, M., Sedeño, L., Hesse, E. … & Ibáñez, A. (2015) Cortical dynamics and subcortical signatures of motor-language coupling in Parkinson's disease. *Sci Rep* **5**, 11899.

Meteyard, L., Cuadrado, S. R., Bahrami, B., & Vigliocco, G. (2012). Coming of age: A review of embodiment and the neuroscience of semantics. *Cortex*, *48*(7), 788-804.

Mollo, G., Pulvermüller, F., & Hauk, O. (2016). Movement priming of EEG/MEG brain responses for action-words characterizes the link between language and action. *cortex*, *74*, 262-276.

Orgs, G., Dombrowski, J. H., Heil, M., & Jansen‐Osmann, P. (2008). Expertise in dance modulates alpha/beta event‐related desynchronization during action observation. *European Journal of Neuroscience*, *27*(12), 3380-3384.

Papeo, L., Lingnau, A., Agosta, S., Pascual-Leone, A., Battelli, L., & Caramazza, A. (2015). The origin of word-related motor activity. *Cerebral Cortex*, *25*(6), 1668-1675.

Patterson, K., Nestor, P. J., & Rogers, T. T. (2007). Where do you know what you know? The representation of semantic knowledge in the human brain. *Nature reviews neuroscience*, *8*(12), 976-987.

Postle, N., McMahon, K. L., Ashton, R., Meredith, M., & de Zubicaray, G. I. (2008). Action word meaning representations in cytoarchitectonically defined primary and premotor cortices. *Neuroimage*, *43*(3), 634-644.

Pfurtscheller, G., & Da Silva, F. L. (1999). Event-related EEG/MEG synchronization and desynchronization: basic principles. *Clinical neurophysiology*, *110*(11), 1842-1857.

Pulvermüller, F., Hauk, O., Nikulin, V. V., & Ilmoniemi, R. J. (2005). Functional links between motor and language systems. *European Journal of Neuroscience*, *21*(3), 793-797.

Pulvermüller, F. (2013). How neurons make meaning: brain mechanisms for embodied and abstract-symbolic semantics. *Trends in cognitive sciences*, *17*(9), 458-470.

Pulvermüller, F. (2018). Neural reuse of action perception circuits for language, concepts and communication. *Progress in neurobiology*, *160*, 1-44.

Ralph, M. A. L., Jefferies, E., Patterson, K., & Rogers, T. T. (2017). The neural and computational bases of semantic cognition. *Nature reviews neuroscience*, *18*(1), 42-55.

Rosanova, M., Casali, A., Bellina, V., Resta, F., Mariotti, M., & Massimini, M. (2009). Natural frequencies of human corticothalamic circuits. *Journal of Neuroscience*, *29*(24), 7679-7685.

Rüschemeyer, S. A., Brass, M., & Friederici, A. D. (2007). Comprehending prehending: Neural correlates of processing verbs with motor stems. *Journal of cognitive neuroscience*, *19*(5), 855-865.

Schmahmann, J. D. (2010). The role of the cerebellum in cognition and emotion: personal reflections since 1982 on the dysmetria of thought hypothesis, and its historical evolution from theory to therapy. *Neuropsychology review*, *20*, 236-260.

Sereno, S. C., Rayner, K., & Posner, M. I. (1998). Establishing a time-line of word recognition: evidence from eye movements and event-related potentials. *Neuroreport*, *9*(10), 2195-2200.

Simmons, W. K., Ramjee, V., Beauchamp, M. S., McRae, K., Martin, A., & Barsalou, L. W. (2007). A common neural substrate for perceiving and knowing about color. *Neuropsychologia*, *45*(12), 2802-2810.

Strick, P. L., Dum, R. P., & Fiez, J. A. (2009). Cerebellum and nonmotor function. *Annual review of neuroscience*, *32*(1), 413-434.

Tettamanti, M., Buccino, G., Saccuman, M. C., Gallese, V., Danna, M., Scifo, P., ... & Perani, D. (2005). Listening to action-related sentences activates fronto-parietal motor circuits. *Journal of cognitive neuroscience*, *17*(2), 273-281.

Thut, G., & Miniussi, C. (2009). New insights into rhythmic brain activity from TMS–EEG studies. *Trends in cognitive sciences*, *13*(4), 182-189.

Tulving, E. (1972). "Episodic and semantic memory," in Organization of Memory. *(No Title)*, 381.

Visani, E., Garofalo, G., Rossi Sebastiano, D., Duran, D., Craighero, L., Riggio, L., & Buccino, G. (2022). Grasping the semantic of actions: a combined behavioral and MEG study. *Frontiers in Human Neuroscience*, *16*, 1008995.

Warrington, E. K. (1975). The selective impairment of semantic memory. *Quarterly Journal of Experimental Psychology*, *27*(4), 635-657.

Zwaan, R. A., & Taylor, L. J. (2006). Seeing, acting, understanding: motor resonance in language comprehension. *Journal of Experimental Psychology: General*, *135*(1), 1.