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Universidad del País Vasco
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The Relationship between Context and Conceptual Access

Peter James Boddy

Supervised by

Dr. Eiling Yee and Dr. Pedro M. Paz-Alonso

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BASQUE CENTER
ON COGNITION, BRAIN
AND LANGUAGE

The Relationship between Context and Conceptual Access

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For Marcus

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Abstract

An important question in the cognitive neuroscience of language regards the nature of the conceptual representations that make up semantic memory. Amodal accounts argue that conceptual representations of objects and their processing is functionally distinct from sensory or motor brain systems. On the other hand, sensorimotor theories maintain that the conceptual representations of objects and their processing involve the same perceptual and action brain areas active when experiencing them online. In a break from current orthodoxy, the current thesis seeks to explore whether concepts and semantic processing are best considered as functionally grounded in sensorimotor systems and contextually sensitive. To this end we report four studies using behavioural-psycholinguistic and neuroimaging techniques in healthy and clinical populations.

In part 1 we show that online perceptual processing in the visual (study 1) and olfactory (study 2) modalities can influence language comprehension, that lifetime sensory experience shapes the representational structure of object concepts, and that the outcome of semantic processing differs depending on an interaction of people's experience and their immediate perceptual context. In part 2, we examine whether motor system degradation due to Parkinson's disease leads to impairments or measurable differences in processing manipulable objects compared to healthy controls. While we do not observe behavioural differences in the way individuals with Parkinson's access the representations of manipulable objects (study 3), this may be due to their treatment context. However, the neuroimaging evidence we report (study 4) does suggest that changes in people's motor capacities lead to measurable alterations in the way that they process action semantics, at the neural level.

Taken together the experiments presented in this thesis provide evidence that the content and format of the conceptual representations of objects is multimodal and grounded in sensory and motor brain systems and people's lifetime sensory and motor experience with objects shapes their representations. Therefore, contrary to amodal accounts, there is functional overlap between sensorimotor and semantic processing, such that sensory, motor and semantic processes mutually interact with context (at many levels) meaning that each time a noun is processed its representational outcome and content varies dynamically. This suggests that exploring the relationship between concepts and context is both necessary and vital in order to properly understand the semantic representations underlying noun words.

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Resumen amplio en castellano

Introducción

El objetivo general de la presente tesis era ampliar nuestro conocimiento sobre la manera en la que se estructuran las representaciones conceptuales a largo plazo de los objetos concretos en la memoria semántica. Estas representaciones conceptuales de los objetos concretos no solo forman la base del significado de los sustantivos que les nombran, sino que además son la base del conocimiento que se deriva de la percepción de dichos referentes y de la actuación con ellos. Rompiendo con la ortodoxia imperante, el trabajo aquí presentado buscó proporcionar pruebas de que los conceptos efectivamente se conciben mejor como representaciones multimodales basadas en el sistema sensomotor, pero también sensibles al contexto.

La presente tesis contó con tres objetivos experimentales. En primer lugar, poner a prueba las predicciones de las teorías sensomotoras del procesamiento semántico (ej. Allport, 1985). Concretamente, que los atributos funcionalmente importantes de las representaciones conceptuales de los objetos concretos están representados en regiones cerebrales dispersas y de distintas modalidades sensoriales, las cuales se activan durante la percepción e interacción motora con dichos objetos. El segundo objetivo era examinar si, como resultado de lo anterior, el procesamiento semántico y el procesamiento sensomotor en línea son interdependientes e interactúan entre sí. El tercer y último objetivo era interpretar los hallazgos a la luz de una predicción de las teorías sensomotoras, hasta ahora relativamente poco investigada: que el contenido de las representaciones semánticas multimodales varía en función del contexto, entendido tanto como contexto inmediato como contexto personal, es decir, la experiencia previa de cada persona con estos objetos a lo largo de su vida.

Estas predicciones son incompatibles con las teorías que sostienen que el formato de las representaciones conceptuales y su procesamiento semántico son de carácter amodal (p. ej. Fodor, 1983), funcionalmente distintos del procesamiento sensorial y motor. Defienden, además, que los contenidos nucleares de la representación conceptual son unidades de significado fidedignas, infrangibles y contextualmente inmutables.

Con el fin de explorar las predicciones anteriores, realizamos cuatro estudios empleando técnicas conductuales y de neuroimágen, e incluyendo tanto participantes sanos como personas pertenecientes a poblaciones clínicas.

Parte 1 – La modalidad visual y la olfativa

Los dos primeros capítulos experimentales de esta tesis presentan dos estudios que exploran los componentes visuales y olfativos de las representaciones de objetos empleando paradigmas conductuales de "interferencia".

1.1.1 Visual

En primer lugar, presentamos dos experimentos (N = 83) diseñados para comprobar si las regiones cerebrales visuales tienen una importancia funcional para los componentes visuales de las representaciones de objetos, y en ese caso, para explorar cómo interactúan *mutuamente* el procesamiento semántico y el visual. Empleamos un paradigma de "interferencia" visual multi-tarea para comprobar: A) si ocupar el sistema visual con una tarea visual causa más interferencia en el procesamiento semántico concurrente de palabras referentes a objetos con una asociación a la experiencia visual relativamente mayor (*más visuales*) que con aquellos asociados con una experiencia visual relativamente menor (*menos visuales*); y B) si procesar nombres de objetos *más visuales* causa una interferencia relativamente mayor sobre el desempeño de la tarea visual que procesar nombres de objetos *menos visuales*. En consonancia con las predicciones sensomotoras, en el experimento 1 observamos que los participantes cometían relativamente más errores en la tarea visual cuando procesaban semánticamente nombres de objetos *más visuales* que cuando lo hacían con nombres de objetos *menos visuales*, y en el experimento 2 comprobamos que los participantes tardaban relativamente más en procesar semánticamente nombres de objetos *más visuales* que *menos visuales* cuando desarrollaban de forma simultánea una tarea visual. Ambos hallazgos fueron corroborados por un análisis estadístico exploratorio más potente, en el que analizamos ambos experimentos de forma conjunta, revelando resultados generales complementarios.

Estos resultados indican que los procesamientos visuales y semánticos concurrentes pueden competir por recursos cognitivos, de manera que las representaciones semánticas de objetos frecuentemente vistos pueden solaparse con áreas cerebrales involucradas en el desarrollo de tareas visuales (es decir, áreas involucradas en el procesamiento visual). Por lo tanto, dichas representaciones semánticas son, al menos en parte, de naturaleza visual. Los resultados también sugieren que el procesamiento semántico y el visual interactúan mutuamente, y que, por lo tanto, el contexto en el que se procesan nombres de objetos afecta al resultado del acceso semántico. Además, ya que los objetos se asignaron a las categorías para cada participante en base a su propia experiencia, las interacciones semántico-perceptuales que observamos sugieren que el grado en el que la representación de un objeto involucra áreas visuales depende de la *cantidad* de experiencia vital que un participante dado haya tenido, *personalmente*, con dicho objeto. En conjunto, parece que lo que vemos en un momento dado depende de lo que estamos pensando en ese momento, y lo que estamos pensando, a su vez, depende de lo que estamos viendo.

1.1.2 ***Olfativo***

A continuación, presentamos un experimento (N = 62) diseñado con un doble objetivo: comprobar si las regiones cerebrales olfativas son funcionalmente relevantes a la hora de procesar los componentes olfativos de las representaciones semánticas de los objetos y, en tal caso, examinar si la experiencia olfativa individual a lo largo de la vida moldea los elementos de estas representaciones. Para tales fines, empleamos un paradigma innovador de "interferencia" pasiva olfativa. En el mismo, la tarea de los participantes era realizar juicios semánticos sobre dos tipos de objetos: objetos fuertemente asociados a olores (*olorosos,* p. ej. ajo) y objetos olfativamente neutros (*neutros,* p. ej. martillo). A su vez, los participantes realizaban los juicios en dos contextos perceptuales distintos: sin aroma o expuestos a un aroma ambiental fuerte. Nuestra hipótesis principal era que el aroma ambiental fuerte "ocuparía" el sistema olfativo, produciendo una interferencia en la comprensión de las palabras de objetos *olorosos* en dicho contexto, al compararlo con el mismo procesamiento en un ambiente sin aroma. Además, otra de nuestras predicciones era que el nivel de interferencia sería proporcional a la experiencia de los participantes con el olor del objeto a lo largo de la vida. En consonancia con nuestras hipótesis, los resultados revelaron que la exposición a un olor ambiental fuerte dificulta (esto es, ralentiza) ligeramente el procesamiento de objetos *olorosos* en comparación con objetos *neutros*, y que esta interferencia es proporcional a la experiencia olfativa con los objetos. En conclusión, estos resultados avalan la hipótesis sensomotora de que los procesamientos conceptual y perceptual no son modulares sino continuos y capaces de interacción mutua. La mera presencia de un aroma ambiental es suficiente para provocar interferencia selectiva mientras se procesan objetos *olorosos* (pero no objetos *neutrales*), incluso cuando no se requiere atención explícita a la información olfativa. Asimismo, observamos que la interacción entre el procesamiento semántico y olfativo depende en gran manera del contexto inmediato y de la experiencia del individuo.

Resumen

En términos generales, los hallazgos expuestos en la Parte 1 indican que la comprensión del lenguaje puede influir sobre el procesamiento perceptual en línea, que la experiencia sensorial a lo largo de la vida determina la estructura representacional de los conceptos relativos a objetos y que el resultado del procesamiento semántico depende de la interacción entre la experiencia personal y el contexto perceptual inmediato.

Parte 2 - Parkinson y la modalidad manual

La segunda mitad de la tesis pasó a comprobar las predicciones sensomotoras en el campo manual. Así, examinamos si la degradación del sistema motor debido a la Enfermedad de Parkinson (EP) conduce a deficiencias o diferencias medibles en el procesamiento de nombres de objetos manipulables en comparación con personas sanas.

1.1.3 EP – Parte conductual

Primero, presentamos un experimento (N = 38) diseñado para probar si el sistema motor es importante para los componentes de acción de las representaciones de los objetos. Utilizando un paradigma conductual de denominación de objetos, evaluamos si los pacientes con la EP muestran una mayor interferencia al nombrar objetos *más manuales* como "martillo", que objetos *menos manuales* como "avión", en comparación con controles sanos equiparados. En contra de nuestras predicciones, no encontramos evidencia conductual de deficiencias semántico-motoras. Sin embargo, debido a que los pacientes con EP estaban bajo los efectos de su medicación contar el Parkinson en el momento de la prueba (es decir, habían recuperado su función de bucle motora) este resultado nulo es difícil de interpretar. Podría ser que la EP no provoque impedimentos en el procesamiento de objetos manipulables, pero también puede haber sido consecuencia de una interacción del estado del tratamiento con dichas deficiencias. Si esto fuera así, convendría señalar que esto estaría en línea con las ideas expuestas en esta tesis de que el contexto es clave para la comprensión de conceptos. En este caso, el contexto del tratamiento podría llevar a variaciones en contenido conceptual. Todo ello evidencia la necesidad de más investigación.

1.1.4 EP - fMRI

Teniendo en cuenta la información del estudio conductual, creamos un experimento (N = 34) diseñado para explorar si, a nivel neuronal, las deficiencias motoras debidas a la EP interactúan con las redes cerebrales involucradas en el procesamiento semántico de los nombres de objetos manipulables. En línea con nuestras predicciones, observamos diferencias de conectividad debido a influencias semánticas entre los controles sanos y los pacientes con la EP cuando procesaban nombres de objetos *más manuales*. En particular, observamos una conectividad funcional relativamente reducida para nombres de objetos *más manuales* para pacientes con la EP en redes cerebrales asociadas con la acción sobre los objetos. Este patrón de resultados sugiere variaciones sutiles en el procesamiento de objetos manipulables debido a un trastorno motor, en línea con las predicciones sensomotoras.

Resumen

En esta segunda parte de la tesis no observamos diferencias conductuales en la forma en la que los pacientes con la EP acceden a las representaciones de objetos manipulables, pero esto puede deberse al contexto de su tratamiento. Sin embargo, sí que encontramos evidencia de neuroimágen que sugiere que cambios en las capacidades motoras de los participantes pueden conducir a alteraciones medibles en la forma en la que procesan la semántica relativa a la acción, a nivel neuronal.

Conclusiones

Tomando los experimentos presentados en esta tesis de forma conjunta, tenemos evidencia de que el contenido y el formato de la representación conceptual de los objetos son multimodales y de que están basados en los sistemas cerebrales sensoriales y motores. También hemos mostrado evidencia de que la experiencia vital motora y sensorial de las personas modula sus representaciones de forma profundamente personal. Así, contrariamente a lo que defienden las teorías amodales, existe un solapamiento entre el procesamiento semántico y el sensomotor, de tal forma que los procesamientos sensorial, motor y semántico interactúan mutuamente con el contexto a varios niveles. Así, cada vez que se procesa un nombre, su representación final y su contenido varían dinámicamente.

El trabajo presentado en esta tesis es novedoso y notable en varios aspectos. Para empezar, nuestros resultados se obtuvieron de tres modalidades o campos sensoriales: el visual, manual y (el gran ignorado) olfativo. El hecho de que encontremos patrones similares en las diferentes modalidades, utilizando paradigmas novedosos, refuerza nuestras conclusiones considerablemente. Como segundo aspecto, destacamos que nuestros resultados de interferencia de multi-tarea en los campos olfativos y visuales variaron acorde a la experiencia vital. Varios estudios que han comprobado hipótesis similares utilizan puntuaciones de experiencia individuales agrupadas en medias grupales, o las obtienen de otros estudios o corpus. Nosotros, en cambio, mostramos los efectos a nivel individual. El tercer elemento a subrayar es que nuestras metodologías de interferencia son demostraciones no correlacionales de una relación funcional entre el procesamiento sensorial y semántico. Esto lo hace libre de cualquier crítica potencial relacionada con el argumento (asiduamente usado contra evidencias de neuroimágen) que la activación en áreas sensoriales y motoras no guarda ninguna relación con el procesamiento semántico, argumentando que sería simplemente una activación posterior epifenoménica o una activación extendida. Como cuarto aspecto, la evidencia de neuroimagen presentada en el cuarto capítulo experimental mejora el trabajo previo, ya que incluye un grupo control saludable, por lo que es informativo respecto a las diferencias en el procesamiento semántico debido a la EP. También emplea métodos de conectividad funcional, lo cual puede ser más informativo que las comparaciones de activaciones respecto a cuestiones relativas a la compensación conceptual y variaciones debido a cambios de larga duración en las capacidades de las personas. Para terminar, cabe destacar que una gran parte del trabajo realizado en torno a las hipótesis sensomotoras se concentra en estudiar verbos, como ejemplos canónicos de semántica de acción. Sin embargo, aquí examinamos una predicción sensomotora sin explorar hasta ahora, concentrándonos en objetos concretos del día a día con los que las personas tienen diferentes grados de experiencia en diversos ámbitos. Aunque esto haya hecho que nuestra aproximación a estas hipótesis haya sido más arriesgada en términos de poder observar un efecto, también hace que nuestros descubrimientos sean más novedosos.

En conjunto, nuestros resultados están en línea con teorías más recientes que hablan de conceptos "fluidos" (p.ej., Yee & Thompson-Schill, 2016), negando que las representaciones conceptuales estén delimitadas y sean unidades de significado fidedignas, y abogando por procesos dependientes del contexto. Esto sugiere que el contenido de una representación conceptual obtenido en un momento particular sería diferente del contenido de una representación similar en otro momento. Este contenido depende de la interacción entre lo que el cerebro esté ocupado haciendo en el momento que accede a la representación, y la naturaleza y cantidad de la experiencia vital de las personas con el referente de ese concepto. En general, esto sugiere que explorar la relación entre los conceptos y el contexto es necesario y vital para poder entender correctamente las representaciones semánticas.

Chapter 1: General introduction

1.1 Semantic memory

People know things about the world. I know, for example, that Tbilisi is the capital of Georgia, spoons are better than forks for eating soup, the British flag features three colours and Melton-Mowbray pork pies are delicious. We learn about the world through our senses as we develop from newborns to geriatrics, acquiring knowledge, storing it and then, more often than not (with luck), using it to behave intelligently. The faculty which allows us to store and access knowledge is called long-term memory, the purpose of which, succinctly, is to permit us to successfully perceive the world and act within it (Glenberg, 1997). Early accounts of long-term memory (e.g., Squire, 1987) separate it into procedural (or implicit) and declarative (or explicit) memory systems. We do not usually have conscious access to the content of the former and cannot readily express it with words (i.e., how to walk on slippery ice). The latter, declarative memory (i.e., “fact-like” memory) stores knowledge available to conscious consideration which is, for the most part, expressible with language (e.g., Donald Trump won the 2016 US presidential election). Declarative memory has traditionally been further separated into semantic and episodic memory (Tulving, 1972). Generally speaking, semantic memory is thought of as distinct from episodic memory in that it contains general knowledge stored about the world abstracted from particular encounters while episodic knowledge is ephemeral and connected to a particular time or place; consider: “What is a car?” vs. “Where did I leave my car parked yesterday”. As we shall see, modern advances in the cognitive neuroscience of language challenge these distinctions and taxonomies in a number of interesting ways and prompt further questions about the nature of semantic memory.

The conceptual representations or memory traces which constitute semantic memory are fundamental in cognition. One crucial role they play is to underlie the meaning of words and language. Though semantic memory includes the meaning of many classes of words such as verbs and nouns both concrete and abstract, the experiments I report in this thesis were confined to studying the nature of conceptual representations of concrete objects that are commonly referred to with noun words. While in the past semantics has focussed on words and their meanings (Tulving, 1972), nowadays, the term semantic memory means more than just word meaning. For cognitive neuroscience, semantic memory includes not only words but also other kinds of conceptual knowledge which play a central role in sensory perception, action and information processing. Semantic knowledge, in this thesis, is synonymous with conceptual knowledge.

The empirical literature reviewed in this introduction primarily focuses on relevant research into semantic memory focused on concrete objects. In the following introduction I briefly outline an influential cluster of theories of semantics (generally referred to as the amodal account), the characterisations of concepts which emerge from it, and then some challenging criticisms of it. I then outline the prevailing alternative approach to characterising semantic memory; namely, the sensorimotor account, and review empirical evidence in its favour. In turn, I describe prominent critiques of the sensorimotor approach and detail some important open questions for study. Finally, I outline my approach to answering them, thereby contributing to the debate; the experiments reported here.

1.2 Amodal accounts

For much of the history of research into lexical semantics, concepts have been characterised as units in an amodal semantic system called the *mental lexicon*. According to amodal accounts, the mental lexicon is something like a mental dictionary of word meanings which correspond to bounded and reliably reproduced lexical units. The contents of the mental lexicon include the word’s grammatical class, pronunciation and its meaning. In general, understanding the meaning of a noun word means accessing its unitary lexical concept by grasping the semantic entailments that it possesses. These semantic entailments have variously been characterised as; propositional (similar to sentence-like feature lists e.g., Fodor, 1983), evaluable for truth or falsity (Davidson, 1967) & hierarchical (i.e., structured in ontologies which involve hyponymy or hypernymy; Collins & Quillian, 1969). Concepts are compositional (combinable), fundamentally bounded discrete units of meaning and even innate (Chomsky & Smith, 2000). Conceptual representations of object nouns (i.e., lexical knowledge) are symbolic representations, stored in an amodal word-like code (sometimes referred to as “mentalese”), which are arbitrarily related to their referent. This means that irrespective of what specific knowledge is represented i.e., whether the semantic entailments include, e.g., what an object looks like or how it smells, the same symbolic code is used. According to the amodal approach, conceptual representation and processing is functionally separate from other aspects of cognition like perception or action.

1.2.1 Amodal accounts and cognitivism

Amodal accounts are attractive from the perspective of *cognitivism*, the view that computation is the best theoretical metaphor for what the mind does (i.e., that what the brain does is in essence, what computers do). As a metaphor it is tempting; computers (or robots) can receive information from sensors, transduce it into a single (amodal) computable code format, process it according to algorithms, and return outputs; potentially even motor or linguistic outputs. Can't human brains be said to do the same? Another advantage of computational metaphor is that computation is agnostic about hardware. In theory, *any* computation can be carried out on *any* hardware (Turing, 1937), even biological hardware like brains. Cognitivism has incredible explanatory use, and useful models of psychological phenomena that are based on it are plentiful. Its effects can be seen in many of the vast leaps forward in formal logic and linguistics, computer science, and artificial intelligence over the last 50 years. However, because cognition and amodal formal computation differ in important ways the amodal account of semantics faces a number of significant challenges.

1.2.2 Criticisms of amodal accounts: Grounding problem

Firstly, one major challenge for theorists is to explain how conceptual representations (either in computers or in brains) are "correctly" connected to their referents. In other words, what the nature is of the connection between signifiers (words or symbols) and denotations (referents or objects in the world). This problem is known as the grounding problem (Harnad, 1990) and is elegantly laid out in the Chinese room thought experiment (Searle, 1980) which asks us to imagine a monolingual English speaker seated in a cubicle, in possession of a Chinese to Chinese phrasebook. When slips of paper are slipped to him, covered with Mandarin characters, he dutifully transposes, using his trusty manual, the input to a suitable output and pushes responses out of the room. Presumably, if the phrasebook is any good, the responses should be suitable and meaningful to those Chinese speakers outside the room. But crucially, from his perspective, he has no idea whatsoever what any of the symbols mean. The strong intuition here is that computers cannot "understand" the meaning of what they compute, that symbolic systems alone cannot ground knowledge meaningfully. In the case of computers, humans ground the symbols for them. Thus, the work of meaning is kicked down the road. How, then, are the conceptual representations involved in human cognition grounded in the world?

1.2.3 Criticisms of amodal accounts: Architecture

Another criticism of amodal accounts is that their modular structure does not seem to fit well with what we know about brains; that they are highly interconnected and plastic networks of organic neurons. Brains evolved over millions of years to be perfectly integrated with sensory organs and action systems in bodies so as to permit animals to act successfully in their environment. Because symbolic computers did not develop this way, an obvious worry is that the hardware of cognition seems different to that of computation. While architectural differences are not problematic *per se* (as mentioned, symbolic computation is hardware agnostic) it is possible that, because brain architecture is varied and different cortical and subcortical regions process different types of input or output (i.e., visual, auditory, haptic) the processing that symbolic computers do may differ importantly to the processing that brains *in fact* do.

1.2.4 Criticisms of amodal accounts: Representational format

This leads naturally on to a related criticism of amodal accounts – one that challenges the contention that conceptual content and processing is symbolic and amodal in nature. As we have seen, in amodal accounts computation involves abstract symbols which don't reflect any features of its referents. However, content in human cognition seems to involve a variety of different formats of knowledge representation: visual, linguistic, olfactory, motor etc. In line with this, some theorists have tried to include further codes into their models (e.g., dual linguistic and visual codes; Paivio, 1990) however, these theories were developed before a number of important developments in cognitive neuroscience. It is interesting to note that Barsalou's perceptual symbols system are an attempt to bridge the gap between the symbolic and the perceptual by positing *perceptual* symbols (Barsalou, 1999).

To summarise, traditional amodal accounts are not considered to be readily compatible with current understanding of either the neural structure of the brain, or how it has been shown to process information. For example, they fail to adequately explain how meaning can be grounded in the world, capture and store information in formats sensitive to specific sensory modalities or how functional modularity could be implemented in the brain's inter-connected architecture.

1.3 Sensorimotor accounts of semantics

In light of these challenges, a number of competing explanations have developed for semantic content. For example, cognitive linguistics (Lakoff, 1987) sought to provide an *implementable* model of word meaning in terms of brain based meaningful content. In opposition to amodal theories (Chomsky & Smith, 2000; Fodor, 1983), according to cognitive linguistics, the faculty of language is not modular and separate from other areas of cognition such as perception and action. Language is just like other brain-based processes and describing it accurately means making it consistent with our knowledge of the brain. By combining linguistics and psychology, cognitive linguistics posited a bi-directional relationship between language and cognition in which linguistic categories such as concrete object noun words are defined through embodied and situated experience with the world alongside language experience.

Another influential alternative view, in line with cognitive linguistics, has developed, namely the sensorimotor approach[1] (alternatively referred to as embodied approach) (Allport, 1985; Barsalou, 1999; Damasio, 1989; Lakoff & Johnson, 1999). It argues that current amodal or cognitivist accounts are not compatible with our understanding of the brain and how it processes information and highlights that as embodied agents, our interactions with the world and objects within it are mediated through our sensorimotor capacities. It maintains that conceptual representations of objects are grounded in the world because their representations involve the same perceptual and action brain areas active when experiencing those objects and that the representational format of concepts, rather than being amodal, is multimodal. Given that the brain processes information from the senses in a variegated and distributed way over the cortex, representations can be said to resemble their referents insofar as the distribution of labour between sense modalities in experience is mirrored in long-term semantic memory. Specifically, when we identify objects or read their names, our successful recognition or comprehension of them is (at least partly) due to re-activation of those sensorimotor regions involved in our previous experiences of perceiving or interacting with them.

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[1] While not often associated with distributed and dynamic accounts of experience based sensorimotor semantics similar ideas were also suggested or explored by Wernicke & Freud (Gage & Hickok, 2005).

1.3.1 Distributed multimodal semantic representations

Activating the mental representation of an object means re-activating parts of the brain generally active when it is experienced, recapitulating our learned experiences of it. Because of this, sensorimotor representations are sympathetic to featural models of semantics because fragmentary conceptual representations are distributed along a variety of dimensions including (but not limited to) functional (how something is used or what it does), visual (what it looks like), motor (how it can be interacted with) and emotional (what type of affect it is associated with). This information clusters around parts of the brain responsible for acquiring it, meaning that information about an object's taste or odour is stored in olfactory or gustatory brain areas, its shape and colour in visual cortices and how it is manipulated in motor regions etc. For instance, when we hear the word *pen*, both visual regions and regions involved in coordinating the movement of the hand and arm should be activated, while hearing words like *cloud* or *satellite*, which refer to objects that are rarely touched, should in most people, activate predominately visual areas. The functional relationships between noun words (object labels) and their distributed sensorimotor representations may develop as a result of their regular coactivation. In Hebbian terms: those neuronal patterns which fire together, wire together (Hebb, 1949).

1.3.2 Evidence in support of sensorimotor accounts – Neuroimaging

Cognitive neuroscience uses neuroimaging methods such as functional magnetic resonance imaging (fMRI), electroencephalography (EEG), magnetoencephalography (MEG) to measure the activity of the brain while it performs cognitive tasks. Of particular interest to this review are insights gained from fMRI studies. fMRI is a non-invasive method of measuring in-vivo and in context the amount activity happening in the brain at different locations over time. It has a very good spatial resolution (i.e., it is excellent at locating activation to millimetre precision) but relatively poor temporal resolution (on the order of seconds). Its dependent measure is the blood oxygen level dependent (BOLD) signal, which is a measure of the relative amount of oxygen and carbon dioxide present in a given brain location at a given time. The BOLD signal tracks glucose uptake in the neurones of the brain and is treated as a measure of metabolic activity. By comparing the functional brain activity (three dimensional maps of BOLD signal changing over time) of people while they perform different cognitive tasks it is possible to identify which areas of the brain are involved in carrying them out.

Functional maps of the brain have been developed based on the insights of and neuroimaging (along with many other fields such as neuropsychology, neurobiology, basic neuroscience, tractography etc.). These heterogenous functional maps have localised areas of the brain related to many cognitive functions. For the purposes of this review, of particular importance are the areas of the cortex associated with sensory and motor processing and the fact that these areas of the brain are commonly structured (at the structural, connectivity, neuronal and cytoarchitectonic levels etc.) in such a way as to be specialised for processing the peculiarities of the types of information they are associated with. This can be seen in the visual system, for example, where visual input from the eye is fed into a distributed processing stream of increasing complexity with units specialised for processing edges, colours, movement etc, or the motor system which is organised (somatotopically) such that spatially distinct areas are responsible for controlling the hands, legs, mouth etc., resulting in a map like distribution of specialisation. Summarizing, distinct cortical and subcortical parts of the brain are highly specialised to process information from different senses.

In line with the predictions of the sensorimotor approach, cognitive neuroimaging fMRI studies indicate that processing objects (as the result of naming them or reading/hearing their names) results in the selective activation of brain areas involved in their experience (Binder, Desai, Graves, & Conant, 2009; R. F. Goldberg, Perfetti, & Schneider, 2006; Robert F Goldberg, Perfetti, & Schneider, 2006; Alex Martin, 2007; Noppeney & Price, 2003). In the case of vision, for example, visual features such as the shape (Wheatley, Weisberg, Beauchamp, & Martin, 2005) or colour (Simmons et al., 2007) of objects is stored in the ventral occipital cortex in an area known as the fusiform gyrus (the lateral mid FG in the case of the former and an area known as FG-alpha for the latter). Different classes of items such as tools and animals which differ in their typical visual features, and the relative importance of highly specific visual information for their recognition, lead to spatially distinct activation (medial for tools, lateral for animals) in this FG area (Chao & Martin, 1999). Another area, the lateral occipital complex (LOC) seems to represent “whole” objects, i.e., the viewpoint invariant visual composition of specific objects (Grill-Spector, Kourtzi, & Kanwisher, 2001).

In general, seeing photos and reading the names of objects associated with a particular modality leads to specific activation in relevant areas. For example tasty foods or smelly objects lead to activation of the orbitofrontal cortex and insula, parts of the brain involved in actually eating and smelling objects (Barrós-Loscertales et al., 2011; R. F. Goldberg et al., 2006; Robert F Goldberg et al., 2006; González et al., 2006; Simmons, Martin, & Barsalou, 2005), and objects associated with sound (such as musical instruments) cause the selective recruitment of left-lateralised and posterior regions of the superior and middle temporal gyri, areas predominately involved in processing input from the ears (Hoenig et al., 2011; Kiefer, Sim, Herrnberger, Grothe, & Hoenig, 2008).

The representation of simple motor plans is associated with parietal regions, specifically the anterior intraparietal sulcus (aIPS) and the supramarginal gyrus. More sophisticated motor representations are associated with the ventro-lateral pre-motor cortex (vPMC) (for review see: Johnson-Frey, 2004). Activating functional information about how to use or manipulate objects associated with these regions occurs as a result of seeing images or processing their noun word labels (Chouinard & Goodale, 2010; Saccuman et al., 2006). A number of studies indicate that highly specific information about objects is represented in the motor system, for example, detailed knowledge of how they are manipulated (Boronat et al., 2005; Hargreaves et al., 2012; Rueschemeyer, van Rooij, Lindemann, Willems, & Bekkering, 2010; Yee, Drucker, & Thompson-Schill, 2010).

Recent advances in fMRI data analysis and linguistic corpus analysis have resulted in a number of studies reporting that semantic information about nouns is distributed over the cortex in a tiled fashion in which the meaning of words similarly related to certain sensory dimensions cluster around relevant areas of the brain (cf Barsalou, 2017; Huth, de Heer, Griffiths, Theunissen, & Gallant, 2016; Mitchell et al., 2008).

In general, neuroimaging research shows significant overlap in areas associated with online action and perception and accessing semantics through language. As outlined below complementary findings come from neuropsychology and patient data.

1.3.3 Evidence in support of sensorimotor accounts - Neuropsychology

Neuropsychology studies patient populations with cognitive deficits as a result of brain damage or non-standard development. The insights gained from studying cognitive deficits as a result of damage (lesions) are particularly useful because they inform us of which areas of the brain are functionally associated with different cognitive functions. Early neuropsychological findings showing category specific deficits (i.e., living things vs non-living things) in some patients lead researchers to posit that object concepts are distributed in a domain specific way, according to categories (Warrington & Mccarthy, 1987). While some researchers argue for an approach like this because it considers that certain categories are more evolutionarily relevant for us than others (i.e., food, tools etc; Caramazza & Shelton, 1998), and there is some lesion evidence in support of it (Farah & Rabinowitz, 2003), a different account in line with sensorimotor theories has developed. The sensory functional view acknowledges that certain categories of objects tend to correlate with particular modalities, and that the importance of them for a category is differentially weighted (Warrington & Shallice, 1984). For example, visual information about living objects is very important for specific identification or distinguishing of species, whereas the most relevant information about tools seems to be functional. This means that the features or attributes of objects are represented in relevant modalities, as suggested by the sensorimotor approach.

If certain semantic knowledge is reliant on parts of the brain active during experience, as suggested by neuroimaging findings, then damage to those areas should lead to deficits in that knowledge, which seems to be the case: Lesions in sensorimotor regions do indeed lead to semantic deficits for objects which are reliant on that modality (G Gainotti, 2000). For example, lesions to the superior temporal gyrus (STG) lead to impairments to sound related concepts (Bonner & Grossman, 2012; Trumpp, Kliese, Hoenig, Haarmeier, & Kiefer, 2013). Lesions to the visual areas such as the lateral occipital complex (LOC) impair the visual recognition of objects but do not affect encyclopaedic knowledge of those objects (Wolk, Coslett, & Glosser, 2005). Furthermore, computational models of semantics based on the sensory functional approach show similar “semantic failures” in neural network models when their systems are experimentally lesioned (Farah & McClelland, 1991).

It should be noted that it has been argued that neuropsychological data does not fit well with sensorimotor accounts (e.g., Caramazza & Shelton, 1998). However, the balance of evidence seems to be in its favour and that difficulties in activating and integrating stored semantic information from modality specific regions lies behind many semantic agnosias (difficulty naming) in which failures to recognise objects are frequently resolved after individuals are provided with further cues through manipulating, hearing or smelling objects.

1.3.4 Evidence in support of sensorimotor accounts - Psycholinguistics

Further support for sensorimotor accounts comes from psycholinguistics. Eye tracking research shows that a great deal of sensory and motor information about the visual or manipulable characteristics of objects is automatically and quickly activated when we read their names (even when we are not conscious of having done so, (e.g., masked priming studies)) and which can prime us to look at other items which are similar along those dimensions (Yee & Sedivy, 2006). When reading language, we seem to activate visual representations of what the language describes in the visual system which speeds up our responses to matching and slows them to mismatching images later presented (Zwaan, Stanfield, & Yaxley, 2002).

1.3.5 Evidence in support of sensorimotor accounts – Multitasking paradigms

Many behavioural studies designed to test sensorimotor accounts involve variants of multitasking paradigms which are (conceptually), an alternative to lesion studies that do not rely either on accidents of nature like brain damage or on artificial methods of interrupting the neuronal activity at a particular place on the cortex such as transcranial magnetic stimulation (TMS) or transcranial direct current stimulation (tDCS).

The logic behind the multitasking methodology paradigm is that if two concurrent cognitive processes share the same neural resources then; because the brain has limited processing resources, performing one of these cognitive tasks while simultaneously performing another may cause them to interact and affect performance on one or both tasks. In the case at hand, i.e., testing sensorimotor accounts of semantic processing; concurrent semantic processes and other, ostensibly unrelated, perceptual or motor processing should selectively interact *only* when the semantic content being accessed relies significantly on the sensorimotor modalities being taxed.

The dynamics of the interactions in multitasking experiments are complex and depend on a number of factors. First, they may result in facilitation and interference (to one or both tasks) as a result of sympathetic vs antagonistic coactivation (Connell & Lynott, 2012). Furthermore, following the logic of resource conflict in the brain, the degree to which multitasking interacts should scale, on an item by item basis, in relation to how important a particular modality is for its conceptual representation, factors which influence this such as lifetime experience will be discussed below.

One study found that a task which taxes visual brain areas (remembering three coloured shapes) made verifying visual properties of a concept (e.g., “is it green?”) more difficult and conversely a task which taxed the auditory modality (remembering three tones) interfered with verifying auditory properties (e.g., “does it buzz?”) (Vermeulen, Corneille, & Niedenthal, 2008). Other studies have shown similar effects for repetitive hand movement interfering with accessing the representations of manipulable objects (Yee, Chrysikou, Hoffman, & Thompson-Schill, 2013)

These findings provide evidence that conceptual processing, to at least some degree, shares resources with those which are taxed by concurrent sensory or motor tasks and suggest that sensorimotor areas are not peripheral to semantic processing.

1.4 Criticisms of sensorimotor accounts

The convergent evidence in support of sensorimotor theories is sizeable. However, a number of challenges to the approach have been proposed. It is to these that I now turn.

First, a number of behavioural studies which report findings in support of embodied cognition have been challenged on theoretical, design and statistical bases (Firestone & Scholl, 2014, 2016), others have failed to replicate in large pre-registered replication studies (Garrison, Tang, & Schmeichel, 2016). These “technical” criticisms are best addressed by ensuring that experimental design, analyses and adequate replications are carried out with due diligence. The work reported in this thesis was done with these considerations in mind.

Second, the fact that most studies involving word processing do not involve total breakdown in accessing the meaning of nouns, i.e., participants and patients mostly “get there in the end just fine”, might suggest that sensorimotor areas are not “critical” for representing the meaning of nouns. With regards to this criticism, it should be highlighted that, in fact, sensorimotor models are well placed to provide an account for this. Given the highly distributed nature of conceptual representations, almost all objects will be structured along a number of sensory or functional dimensions over relevant parts of the cortex. This means that where one part of a representation is damaged or temporarily inaccessible, other, preserved parts of the representation can “take up the slack”. In other words, sensorimotor representations are, by their nature, more robust to catastrophic failure than amodal representations, and particularly well suited to allow for graceful degradation of meaning.

A similar issue is that evidence from lesion studies is mixed. For example, lesions to motor regions do not always coincide with measurable conceptual impairments to motor concepts and vice versa (Mahon & Caramazza, 2005). That lesion studies sometimes do not line up with the predictions of sensorimotor accounts is indeed a challenge. One potential criticism of patient studies which is less readily levelled at multitasking paradigms is that aggregating data from patients with the “same” lesions is fraught with difficulty not least because of the complexity of the human brain and its interconnected nature. To avoid this criticism, studies which demonstrate modulations of concrete noun processing as a result of *controlled* interventions to sensorimotor areas are needed, interventions such as behavioural multitasking experiments.

A major criticism levelled at the sensorimotor approach concerns neuroimaging findings. The charge is that any activation observed in sensory regions putatively as a result of semantic processing does not definitively demonstrate that these regions are involved in representing the meaning of noun words. It remains logically possible that the observed activation results from a number of processes downstream from semantic resolution such as post-comprehension explicit mental imagery or automatic spreading neural activation (Mahon & Caramazza, 2008). If this criticism is correct, the activation of sensorimotor areas during semantic tasks could be equally well explained by a model of representation in which activation spreads to sensorimotor areas during or after conceptual access, perhaps in order to “enrich” cognition, but in which this sensorimotor activation is not a part of concepts, i.e., the amodal view. One-way researchers try to address this challenge is to show that sensorimotor recruitment happens very quickly, thereby indicating that it is automatic and functionally important rather than incidental and downstream (e.g., Hoenig, Sim, Bochev, Herrnberger, & Kiefer, 2008; Wheatley et al., 2005). While speed is indeed suggestive and informative, it still suffers the criticisms that correlated activity (no matter the speed) does not *definitively* indicate that sensorimotor areas are *part of* conceptual meaning. In order to convincingly show that sensorimotor regions are *functionally* involved in object comprehension (i.e., constitutive of meaning), as opposed to incidentally co-activated (i.e., peripheral or epiphenomenal), non-correlational paradigms must be employed.

1.4.1 Open questions

In order to address the above challenges, further work needs to be done to demonstrate that sensorimotor areas are functionally related to meaning and that semantic processing is not amodal and insulated from other perceptual and motor processing, but rather that these processes interact in deep and important ways. As well as addressing criticisms, much work needs to be done on unpacking as yet under emphasized but nonetheless critical aspects of the sensorimotor theory. One such aspect is the need to study sensorimotor concepts "in context". It is to this topic that I now turn.

1.5 Concepts in context

Early on, cognitive linguistics (Lakoff, 1987) emphasised the importance of studying human cognition in ways sympathetic both to insights about the brain, but also as embodied and situated or embedded in social, linguistic and sensory contexts. Much of cognitive science now acknowledges the importance of this insight (Clark, 2001; Di Paolo, Cuffari, & De Jaegher, 2018; Varela, Thompson, Rosch, & Kabat-Zinn, 2016). In line with this, the sensorimotor view maintains, in contrast to amodal accounts, that the conceptual system is not separated from sensation or action, that sensory experience with objects shapes their representations and that ongoing activity in perceptual or motor areas affects how meaning is activated (Yee, Chrysikou, & Thompson-Schill, 2013). If the nature of object concepts is as suggested by the sensorimotor account then they are not clearly-delimited context-free "nuggets" of meaning which are reliably and consistently activated each time we read their names. Rather, the concepts which underlie the meaning of words are best characterised as contextually fluid to a functionally relevant degree.

While some theorists suggest that thought is so fundamentally dynamic and that even the notion of conceptual representations is unnecessary (Chemero, 2011; Elman, 2009), for the purposes of this thesis I will focus primarily on the more circumscribed insight that viewing conceptual representations as stable and context free is a problematic oversimplification (D Casasanto & Lupyan, 2015; Connell & Lynott, 2014; Spivey, 2008; Yee, 2017; Yee & Thompson-Schill, 2016). Specifically, considering concepts in context here means: A) studying a person's immediate sensory or motor context and how that interacts with semantic processing i.e., studying the dynamics between concurrent sensory and semantic processing. B) Studying personal context: either in terms of an individual's particular lifetime sensorimotor experience with objects and/or fundamental changes in a person's sensorimotor capacities as a result of illness. In the following sections I describe these "contexts" in more detail (for further discussion see; Yee & Thompson-Schill, 2016).

1.5.1 Immediate context

In the first case, because of resource competition (as in multitasking paradigms), what the brain is busy doing at any moment (e.g., sensing, perceiving) can affect other processes (e.g., accessing semantics). This means that semantic information retrieved at a given moment varies from other moments. Perhaps this is because not all aspects of a representation is available, possibly due to interference or lesioning (Bub, Masson, & Cree, 2008; Yee, Chrysikou, Hoffman, et al., 2013) or certain featural dimensions that are more strongly activated, or perhaps because attention has been directed to them as a result of a task (Yee, Ahmed, & Thompson-Schill, 2012). Or particular dimensions are under activated because they are not relevant for a particular context (Barsalou, 1983). More work needs to be done on mapping out the ways that immediate context and semantics interact

1.5.2 Lifetime experience

Because, at a certain level, people's lifetime experiences are largely similar, enormous progress has been made with "averaging approaches" to studying semantic memory, however, as an important prediction of sensorimotor-based accounts of object concepts is that an object concept's representation is (at least partially) constructed from our lifetime experiences with that object, it also follows that variability in people's sensorimotor experience with objects should affect, at the individual level, how a concept's representation will be instantiated in the brain. At a fundamental level, because individual brains develop and change over the lifetime and because the content of language and the brain are interconnected, then the representations underlying word meaning are *personal*. Personal semantics involves representations which are labile and shift as we gain new knowledge through sensory and motor interactions with objects in the world. Important to note is that while it seems possible (and likely) that semantic knowledge can be gained through other experiential paths (Renoult, Davidson, Palombo, Moscovitch, & Levine, 2012) e.g., book learning or internal thought processes such as mental rehearsal etc., further discussion of these topics is, unfortunately, beyond the scope of this introduction.

According to sensorimotor accounts, as a result of experience, the semantic representations of particular concrete objects should be represented to a greater degree over brain areas supporting some modalities than others. As a first example, in the case of cutlery, our previous experience of using them with our hands should result in their representations extending into areas of the brain related to manual manipulation However, our representations of clouds, which we almost exclusively experience visually, should load very little on manual but rather more heavily onto visual areas of the brain. However, many objects are less ubiquitously experienced than cutlery and clouds. Objects for which there is more personal variability in experience are good test cases for the predictions of sensorimotor accounts. For these objects, over time their representations should alter subtly insofar as the distribution of their sensorimotor representations would "gravitate" to different modalities as a result of variegated individual experience. There is evidence that this is true, with respect to relatively long-term experience where it has been found that musicians show differences to non-musicians in auditory cortex when reading the names of or naming pictures of musical instruments (Hoenig et al., 2011; Trumpp et al., 2013), the handedness of people (i.e., the hand they use to manipulate objects with) leads to complementary differences in the lateralisation of activation of the premotor cortex when naming tools (Kan, Kable, Van Scoyoc, Chatterjee, & Thompson-Schill, 2006) and that lifetime tactile experience with a variety of everyday objects changes the recruitment of parietal cortex for processing their names (Oliver, Geiger, Lewandowski, & Thompson-Schill, 2009). Similarly, with respect to relatively shorter-term experience, periods of olfactory, visual or manual training on previously unknown objects have been shown to affect how objects are represented in related modality specific regions of the brain (Bellebaum et al., 2013; Ghio, Schulze, Suchan, & Bellebaum, 2016; Oliver et al., 2009; Weisberg, Van Turennout, & Martin, 2007). Finally, some convergent evidence also comes from a number of behavioural studies which showed that the amount of experience a person has with a given object in a particular modality shapes the degree to which their *personal* representation of that object is represented over that modality (Chrysikou, Casasanto, & Thompson-Schill, 2017; Yee, Chrysikou, Hoffman, et al., 2013).

1.6 The current thesis

The objective of the experimental chapters reported in this thesis is to examine whether sensorimotor areas are *functionally* (not epiphenomenally) related to semantic representations by employing non-correlational multitasking methodologies which are not susceptible to some prominent criticisms levelled at neuroimaging evidence. Furthermore, these methodologies allow us, simultaneously, to challenge the amodal approach's tenet; that semantic memory is amodal and modular (i.e., separate from other perceptual and motor processing systems), by demonstrating that what the body is doing at a given moment influences cognition and by measuring those semantic-sensory-perceptual interactions. In addition, in order to further extend our understanding of semantic memory in a novel direction, these experiments were designed to explore the dynamic interplay of context (whether personal; i.e., in lifetime sensorimotor experience, momentary or acquired, across three distinct sensory modalities) and conceptual processing, to test *how* the content of distributed sensorimotor concepts available for thought varies dynamically; to explore concepts in context. The research presented in this thesis departs from much work to date which seeks generalizable models of semantics focusing predominately on commonalities in cognition; i.e., findings averaged over people and in simplified contexts, and instead focuses on the way semantic phenomena vary according to the particulars of individual experience and the complex contexts in which human thought occurs.

Part 1 – Visual and olfactory modalities

The first two experimental chapters of this thesis report two studies designed to test visual and olfactory components of object representations.

Chapter 2: Visual experience and object representations

2.1 Introduction

Vision is an extremely important perceptual modality for experiencing the world and is often vital for object recognition. This is because many objects are most readily or commonly differentiated based on visual properties like their form, size or colour (e.g., species of animals or tools). Experience with concrete objects is sometimes entirely mediated through vision (e.g., moon), else, visual information still commonly forms an important part of multimodal experience with objects. Sensorimotor theories predict that if objects are visually experienced then their representations should extend over brain regions related to visual processing. For these reasons, vision is a promising modality in which to test the predictions of sensorimotor accounts.

As discussed in the general introduction, many neuroimaging (fMRI) studies have shown that when people think about the visual features of objects the ventral stream (including many areas of the brain responsible for vision) are activated (e.g., Anderson, Bruni, Lopopolo, Poesio, & Baroni, 2015; Chao & Martin, 1999; Coutanche & Thompson-Schill, 2015; A. Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995; Simmons et al., 2007; S. Thompson-Schill, Aguirre, D'Esposito, & Farah, 1999; Wheatley et al., 2005). Furthermore, neuropsychological research suggests a functional relationship between the semantic representations of objects and these areas as lesions in the LOC, an area involved in processing visual objects, lead to impairments in the visual recognition of objects (e.g., Wolk et al., 2005).

Similarly, psycholinguistic research suggests that when language describing objects is processed, a rich visual "simulation" of what is conveyed is activated. After people hear verbal descriptions of an object, they recognise visually congruent depictions of what is described more quickly than incongruent images, i.e., if they hear "the man picked up the nail from the table", a picture of a nail lying in a box is recognised faster, or named more quickly, than a picture of one ready to be hammered (Pecher, van Dantzig, Zwaan, & Zeelenberg, 2009; Zwaan et al., 2002). Crucially, because the sentences *imply* certain visual properties, but do not explicitly state them, and pictures in both conditions (i.e., matching or mis-matching) depict the *same object*, picture-sentence match-facilitation is taken as evidence of people routinely activating more fulsome visual simulations of the language than provided by the individual words alone. Using such tasks, it has been shown that implied orientation (Stanfield & Zwaan, 2001) and shape (Zwaan et al., 2002) information is activated by language.

Some authors have failed to replicate the orientation simulation effects (Rommers, Meyer, & Huettig, 2013) and argue that visual simulation is not automatic and is task dependent. However, a large online replication of both the orientation and shape effects (Zwaan & Pecher, 2012), and supporting evidence from eye tracking (Wassenburg & Zwaan, 2010) suggests, on balance, that rich visual mental simulations of what is described by language arise online as we process it, at least for some properties (see: Connell, 2007; for evidence that colour information is different).

While the above experiments involve sentence comprehension, there is further behavioural evidence that even single words like object names activate the visual features of their referents. In visual search tasks, hearing the name of a target (e.g., "cat") boosts people's ability to find an image of that item more than non-linguistic, but valid, cues like canonically associated sounds (e.g., "miaow") (Lupyan, 2012) and makes people more likely to correctly predict its presence, even when targets are placed out of conscious visual awareness using constant flash suppression techniques (Lupyan & Ward, 2013). It is also well established that processing the names of objects primes us to think about things that have similar shapes (Pecher, Zeelenberg, & Raaijmakers, 1998; Schreuder, Flores d'Arcais, & Glazenborg, 1984; Yee, Huffstetler, & Thompson-Schill, 2011).

While these findings are very suggestive, as outlined in the introduction, it is important to show that visual areas are *functionally* related to semantic processing. If, as the sensorimotor account maintains, overlapping visual brain regions are involved both in visual perception and semantic processing, then concurrent processes, both reliant on those regions, should interact with one another. Some research, employing visual-semantic multitasking paradigms suggests that this is the case. For example, people's sensitivity to identifying the direction of dot array motion is interfered with by simultaneously processing "incongruent" language e.g., hearing the verb fall while viewing arrays suggesting upwards movement (Meteyard, Bahrami, & Vigliocco, 2007; Meteyard, Zokaei, Bahrami, & Vigliocco, 2008), or alternatively people's ability to process directional language (verbs) is facilitated by congruent motion (Kaschak et al., 2005). While these examples support the view that visual processing and semantic processing can interact, at least with sentence or verb processing, little work has thus far been done on the question of whether similar effects can be observed when processing single object names. One study found that a short-term memory task, designed to tax visual brain areas, made verifying visual properties of an object more difficult as compared to a task which taxed the auditory modality (Vermeulen et al., 2008) and another similar experiment even found that simply presenting probe questions visually incurred a processing cost for visual (but not auditory) property verification (Vermeulen, Chang, Corneille, Pleyers, & Mermillod, 2013). One recent study (Edmiston & Lupyan, 2017) demonstrated that visual interference (quickly flashing rectangles) disrupted participant's ability to verify explicitly probed information about visual properties rather than encyclopaedic information about objects (though see: Ostarek & Huettig, 2017 for evidence that these effects are task dependent). Finally, one study (Rey, Riou, Vallet, & Versace, 2017) observed that a visual mask, perceptually absent (but reactivated from visual memory), interfered with making semantic judgements on object names and that the magnitude of this dual-task-interference was correlated with ratings of each item's visual perceptual strength i.e., the relative degree to which visual features are important to that object's representation (see: Lynott & Connell, 2013). It seems, therefore, that accessing object representations associated with visual experience can be interfered with concurrent visual tasks.

However, it remains to be seen whether the *amount* of visual experience a person has shapes object representations by determining the degree to which they are represented in visual areas. While there is little evidence examining this in the visual modality (though see: Davis et al, 2019: a study conducted after the ones described in this chapter, which we return to in the general discussion), in the manual modality one study (Yee, Chrysikou, Hoffman, et al., 2013) employed two concurrent tasks, intended to selectively occupy the motor system or the mental rotation system while participants made semantic judgements about objects which varied in how much lifetime manual *versus* visual experience participants had had with them. Promisingly, they found that lifetime manual experience with a given object predicted how much the manual task interfered with making the semantic judgement. However, their mental rotation control task, which might be construed as a visual task, did not cause relatively greater interference to the semantic processing of more-visually-experienced objects. This may have been because, as the authors pointed out, mental rotation is thought to be sub-served by the superior parietal lobe (Isabel Gauthier et al., 2002), which is not the part of the visual system that has been commonly linked to visual object recognition (i.e., the Lateral Occipital Complex; Farah & Hammond, 1988). If this is the case, then the absence of interference between the retrieval of object semantics for more visual objects is not surprising. Thus, it is still unclear whether lifetime visual experience influences the representations of concrete objects in the same way as suggested for manual experience. Given this gap in the literature, here we sought to explore these issues more fully.

2.1.1 Questions

In this chapter I report two experiments which were designed to explore central predictions of sensorimotor accounts and to gain new insights into the interplay between language and perception. Firstly, we wanted to test whether visual brain areas are functionally (not incidentally) important for visual components of object representations. Therefore, we tested if occupying the visual system with a visual task causes greater interference to the processing of words referring to more-visual objects than to less-visual object names. Secondly, because we wanted to explore how semantic and visual processing mutually interact, we tested if thinking about words referring to more-visual objects causes greater interference to doing a visual task than less-visual object names. Finally, because we were interested in how *personal* visual experience with objects affects their representations, we used participants' own ratings of lifetime visual experience with items in our analyses.

2.1.2 Predictions

If the semantic representations of objects associated with more visual experience involve the same brain areas as those employed in the visual task (i.e., visual areas), we predict that conceptual processing and visual processing will interfere with each other. Furthermore, we predict that interference will relate to the amount of lifetime visual experience people have with objects.

2.1.3 The experiments

An early analysis of data from the semantic task of experiment 1 was previously reported (Boddy & Yee, 2013 unpublished Master thesis). However, multitasking interference effects could have manifested in a number of ways in that experiment, i.e., in both tasks, only in the semantic task or only in the visual task. Thus, here we present an analysis designed to examine a possibility that was not explored in the prior work – that interference will manifest in the visual task. To do this, we use a dependent variable that was collected, but not analysed in the earlier work, namely participants' responses to the visual task. We also present a re-analysis of the semantic task data from experiment 1. In experiment 2, we present new data from a follow-up experiment which modified the procedure of experiment 1 and also included several other refinements designed to optimise the experiment's statistical power to detect any effect of concurrent visual task processing on conceptual processing and vice versa.

2.2 Experiment 1

2.2.1 Motivation

Because, at the time of this study, previous work did not observe semantic-perceptual interference in the visual domain (Yee, Chrysikou, Hoffman, et al., 2013), we decided to use a visual task intended to be more likely to interfere with parts of the visual system that support visual object recognition (i.e., the lateral occipital cortex) than a mental rotation task: namely Multiple Object Tracking (MOT) (Pylyshyn & Storm, 1988). This task, which requires participants to track a number of pre-cued moving targets in a field of identical distractors over a short period, is broadly similar to those used in the literature previously (e.g., moving dot arrays or spirals: Kaschak et al., 2005; Meteyard et al., 2007), but differs from those tasks in that the movement component of the visual task was orthogonal to the content probed in the semantic task (i.e., single concrete nouns referring to a wide range of objects not associated with canonical directional movement). In our experiment, because the visual stimuli do not resemble the tested objects, and motion was not relevant to making judgements, the required visual processing demand for the task, *per se*, was predicted to interfere with semantic processing alone. Another benefit of the MOT task is that because continuous visual tracking (i.e., sustained visual attention over time) is required for successful task completion, it is appropriate for use as an interfering concurrent task to auditory language processing, which itself unfolds over time (Connell & Lynott, 2012). Finally, performance on the MOT task has the added advantage of providing a measure of accuracy, which, as described below, affords an extra dependent variable of interest and therefore a more fine-grained way of looking at interactions between concurrent semantic and visual processing. Furthermore, there is some suggestive evidence of the MOT task interacting with language (Kunar, Carter, Cohen, & Horowitz, 2008) though that study did not test sensorimotor-semantic hypotheses.

2.3 Methods

2.3.1 Participants

The final study sample consisted of 33 (M age = 23 years, range = 19-36 years, 14 male) native Spanish speakers with normal or corrected-to-normal vision who were paid for participating in the 1hr study. Exclusion criteria included: physical disability or injury to relevant response effectors (hands or feet) or not being a native Spanish speaker.

2.3.2 Ethics statement

We obtained written informed consent, in compliance with the regulations established by the BCBL ethics committee in line with the guidelines of the Helsinki Declaration, from all participants before taking part in the study.

2.3.3 Stimuli

Semantic task

Our stimuli were 200 concrete object names (e.g., *leaf*) and 200 abstract noun words (e.g., *approval*) (The stimuli were in Spanish. See Table 11 in the appendix for a full list). The concrete objects included: man-made; tools (56), objects (56) & natural: food/plants (44), animals (44). For counterbalancing purposes, we split the stimuli in half and created two counterbalance lists, approximately balanced for log-frequency and semantic category and equally varied on visual experience ratings[2]. Each participant saw all of the stimuli once, but we arbitrarily allocated the order of presentation of each counterbalance list to participants ensuring that one half saw one in the concurrent-visual-task condition and the other saw it in the no-concurrent-visual task condition. Within both counterbalance lists, words were presented in a pseudo-randomised fashion with no more than four items of the same category (i.e., concrete or abstract) presented in succession.

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[2] We collected preliminary visual experience ratings online from 62 paid participants who did not participate in the main experiment. The rating question was identical to that described below.

Visual task

For the visual task we created fifty stimuli videos in MATLAB, using the Psychophysics Toolbox extensions (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007; Pelli, 1997) with adapted scripts from the Bavelier Brain & Learning Lab (Bavelier, Achtman, Mani, & Föcker, 2012).

2.3.4 Procedure

The experiment was presented using Presentation® software (Version 18.0, Neurobehavioral Systems, Inc., Berkeley, CA, www.neurobs.com) on a CRT monitor. Participants performed the experimental blocks in a sound proofed behavioural cabin and audio stimuli were presented through headphones. Task instructions, volume level, participant distance from monitor and position of response box and keyboard were kept constant across participants. Standardised written task instructions and diagrams were used during task explanations and were clearly visible to participants throughout the experimental blocks. There were 200 trials per experimental block with a pause after 100 trials. Each participant performed two experimental blocks: one whilst performing the perceptual task and one while not. There was a block of 10 practice trials before the concurrent task experimental block during which feedback about accuracy and concurrent task performance was given. Because the experiment design required a condition in which the visual system was relatively less occupied than in the perceptual task condition, in the no-interference blocks participants were instructed to close their eyes and wore a sleeping mask while they performed the semantic task. The order of interference and non-interference task blocks was arbitrarily determined and counterbalanced across participants. At the end of the experimental session, all participants rated the concrete noun words according to the following question: “How much relative lifetime experience do you have touching this object with your hands or seeing it?” from 1 = relatively more experience touching, to 7 = relatively more experience looking. Finally, they were debriefed as to the objectives of the study.

Trial structure

After 500ms of a white fixation cross on a black background, a large grey circle appeared containing ten smoothly moving small yellow circles which bounced off one another and the edge of the grey circle on contact. Initially, two of the moving balls turned blue, to mark them as targets, before eventually turning yellow after 1000ms. At this point the fixation cross became a white question mark and auditory words for the semantic task were presented. While continuously fixating in the centre and tracking the two previously-marked targets, participants made concrete/abstract judgements on the words, with their toes, as quickly and accurately as possible. When they responded, the white question-mark disappeared. After 2500ms from word onset the balls stopped moving, one of them turned red, and a red question mark appeared in the centre of the screen. Participants had 1500ms to respond, with their toes, if the stationary red ball was one of the previously marked targets or not, before the next trial began. See Figure 1 and Figure 2 for diagrams.

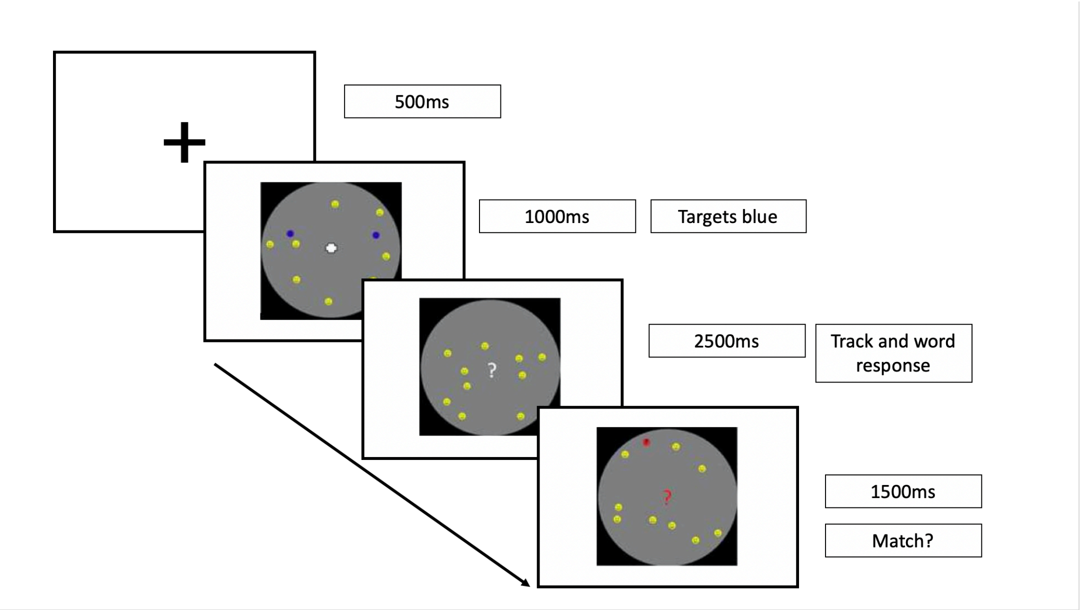


Figure 1. Visual experiment 1 trial structure.

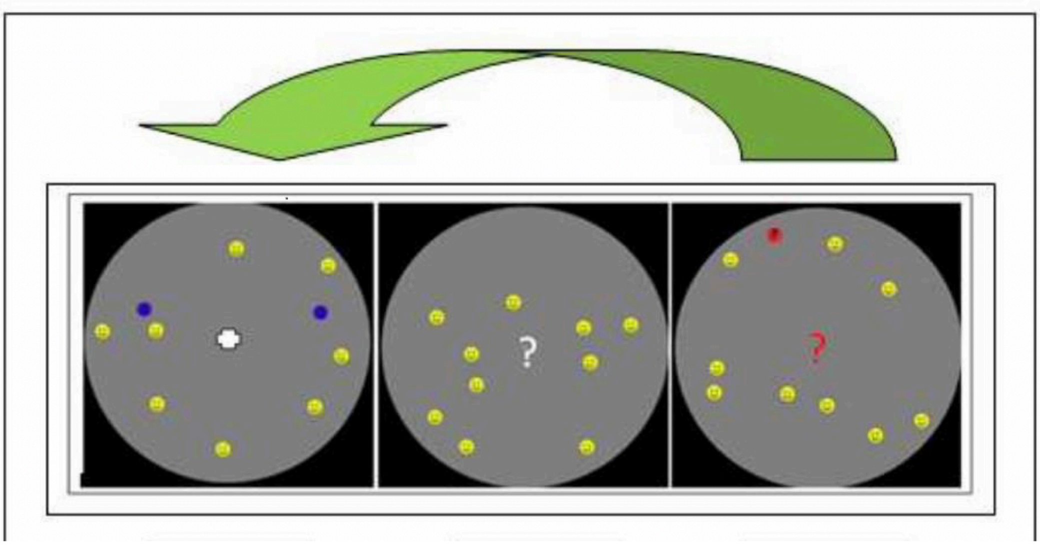


Figure 2. Visual experiment 1 & 2 visual task.

2.3.5 Statistical analysis

We performed analyses using the lme4 package (Bates, Maechler, Bolker, & Walker, 2015) in the R programming environment (R Core Team, 2018). Response times (RTs) were submitted to linear mixed effects regression models (LMERs) and errors were submitted to generalised linear mixed effects (logistic) regression models (GLMERs). The significance of the effects was assessed using the likelihood-ratio tests (i.e., chi-squared tests of fit) between a model with and one without the critical term. To approximate degrees of freedom and *p* values for individual predictors in the models we used the lmerTest package (Kuznetsova, Brockhoff, & Christensen, 2017). For analyses we report relevant regression coefficients (either RTs or odds ratios (ORs)) with 95% CIs and t-values (LMER) or z-values (GLMER).

As counterbalanced-crossed random effects we always included participant and item as intercepts. We also included random slopes of the fixed effects, by subject and by item, when they: improved the fit of the model, were theoretically motivated, justified by the data and design, computationally converged, and did not lead to underspecified estimates (i.e., random effect correlations of >.8/-.8). We aimed to be as maximal (Barr, Levy, Scheepers, & Tily, 2013) as was warranted without sacrificing parsimony (Bates, Kliegl, Vasishth, & Baayen, 2015; Matuschek, Kliegl, Vasishth, Baayen, & Bates, 2017).

In the semantic task analyses, as fixed effects we entered object-type (a categorical variable with two levels: less-visual objects (baseline) and more-visual objects), interference condition (a categorical variable with two levels: no-interference (baseline) and visual-interference) and their interaction. A significant critical positive interaction between object category and interference condition, would indicate more relative interference, due to a visual task for objects associated with more visual experience than with less. In the visual task analyses, as a fixed effect we entered object-type, for which a positive critical main effect would indicate more interference on the visual task as a result of processing objects associated with more visual experience than with less.

Because we had no predictions for the abstract "foil" items we did not include their data in the analysis. Similarly, because we are interested in the mutual interaction of semantic processing and visual processing, in each task's analysis we include only trials in which participants also made correct responses in its corresponding concurrent task i.e., those trials where we could be sure either that the semantic information had been accessed or visual tracking had succeeded (<9% of total data excluded). In the semantic task valid response times (i.e. those logged between 300ms-2500ms of word onset) to the semantic task were trimmed, by participant and for each condition, to ±3 SD of the mean (<1% of total data excluded). In the visual task, latencies are uninformative with regards to semantic interference because it involves a delayed binary response to a probe based on continuous visual tracking. This means that the participants have either tracked successfully and can accept or reject the probe, or they have tracked ineffectively and are forced to guess; therefore, we only analysed accuracy. Analyses of interference as measured in accuracy for the semantic task in both experiment 1 and 2 revealed no differences and are not described further here.

2.4 Results

Data Exclusion

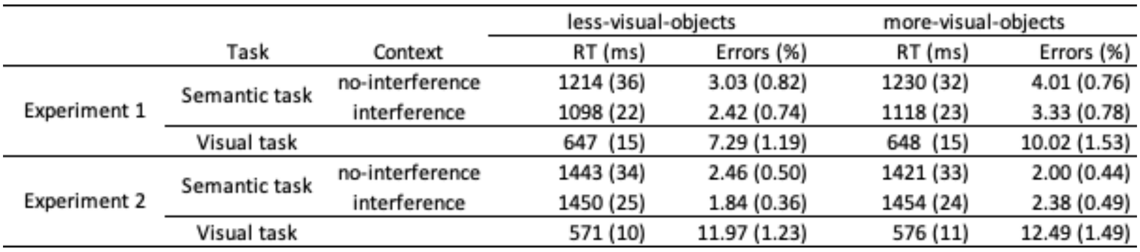
We excluded the data from nine participants (20% of sample), not included in the final sample described in the participants section, for the following reasons: lost data (3), sleeping during task (1), procedural errors e.g., a cable coming loose from the response box (5). Following a preliminary analysis, the data from a further two participants (5% of sample) were excluded due to: poor performance on the visual task (i.e., accuracy < 50% & > ±3 SDs from the sample mean) (1), low variability in ratings (i.e., exclusively values of 1 and 7) making stimuli categorisation impossible (1).

Object condition assignment

Using each participant's individual experience ratings, by subject we divided the objects into two conditions: The bottom tercile of the objects became the relatively-less-visually-experienced-objects (less-visual) condition (M=2.42, SD=1.34) and the top tercile the relatively-more-visually-experienced-objects (more-visual) condition (M=6.48, SD=0.79).

2.4.2 Semantic task

On the semantic task, overall, participants were (unexpectedly) slower in the *no*-interference condition than in the interference condition (RTs ± 1 SD: M = 1222, ± 191 ms and M = 1119, ± 119 ms respectively), but accuracy was similarly high in both conditions (errors ± 1 SD: M = 3.8 ± 3.7 % and M = 4.1 ± 3.8 %, respectively). See Table 1 for raw aggregated reaction times and error rates.



			less-visual-objects		more-visual-objects	
	Task	Context	RT (ms)	Errors (%)	RT (ms)	Errors (%)
Experiment 1	Semantic task	no-interference	1214 (36)	3.03 (0.82)	1230 (32)	4.01 (0.76)
		interference	1098 (22)	2.42 (0.74)	1118 (23)	3.33 (0.78)
	Visual task		647 (15)	7.29 (1.19)	648 (15)	10.02 (1.53)
Experiment 2	Semantic task	no-interference	1443 (34)	2.46 (0.50)	1421 (33)	2.00 (0.44)
		interference	1450 (25)	1.84 (0.36)	1454 (24)	2.38 (0.49)
	Visual task		571 (10)	11.97 (1.23)	576 (11)	12.49 (1.49)

Table 1. Visual experiment 1 & 2 results table: By participant aggregated mean RTs and % errors for experiment 1 & 2 for the visual and semantic tasks separately, by interference context and object-type. Standard error of the mean is given in brackets.

The results of an LMER model to predict visual-interference in RTs based on object category revealed that while participants were indeed about 112 ms (95% CI [58, 166]) faster overall in the interference condition than in the no-interference condition ($t(39.92) = -4.15$, $p < .001$), no main effect of object category was observed ($t(160.8) = 1.16$, $p = .25$) and the critical interaction of object category and interference condition was not significant $\chi 2(1) = 0.17$, $p = .68$. See Figure 3 for an indicative graph.

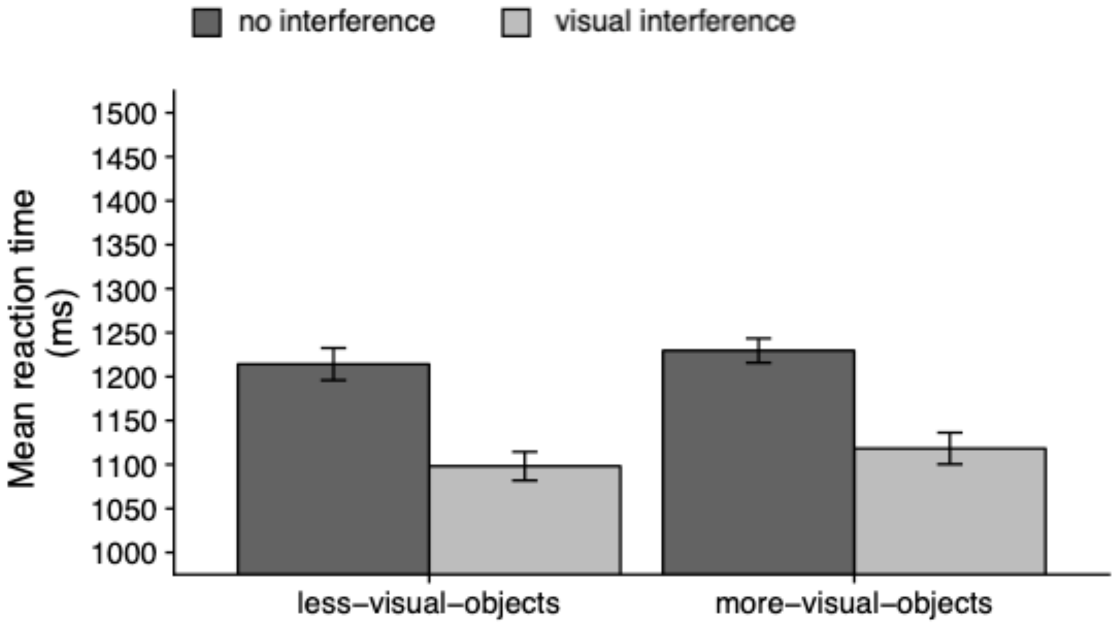


Figure 3. Visual experiment 1 semantic task RTs: Mean reaction time, by participant, as a function of object-type and interference context. Error bars represent within-subject standard error of the mean (Morey, 2008).

2.4.3 Visual Task

Overall, on the visual task, accuracy was high (errors ± 1 SD: M = 9.4 ± 7.5 %). The results of a GLMER model to predict visual task errors based on object category revealed a main effect of object category ($z = 2.17$, $p < .03$) such that the odds of making an error to the video were higher (OR =1.42, 95% CI [1.03, 1.94]) if the word concurrently responded to was more-visual than less-visual[3]. See **Error! Reference source not found.** for an indicative graph.

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[3] Furthermore, using ratings of visual experience (i.e., by item averages) as a continuous fixed predictor we observed that errors reliably scaled in proportion to rating (z = 3.09, p = .002) such that with each unit increase in visual experience with an object the odds of making an error on the concurrent visual task increased (OR =1.17, 95% CI [0.85, 1.60]).

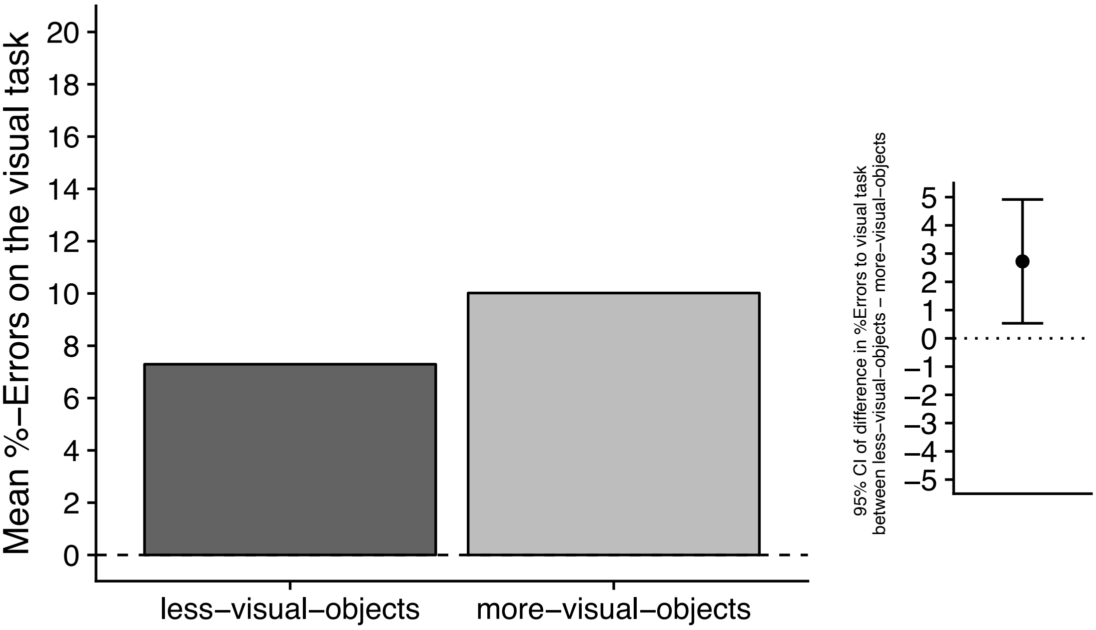

Figure 4. Visual experiment 1 semantic task %-errors: Mean %-errors as a function of object-type. On the right is the 95% CI of the mean of the within-subject-paired differences in errors to the visual task after responding to less-manual-objects minus more-visual-objects.

2.5 Interim discussion

In line with a previous report (Boddy, 2013), following a re-analysis of the semantic task data we confirmed that, contrary to sensorimotor predictions, participants did not experience significantly more interference to thinking about more-visual-objects than less-visual-objects as a result of performing a concurrent visual task. On the other hand, in line with sensorimotor predictions, we *did* observe interference on the visual task such that participants made more errors on the visual task after having made semantic judgements about more-visual-objects than less-visual-objects. These results partially support sensorimotor theories but the fact that we did not observe dual task interference effects on the semantic task requires further explanation.

Results from the semantic task of this experiment (as first reported in : Boddy & Yee, 2013) were counter to our expectations – participants were faster to respond to the semantic task while concurrently performing a visual task than when not. This pattern of results was unexpected because, generally speaking, performing two tasks simultaneously rather than only one should lead to an overall drop in performance.

In retrospect we believe this overall dual-task-facilitation to have been due to a feature of the procedure. A visual prime in the form of a question mark, was present in the visual task condition, but unavailable in the no-concurrent task condition (because participants had their eyes closed). This cue provided 500ms advance notice that a word was about to be heard and allowed participants to prepare to make faster responses as compared to in the eyes closed condition where a word was heard every 5100ms with no cuing (this was also a very slow pace, which may have produced an atmosphere that was not conducive to rapid responses). If this interpretation is correct, then because our design requires that the time-course of processing the words be relatively comparable in both interference conditions and the time course of single word processing unfolds very quickly, the artificially delayed latencies in the non-interfering-context may be obscuring any effects on the semantic task. Therefore, in experiment 2, we ran an adapted follow up study to test this possibility.

2.6 Experiment 2

2.6.1 Motivation

Following the results of experiment 1, we hypothesised that a number of alterations to the experimental design would increase our sensitivity to semantic/perceptual interference: a) a larger sample size (i.e., 50 vs. 33), b) 50% fewer abstract-noun catch-trials, c) limiting abstract nouns to those lacking morphological markers (e.g., suffixes such as “-cion” or “–ad”) which could potentially provide clues as to their class (Reilly, Hung, & Westbury, 2017). This was intended to discourage strategy-based heuristic responses i.e., focusing on these common markers to perform the semantic task. If used, these “linguistic shortcuts” could permit participants to avoid “deeply” accessing semantic information about the words they hear, in an un-natural way (i.e., normally we don’t use pure heuristics to understand words) thereby potentially ameliorating or nullifying semantic-perceptual interference (see: Connell & Lynott, 2012, for a discussion). Given the suggestive interference effects observed on the visual task in experiment 1, but considering the fact that accuracy was generally high, we endeavoured to make it more challenging by shortening both the target-marking stage, and the response period by 500ms respectively. On each trial we introduced a short beep before word onset to ensure that participants in the both conditions were similarly primed for word responses. Finally, responses to the semantic task were collected using a voice key activated microphone on a headset in order to more closely reflect previous studies (Yee, Chrysikou, Hoffman, et al., 2013) and to avoid making responses with feet, which is less standard in the field. Aside from these changes, the methods for experiment 2 were the same as those used in experiment 1 when not explicitly specified below.

2.7 Methods

2.7.1 Participants

The final study sample consisted of 50 (M age = 23 years, range = 18-35 years, 14 male).

2.7.2 Stimuli

Semantic task

Our stimuli were 210 concrete object names and 68 abstract noun words. The concrete objects included: (man-made; tools (54), objects (52) & natural: food/plants (52), animals (52)). We used SOS software (a tool for automatically optimising experimental lists; Armstrong, 2012), to split the stimuli in half and create two counterbalance lists approximately balanced for log-frequency, semantic category and visual experience ratings[4]. See Table 12 in the appendix for a full list of stimuli.

2.7.3 Procedure

There were 139 trials per experimental block with a pause after 70 trials. Verbal responses were coded as errors in cases of: verbal disfluency, hesitations, false starts and non-target responses.

Trial Structure

After the initial fixation cross of 500ms participants now heard a beep which cued them (in both interference and no-interference conditions) to prepare to hear a word. Then, for a period of 500ms (500 ms shorter than in experiment 1) two of the moving circles were identified as targets. As before, at this point the fixation cross became a white question mark and all the moving circles turned yellow for the 2500ms tracking phase. Within the tracking phase participants heard noun words and now made concrete/abstract judgements on them by verbally responding “pop” for concrete and “too” for abstract. As before, when they responded the white question mark disappeared. Lastly, in the final 1000ms of each trial (500 ms shorter than in experiment 1), one of the eight circles again turned red and participants had to respond,

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[4] Collected online from 58 new paid participants who did not participate in the main experiment.

with their toes if it had been a marked target, before the next trial began. See Figure 5 and Figure 2 for diagrams.

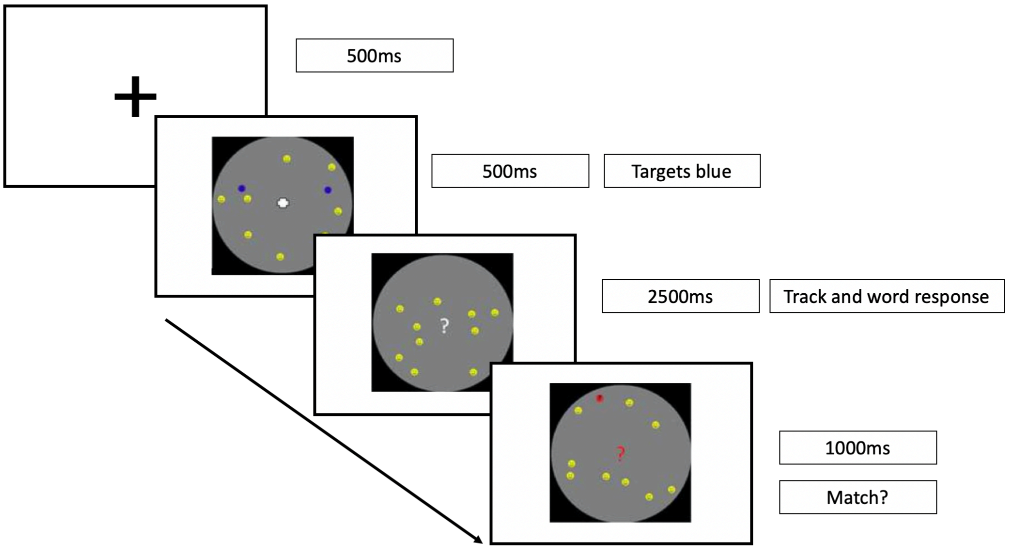

Figure 5. Visual experiment 2 trial structure.

2.8 Results

Data Exclusion

Following a preliminary analysis, we excluded the data from two participants (<4% of sample), not included in the final sample described in the participants section, due to poor performance (i.e., accuracy < 50% & >±3 SDs from the sample mean) on the semantic task (1) and on the visual task (1).

Object condition assignment

Using experience ratings from the participants, in the same way as in experiment 1, we divided the stimuli into two conditions: less-visual-objects (M=2.39, SD=1.37) and more-visual-objects (M=6.73, SD=0.53).

2.8.2 Semantic task

On the semantic task, descriptively, participants were slightly faster in the no-interference condition than in the interference condition (RTs ± 1 SD: M = 1432, ± 189 ms and M = 1470, ± 135 ms respectively) and made numerically more errors (errors ± 1 SD: M = 2.3 ± 3.0 % and M = 3.8 ± 3.1 %, respectively). This suggests that our alterations to the experimental methods in experiment 2 were successful in that we did not observe the counterintuitive dual task *facilitation* in RTs. See Table 1 for raw aggregated reaction times and error rates.

The results of an LMER model to predict visual-interference in RTs based on object category revealed no main effect of condition (*t*(62.7) = 0.44, *p* = .66), or of object category (*t*(192.7) = 0.004, *p* = .99) but, as predicted by the sensorimotor approach, the critical interaction of object category and interference condition was significant ($\chi 2(1) = 3.72$, *p* = .05) indicating that visual-objects suffered more relative interference as a result of a visual task than less-visual-objects (26ms, 95% CI [-0.01, 52.90]). See Figure 6 for an indicative graph.

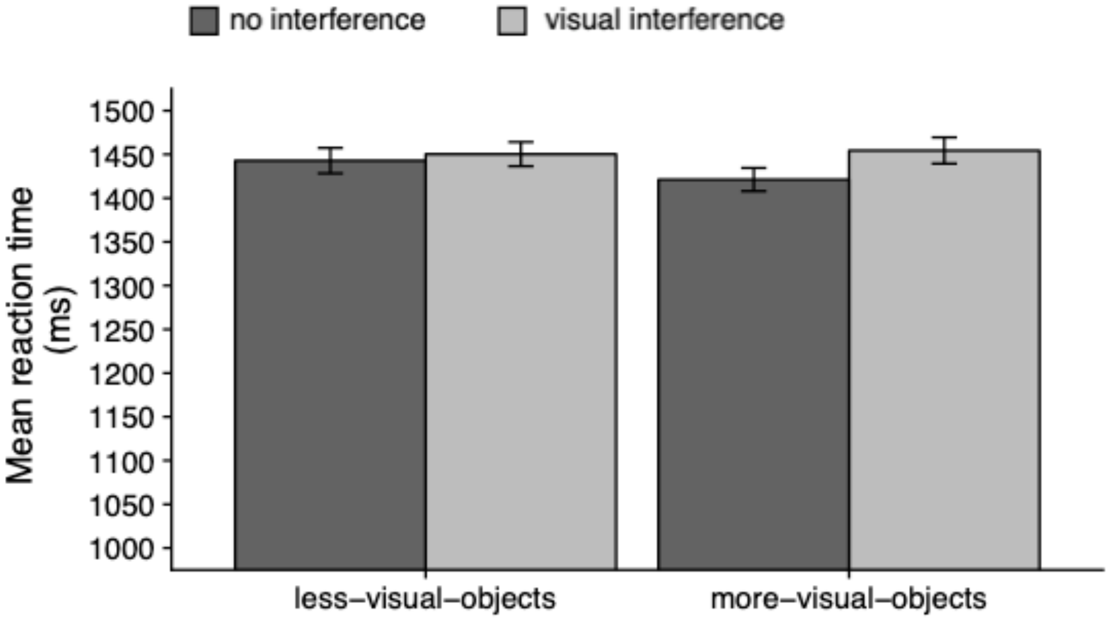

Figure 6. Visual experiment 2 semantic task RTs: Mean reaction time, by participant, as a function of object-type and interference context. Error bars represent within-subject standard error of the mean (Morey, 2008).

2.8.3 Visual task

While accuracy on the visual task was similar to experiment 1 (errors ± 1 SD: M = 13.4 ± 8.2 %), the results of a GLMER model to predict errors to the video based on object category revealed no main effect of object category (*z* = 0.64, *p* = .53) and therefore no evidence of visual-semantic interference to the visual task. See Figure 7 for an indicative graph.

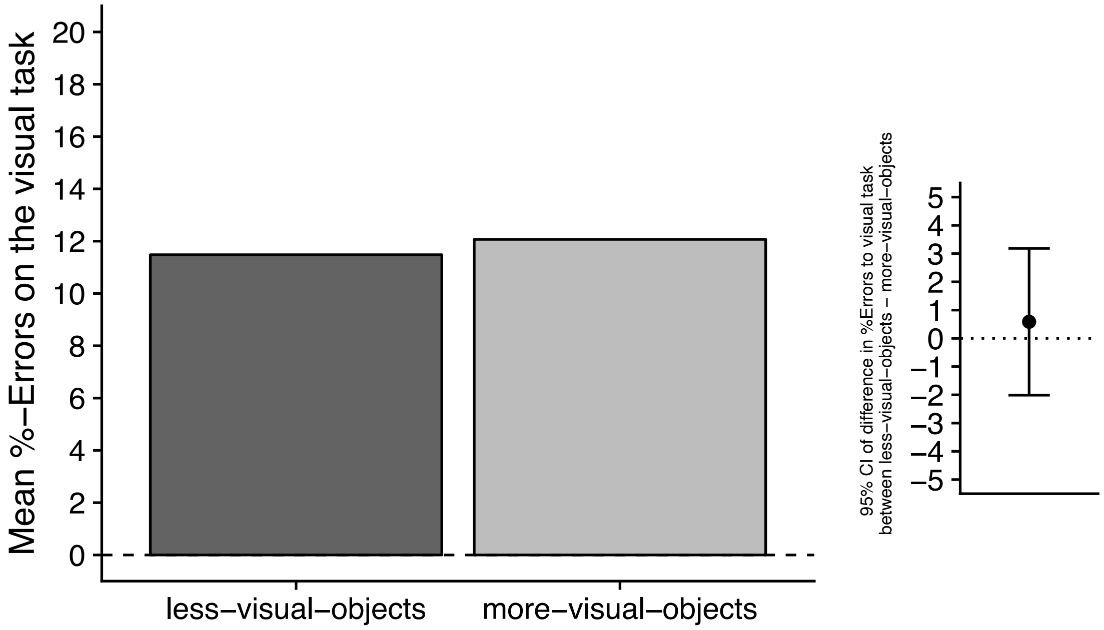

Figure 7. Visual experiment 2 semantic task %-errors: Mean %-errors as a function of object-type. On the right is the 95% CI of the mean of the within-subject-paired differences in errors to the visual task after responding to less-manual-objects minus more-visual objects.

2.9 Interim discussion

Firstly, the addition of an auditory prime to our experimental design succeeded in nullifying the counterintuitive dual-task-facilitation observed in experiment 1. In fact, results on the semantic task in experiment 2 indicate, as predicted by sensorimotor accounts, that relatively more interference was caused by making judgements about more-visual objects as compared to less-visual-objects. In the visual task, on the other hand, in contrast to experiment 1, we did not observe that participants made more errors on the visual task after responding to more visual than less-visual objects.

Again, these results provide a degree of support for our initial hypothesis; that a concurrent visual task would interfere with thinking about objects with which people have had relatively more visual experience, However, our lack of a replication of the findings of experiment 1: that performance on a visual task was disrupted by semantic processing related to the visual modality requires further exploration.

2.10 Experiment 1 & 2 collapsed – Cumulative analysis

2.10.1 Motivation

With this in mind we decided to compare and collapse the effects of experiment 1 and 2 in order to see if an increase in power might illuminate whether the effects we observe are more or less stable. While experiments 1 and 2 differed in a number of ways, they were also very similar in design, and the hypotheses they tested were identical. The analyses of both experiments suggested trends in the predicted directions[5]. There was also no evidence of a task trade off i.e., a semantic effect at the cost of a perceptual effect or the reverse; there were no correlations between the RT interference effect on the word task and the error interference effect in experiment 1 (r= -0.03, $p > .8$) or in experiment 2 (r= 0.02, $p > .9$). Therefore, in exploratory mode, using all the data from experiment 1 and 2, we tested whether the effects which were reliable in one experiment but not in the other were reliable overall.

2.11 Results

2.11.1 Semantic task

The results of an LMER model to predict interference to the semantic task by object category in RTs revealed no interaction between experiment and our critical interaction of object category and interference condition ($t(10078.952) = 0.78$, $p = .44$). Therefore, we collapsed over experiments, while including experiment as a control factor. We found that the critical interaction of object category and interference condition was significant ($\chi2(1) = 3.89$, $p < .05$) suggesting that, overall, visual-objects suffered more relative interference as a result of a visual task than less-visual-objects (18 ms, 95% CI [0.1, 36.2]).

2.11.2 Visual task

Similarly, we fit a GLMER model to predict errors to the visual task based on the category of the word responded to in that trial. This model also revealed no interaction

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[5] In fact, while in both experiments LME models with simplified random effects structures show significant critical effects in our predicted direction, the necessary addition of random slopes nullified them. This is most commonly because between subject variability in trends are too high for low powered experiments to make reliable estimates. One way to address this, is to increase the power of analyses.

between experiment and word category ($z = -1.32$, $p = .19$), but did reveal a main effect of experiment ($z = 2.43$, $p < .02$) such that participants were generally more likely to make an error in the visual task in experiment 2 (OR =1.72, 95% CI [1.11, 2.65]). Most importantly, it also revealed a significant difference in the critical main effect of object category ($z = 2.092$, $p = .04$) suggesting that, overall, making semantic judgements about more-visual object names made making errors on a concurrent visual task more likely (OR =1.41, 95% CI [1.02, 1.94]) than when making the same judgement about less-visual objects.

2.12 Interim discussion

Collapsing over experiments suggests that both the semantic and perceptual effects we observe in experiment 1 and 2 are, overall, stable when the data is analysed together.

2.13 Discussion

Because amodal accounts treat perceptual and semantic processing as entirely distinct they would predict that concurrent visual tasks, if they interfere with semantic processing at all, should do so to the same degree for all object representations, irrespective of whether they are associated with more or less visual experience. However, if as suggested by sensorimotor accounts retrieving visual semantic information and performing an unrelated visual task share cognitive resources, they should, if performed simultaneously, mutually interact with one another due to competition for those resources. Therefore, in two experiments we tested if it is relatively more difficult to think about objects with which people have more visual experience while simultaneously performing a concurrent visual task and, correspondingly, if performing the visual task itself was made similarly more difficult by thinking about them.

We found in experiment 1 that participants did indeed have more difficulty in performing a visual task while thinking about objects associated with more visual experience than those associated with less visual experience. Then, in experiment 2 we found that participants' ability to think about objects associated with more visual experience was compromised by the performance of a concurrent visual task. Both findings were further supported by a more statistically powerful exploratory analysis in which we collapsed over experiments and show complementary findings overall.

Because these results indicate perceptual and semantic processing are competing for cognitive resources, they suggest that semantic representations of frequently seen objects overlap with parts of the brain involved in performing the visual task (i.e., brain areas involved in visual processing) and therefore are, at least partly, visual in nature. Generally, this suggests the same parts of the brain involved in experiencing objects are involved in their long-term cortical representations. Furthermore, because the less- and more-visually experienced object categories were assigned, by participant, based on their own experience ratings, the semantic-perceptual interactions we observe suggest that the degree to which an object's representation is reliant on visual areas is dependent on the *amount* of lifetime visual experience that a given participant has *personally* had with it. Therefore, individual lifetime visual experience shapes semantic representations. These findings support and extend work in the manual domain (Yee, Chrysikou, Hoffman, et al., 2013).

Some recent work has shown that viewing visual noise interferes more with making judgements about visual properties of objects than making judgements about encyclopaedic properties of them (Edmiston & Lupyan, 2017). Similarly, it interferes with making concreteness judgements about concrete concepts more than abstract ones (Ostarek & Huettig, 2017). However, because the former study involved making *explicit* judgements about visual properties and the latter *implicitly* so (because all the concrete items were very visualisable in contrast to the abstract ones) it could be argued that participants might have been encouraged to use explicit visual imagery to perform the tasks. If this is the case, then visual interference could be attributed to "downstream" processes such as mental imagery as opposed to core semantic processing itself. In our study we observe visual interference *between concrete items* to a task that does not explicitly probe visual information. Even if visual imagery were recruited for strategic task-based responses to concreteness judgements (perhaps because concreteness is correlated with perceptual strength, e.g., Connell & Lynott, 2012), it would not explain the interference we observe *between* the concrete objects in the less and more-visually experienced object conditions. All our objects were similarly perceivable, and our conditions differed on the *amount* of visual experience participants had with them.

Because the same words featured (between-subjects) in both interference conditions (interference-condition order was counterbalanced across participants and participants and items were counterbalance-crossed random effects) our analysis suggests that visual semantic interference cannot be attributed to properties of the words themselves.

Furthermore, the inclusion of item as a random effect in our linear mixed effects models also suggests that our findings should extend to as yet untested items.

It might be asked why we did not observe both semantic and visual task effects in both experiments separately, i.e., why they were only collectively observed in a collapsed analysis. We have a number of suggestions for why this might be the case. One might be that each experiment, independently lacked sufficient statistical power to detect both semantic-perceptual interference effects. While we based our power estimates for sample size on the effects observed in previous work in the manual domain (Yee, Chrysikou, Hoffman, et al., 2013) it is possible that the size of the effect of *visual*-semantic interference is smaller. A methodological reason that this could be the case might be relative ease of our visual task compared to other interference tasks. It is worth noting that our experiments only tasked participants to track two targets, in comparison with conventional standards in the MOT literature in which participants typically track four or more (Cavanagh & Alvarez, 2005). Future work could modulate the difficulty of the visual task parametrically (as in: Vermeulen et al., 2008) and observe if the size of the interference effect varies accordingly.

A theoretical reason that the size of interference effects may be diminished in the visual domain is because of the processing capacity of the visual system itself. As outlined in the introduction of this chapter, the visual system is very important for humans. We live our waking lives perceiving the world while also using language and thinking about objects. If our cognitive resources were not sufficient to regularly handle visual and semantic processing simultaneously, then this would not be adaptive. Therefore, it is likely that visual bandwidth is large; we are capable of perceiving many objects at the same time, whereas in the manual domain we are relatively limited, i.e., we can only really handle a couple of things simultaneously. It is therefore possible that the visual system is more robust to interference from semantics than is the motor system.

Another possible reason that these experiments (individually) have weak effects could be the fact that all of the concrete objects that we used as stimuli can be (and frequently are) experienced multimodally; they are, for example, smelt, touched, heard and tasted, meaning that their representations should extend over a variety of sensory or motor modalities giving them some “representational redundancy”. This, in turn, could make even the objects that were frequently visually experienced relatively resilient to visual interference. It could also explain why interference was not catastrophic (i.e., the participants still responded correctly), but rather slowed processing. Following these promising results, we have conducted another, well-powered and conceptually similar study. It included among the stimuli those with which people have varying degrees of visual experience (i.e., like those reported here) as well as things with which we have virtually *no* visual experience e.g. “thunder” (Davis, Joergensen, Boddy, Dowling, & Yee, n.d.). This study, which replicates the findings described here, will be discussed briefly in the general discussion.

This work converges with previous research suggesting that the visual-semantic interaction occurs when simultaneously performing visual tasks and processing verbs (Kaschak et al., 2005; Meteyard et al., 2007, 2008) as a result of their specific content (i.e., directional mismatches between word meaning and what is seen). However, it shows that unrelated visual processing *per se* interacts with semantics, presumably as a result of object concepts’ experience-driven representational overlap with visual areas. Also, similarly, it lends support to studies employing *memory-based* “visual” interference paradigms to the semantic processing of objects (Rey et al., 2017). More generally, these findings support the fluid semantics view (Yee, 2017); that the way people think about objects changes depending on an interaction between the immediate demands of their context and their lifetime experience with those objects, as outlined in the introduction of the thesis.

In conclusion, contrary to amodal accounts, our results show that conceptual and perceptual processing mutually interact. This finding suggests that visual properties of object representations are stored in a perceptual format, and that visual areas are functionally related to accessing object semantics even when simply processing single noun words *without* explicitly probing visual information. We show that online visual processing can be influenced by language comprehension, and that because visual experience in the world shapes the representational structure of object concepts, the outcome of semantic processing differs depending on an interaction of personal long-term experience and immediate context.

Chapter 3: Olfactory experience and object representations

3.1 Introduction

While the *absolute* importance of our sense of smell (or olfaction) may have diminished since humans were predominantly hunter-gatherers (Gilad, Man, Pääbo, & Lancet, 2003) it is arguable that *relatively* among the senses, is remains one of the most crucial. From an evolutionary perspective, it was hugely important for our phylogenetic ancestors because knowledge derived from the chemical senses of smell or taste is highly relevant for an organism's survival; i.e., for seeking nutrition and avoiding toxins. Also, olfactory features of objects are often usefully diagnostic of their class or condition (e.g., *foods*) or very important for fully understanding their nature (e.g., *natural gas, bonfires, perfumes* etc.). Therefore, if multimodal sensory experience with objects determines their conceptual representations (Allport, 1985), then olfactory brain regions[6] should play a prominent role in the cortical representation of objects associated with odour experience. While research into sensorimotor representations of object concepts has increased in recent years (see the thesis introduction and e.g., Alex Martin, 2007), much of the work has been focused on visual and tactile features of objects and research into features perceived through the "chemical" senses (i.e., smell and taste) has been comparatively limited. I briefly review relevant findings below.

Neuroimaging

Processing the names of objects associated with odours leads to activation of olfactory brain areas. For example, making similarity or property verification judgements on fruit names leads to activation of bilateral orbitofrontal cortex (R. F. Goldberg et al., 2006; Robert F Goldberg et al., 2006). Even reading the names of odour associated objects (e.g., *cinnamon*), without any specific semantic task leads to activation of the piriform cortex and amygdala (González et al., 2006).

Neuropsychology

Neuropsychological research suggests a comorbidity of semantic-olfactory impairments such as deficits in odour-naming and the naming of objects typically

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[6] The primary olfactory system in humans centres around the piriform, insula and orbitofrontal cortex, however, a more extended olfactory network includes the hypothalamus, amygdala and hippocampus (Gottfried, 2010; Zatorre, Jones-Gotman, Evans, & Meyer, 1992).

associated with odours with some neurodegenerative diseases. This might be due to the proximity of primary and secondary olfactory regions and those affected by Alzheimer's, dementia, primary progressive aphasia and Parkinson's, i.e., frontotemporal regions, insula and orbitofrontal cortex (Hudry, Thobois, Broussolle, Adeleine, & Royet, 2003; Luzzi et al., 2007; Olofsson, Rogalski, Harrison, Mesulam, & Gottfried, 2013). While this suggests a functional relationship between the representation of olfactory semantics and these areas, given that frontotemporal regions e.g., the anterior temporal lobe (ATL), are also thought to play a crucial role in semantic processing, i.e., as convergence hubs for distributed representations (e.g., Patterson & Lambon Ralph, 2016) it is difficult to disentangle general semantic deficits from olfactory specific ones using patient data such as lesion studies.

Psycholinguistics

The relationship between language and online olfactory perception is complicated. For example, it is well documented that even in healthy individuals translating olfactory information (i.e., smells) into verbal information (i.e., its name) is generally difficult, a phenomenon referred to as the "tip-of-the-nose" phenomenon (Cain, 1979). It is similarly difficult for people to conjure vivid mental imagery of odours in their absence (Crowder & Schab, 1995). On the other hand, *linguistic* cues significantly improve people's ability to categorise olfactory stimuli; i.e., word labels behaviourally prime matching odours in a privileged manner even compared to matching images of an odour's canonical source (De Wijk & Cain, 1994). Furthermore, word-scent matches, but *not* picture-scent matches, lead to activation in the OFC and ATL suggesting that olfactory language is particularly closely connected to olfactory brain areas (Olofsson et al., 2013). That words are so useful for naming scents suggests that they activate specific olfactory features in perceptual regions, just as predicted by sensorimotor accounts.

Although little psycholinguistic work has been done on whether processing the names of objects associated with olfactory experience automatically recruits olfactory brain areas in service of semantics (as predicted by sensorimotor accounts), two relevant behavioural studies appear in the literature. In one study (Cimatti, Flumini, Vittuari, & Borghi, 2016) participants read the names of objects associated odours and were asked to respond (using buttons near-to or far-from them) whether their odours were pleasant or unpleasant. The motivation for the study was the observation that the presence of *real* unpleasant odours unconsciously leads to "avoidant" behaviour (faster near responses) and *real* pleasant ones to “approach” (faster far responses) behaviour. In line with sensorimotor predictions, the authors hypothesised that *words alone* would sufficiently activate their referent’s associated olfactory features to lead to measurable action compatibility effects: i.e., relatively faster responses to pleasant-far matches and unpleasant-near matches. While they did observe such an affect there are a few issues with the study which merit mentioning. One concerns the explicit nature of the task which required participants to judge the pleasantness of the aroma of each object. Given that participant’s attention was directed to the olfactory modality, it is unclear whether the putatively activated olfactory information is recruited automatically (i.e., as part of semantic processing) or only when specifically probed. Further concerns revolve around the analysis strategy of the paper; primarily the absence of an analysis of the interaction of near/far, pleasant/unpleasant, a more standard way of testing for multitasking interference. Overall, this study might be considered suggestive of olfactory-semantic interactions, but its findings are difficult to interpret.

In another study (Speed & Majid, 2018), participants read the name of an object associated with an odour and had to retain it in memory. They were then exposed to an odour (either matching or mismatching the word’s referent), asked to rate its intensity and finally asked to recall the previously seen word. The authors hypothesised that if retaining the name of an object in memory leads to sustained activation of its distributed representation (and therefore its olfactory features) then matching trials should lead to odour recognition facilitation and mismatching trials to interference. However, unlike in a comparable experiment involving auditory features, the authors observed no such effects and argue that odour words do not lead to olfactory simulation. Yet, because their experiment employed word recall as the primary dependent variable it is possible that retaining a word in phonological memory does not require the sustained activation of its referent’s distributed representation (and therefore olfactory areas) but rather could be achieved using auditory short-term memory alone. If this is the case, their failure to observe interactions between olfactory semantics and word retention is unsurprising. On the other hand, the auditory interference condition of their study may have interfered with word retention because phonological memory and the auditory brain areas activated in service of semantics *do* overlap. A stronger test of sensorimotor predictions is a paradigm which involves *online* and *concurrent* semantic-perceptual multitasking such as those described in the visual chapter of this thesis. In fact, the authors themselves acknowledge that tasks involving more complex semantic judgements and carefully measured response times might be more informative about online olfactory-semantic simulation.

Experience

As outlined in the introduction to this thesis, sensorimotor accounts hold that the amount of lifetime experience people have with objects through different sensory modalities shapes how their knowledge is represented over modality specific brain areas. In the olfactory domain there is neuroimaging evidence (for a review see: Royet, Plailly, Saive, Veyrac, & Delon-Martin, 2013) that individuals who have a lot of experience smelling objects or using olfactory mental imagery such as perfumers exhibit functional reorganisation (Plailly, Delon-Martin, & Royet, 2012) and structural alterations (Delon-Martin, Plailly, Fonlupt, Veyrac, & Royet, 2013) in olfactory brain areas (i.e., orbitofrontal cortex, piriform cortex and hippocampus). However, to date there is only one fMRI study which explicitly tested whether smell experience with objects leads to olfactory regions becoming active when thinking about them (Ghio et al., 2016). In this study, individuals who were trained to recognise novel objects in the presence of an ambient aroma showed increased activation in the extended olfactory network (anterior hippocampus) when performing a later old/new recognition task as compared to participants trained on the same items but without an ambient aroma. Together, these results support the idea that olfactory regions are important for some object representations and that the degree to which this is true varies according to personal olfactory experience.

Summary

To summarise, there is limited but converging evidence from neuroimaging and neuropsychology and mixed evidence from psycholinguistics that olfactory brain regions play an important role in the semantic representations of objects associated with odours and odour experience. However, as explained in the general introduction, it has been pointed out that putative semantic-sensorimotor imaging results are not direct proof that these regions are *functionally* related to semantics (Mahon & Caramazza, 2008). It is logically possible that activation of olfactory regions while processing smell related concepts results from peripheral processes. For instance, it has been observed that simply the act of sniffing, in the absence of an odour, activates the piriform cortex (N. Sobel et al., 1998). Could olfactory-semantic neuroimaging findings such as those reviewed above be equally well explained by such non-semantic processes? It remains to be demonstrated that olfactory regions of the brain are *functionally* involved in the representation of objects associated with odour. Similarly, that an individuals' olfactory experience with an object mediates how functionally involved these regions are remains to be behaviourally tested.

3.1.2 Motivation

One approach to addressing these questions is to use behavioural dual-task paradigms to test if occupying (with non-linguistic activity) an area of the brain which is important for a concept's representation influences our ability to access it, due to competition for shared neural resources. Furthermore, the amount of lifetime modality specific experience an individual has with an object in that modality should determine the degree of interference they experience. There is evidence that this approach works in the manual (Yee, Chrysikou, Hoffman, et al., 2013) and visual domains (see the first experimental chapter of this thesis) and therefore, we set out to test whether it holds in the olfactory domain.

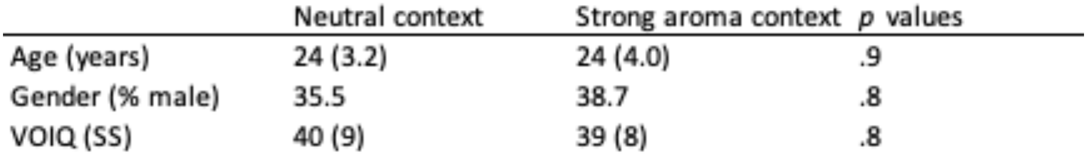
3.1.3 Questions and Predictions

In this chapter I report the results of one experiment designed to explore whether olfactory brain regions are *functionally* important for the representation of odour associated concepts (like garlic) and if so; how object representations are shaped by individual lifetime olfactory experience with referents. As in the visual chapter of this thesis we used an interference paradigm to test our predictions. We reasoned that if in one condition the olfactory system is occupied with a strong odour while participants make semantic judgements on the names of objects, then it should interfere more with understanding words like "garlic" than words like "hammer, relative to a condition with no added aroma. Furthermore, we predicted that interference would scale in proportion to the amount of lifetime olfactory experience people have with the objects.

3.2 Methods

3.2.1 Participants

The final study sample consisted of 62 (M age = 24 years, range = 18-35 years, 23 male) native Spanish speakers with normal or corrected-to-normal vision who were paid for participating in the 1.5hr study. Exclusion criteria included: habitual smoking (more than 5 cigarettes a day), olfactory issues such as a cold or anosmia, allergies to essential oils or not being a native Spanish speaker[7]. The participants in each interference condition did not differ on age, gender or VOIQ score. See Table 2 for further information.



	Neutral context	Strong aroma context	*p* values
Age (years)	24 (3.2)	24 (4.0)	.9
Gender (% male)	35.5	38.7	.8
VOIQ (SS)	40 (9)	39 (8)	.8

Table 2. Olfactory experiment participant demographics by interference condition. Standard deviations in parentheses. SS = standard score. All p's are t-tests except for gender which is chi-squared proportion test.

3.2.2 Ethics statement

We obtained written informed consent, in compliance with the regulations established by the BCBL ethics committee in line with the guidelines of the Helsinki Declaration, from all participants before participation.

3.2.3 Stimuli

Our stimuli were 200 concrete object names (e.g., *cheese*), 200 animal names (e.g., *tiger*) and 20 adjectives (e.g., *shiny*) for 1-back probe trials (taken from: Yee et al., 2010). The concrete objects included: tools (25), objects (88), food (53), plants (28), spices (6). The animals included: birds (39), insects (25), mammals (97), reptiles (16) & sea creatures (23). The adjectives included: functional (5), tactile (5), visual (5), other (5). See Table 13 in the appendix for a list of stimuli. For counterbalancing purposes, we collected preliminary olfactory experience ratings online from 62 paid participants who did not participate in the main experiment following as similar approach to the methods used in (Lynott & Connell, 2009). Using these we separated the concrete objects into two conditions: relatively-less-smell-associated-objects (neutral objects) (M rating = 1.27, SD = 0.79) and relatively-more-smell-associated-objects (smelly objects) (M rating = 3.69, SD = 0.82). Finally we split the stimuli in half using SOS software (Armstrong, Watson, & Plaut, 2012) creating two lists

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[7] We eliminated the data from twenty participants (23% of data) for not meeting exclusion criteria: cold or smoker (19), non-native Spanish speaker (1).

approximately balanced for log-frequency, number of letters and equally varied on olfactory experience ratings. Each participant saw all of the stimuli once, but we arbitrarily allocated the order of presentation of each counterbalance list to participants ensuring that one half saw one first the other saw it second. Within both counterbalance lists, words were presented in a pseudo-randomised fashion with no more than 3 items of the same category (i.e., animal, neutral-object or smelly-object) presented in succession.

3.2.4 Olfactory interference context

The interfering strong added aroma was diffused in a similar way to the methodology employed in previous studies (Moss & Oliver, 2012) i.e., we soaked 10 drops of essential oil into a pad for an aromatherapy fan diffuser and then placed it under the desk in the cabin out of sight of the participants. It was switched on at maximum speed for 5 minutes and then reduced to medium speed immediately before participant entry. The essential oil we chose was cypress based on an informal pre-experiment survey which indicated that it was very difficult to identify and un-associated with the aromas of any stimuli items. Because in everyday life, olfactory stimulation is always occurring (Noam Sobel et al., 2000), i.e., from the experimental cabin, participant's perfume etc., our conditions are best characterised as relatively-less-ambient-aroma in the no-interference condition and relatively-more in the interference condition.

3.2.5 Procedure

The experiment was presented using Experiment Builder software (Version 1.10.1063) on a CRT monitor. Participants performed the experimental blocks in a sound proofed testing cabin measuring 2 x 1.8 x 2.2 m of which the door was kept closed except for participant and experimenter access. During the experiment auditory feedback was presented through headphones and participants responded with a 9-button response box on the table in front of them. Task instructions, volume level, participant distance from monitor and position of response box and keyboard were kept constant across participants. Standardised written task instructions and diagrams were used during task explanations and were clearly visible to participants throughout the experimental blocks. There were 400 trials per experimental block with a 30 second pause after 200 trials. There was a block of 10 practice trials before participants entered the cabin during which feedback about accuracy and concurrent task performance was given.

The interference context was between subjects and therefore we arbitrarily assigned half the participants to the no-added-aroma condition (no-interference) and half to the strong-ambient-aroma condition (interference). At the end of the experimental session, participants rated the object names according to the following question: “When you think of this object, how much does its aroma come to mind?” from 1 = very little, to 7 = a great deal. After rating the objects, participants were asked to complete the Vividness of Olfactory Imagery Questionnaire (VOIQ) (Gilbert, Crouch, & Kemp, 1998) in which they are asked to imagine four specific “odour-scapes” and rate the vividness of their mental images from 1 = as real and vivid as perception, to 5 = no imagery. Finally, we asked whether participants had any suspicions of what the aim of the experiment was, if they had noticed any odour during the experiment, what it was and to rate its intensity from 1-7. They were also asked further questions about if they had any olfactory issues/colds etc., and then debriefed them as to the aims of the study.

Trial structure

After 500ms of a blank screen, a cross appeared for 500ms followed by a word that remained on the screen for 300ms. Afterwards, a cross appeared and remained on screen until the participants responded or the trial timed out after 2500ms. Participants judged if the word on the screen was the name of an animal or not as quickly and accurately as possible. If participants responded correctly, the next trial began, however, if they made an error they heard a tone before the next trial began. If the trial timed out, participants heard a tone and saw a message reading “Faster” on the screen. In order to encourage participants to think deeply about the objects and pay attention to the task, on approximately 10% of trials, after making an animal judgement on a word, participants were then presented with an adjective on the screen for up to 5000ms. On these 1-back probe trials they had to decide whether the adjective, in their opinion, commonly described the object they had just seen. See **Error! Reference source not found.** for a diagram.[8]

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[8] After performing this animal judgment task, but before rating the objects, participants performed two memory tasks for the words they had seen. Our motivation for including these memory tasks and analysis/discussion of the results is beyond the scope of this thesis.

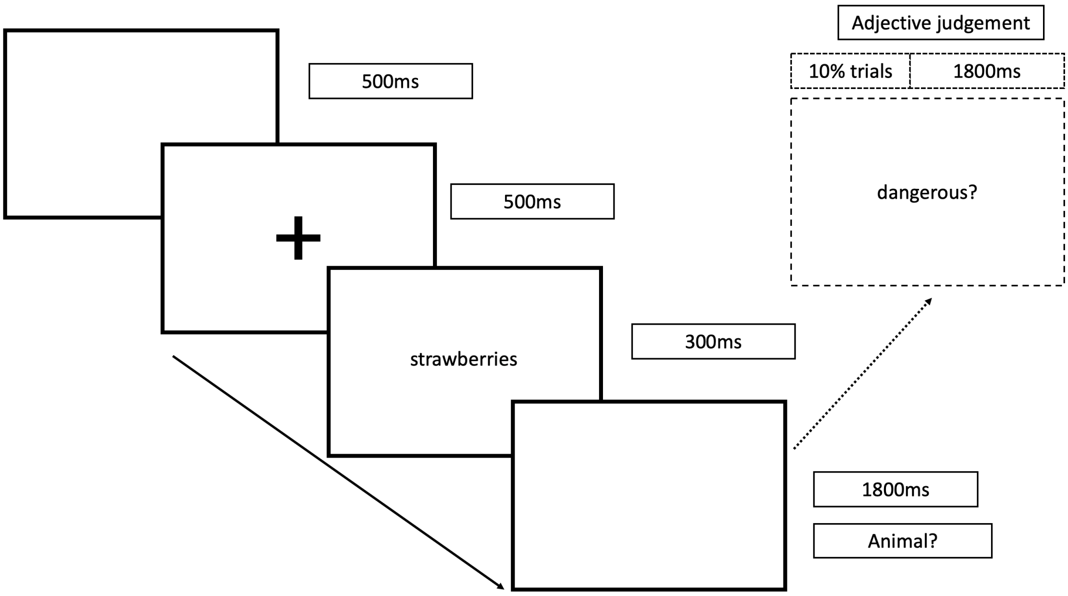


Figure 8. Olfactory experiment trial structure

3.2.6 Statistical analysis

We performed analyses using the lme4 package (Bates, Maechler, et al., 2015) in the R programming environment (R Core Team, 2018). Response times (RTs) were submitted to linear mixed effects regression models (LMERs) and errors were submitted to generalised linear mixed effects (logistic) regression models (GLMERs). The significance of the effects was assessed using the likelihood-ratio tests (i.e., chi-squared tests of fit) between a model with and one without the critical term. To approximate degrees of freedom and *p* values for individual predictors in the models we used the lmerTest package (Kuznetsova et al., 2017). For analyses we report relevant regression coefficients (either RTs or odds ratios (ORs)) with 95% CIs and t-values (LMER) or z-values (GLMER). As participants-within-condition-crossed random effects we always included participant and item as intercepts. We also included random slopes of the fixed effects, by subject and by item, when they: improved the fit of the model, were theoretically motivated, justified by the data and design, computationally converged, and did not lead to underspecified estimates (i.e., random effect correlations of >.8/-.8). We aimed to be as maximal (Barr et al., 2013) as was warranted without sacrificing parsimony (Bates, Kliegl, et al., 2015; Matuschek et al., 2017).

As fixed effects we either entered object-type (a categorical variable with two levels: neutral objects (baseline) and smelly objects) or each participant's olfactory experience ratings (a continuous, mean centred variable from 1-7) with interference condition (a categorical variable with the no-interference condition as baseline).

A significant interaction between object-type/olfactory experience ratings and interference condition, with a positive slope, would indicate that, as predicted, there was more interference due to a strong ambient aroma for objects associated with more olfactory experience. Because we had no predictions for the animal "foil" items or the adjective judgements, they were not included in our analyses. Valid response times (i.e. correct responses logged between 300ms-1800ms of word onset) to the semantic task were trimmed, by participant and for each condition, to ± 2.5 SD of the mean (<3% of total data excluded).

3.3 Results

Data Exclusion

We excluded the data from five participants (6% of sample), not included in the final sample described in the participants section for: sickness (1), experimenter error (2), and low accuracy < 2.5 SDs from the group mean (2). We discarded the data from four object names (2% data loss) because of experimenter error: two because they refer to animals and two because we did not collect participants ratings for them.

Object condition assignment

Using each participant's individual experience ratings, by subject we divided the objects into two conditions: The bottom tercile of the objects became the relatively-less-olfactory-experienced-objects (neutral) condition (M = 1.6, SD = 1.3) and the top tercile the relatively-more-olfactory-experienced-objects (smelly) condition (M = 5.4, SD = 1.7).

3.3.2 Response times

By object category

Overall, participants were similarly fast to respond in the no interference condition (RTs ± 1 SD: 662 ms, ± 108 ms) as in the interference condition (RTs ± 1 SD: 680 ms, ± 77 ms). The results of an LMER model to predict olfactory-interference in RTs based on object category revealed no main effect of condition (*t*(61.92) = 0.46, p > .6), or of object category (*t*(161.88) = -0.83, p > .4). However, the critical interaction of object category and interference condition was significant $\chi2(1) = 3.99, p < .05$. This indicates that smelly objects suffered more relative interference as a result of a strong ambient aroma than neutral objects (12ms, 95% CI [0.22, 24]). See Figure 9 for an indicative graph.

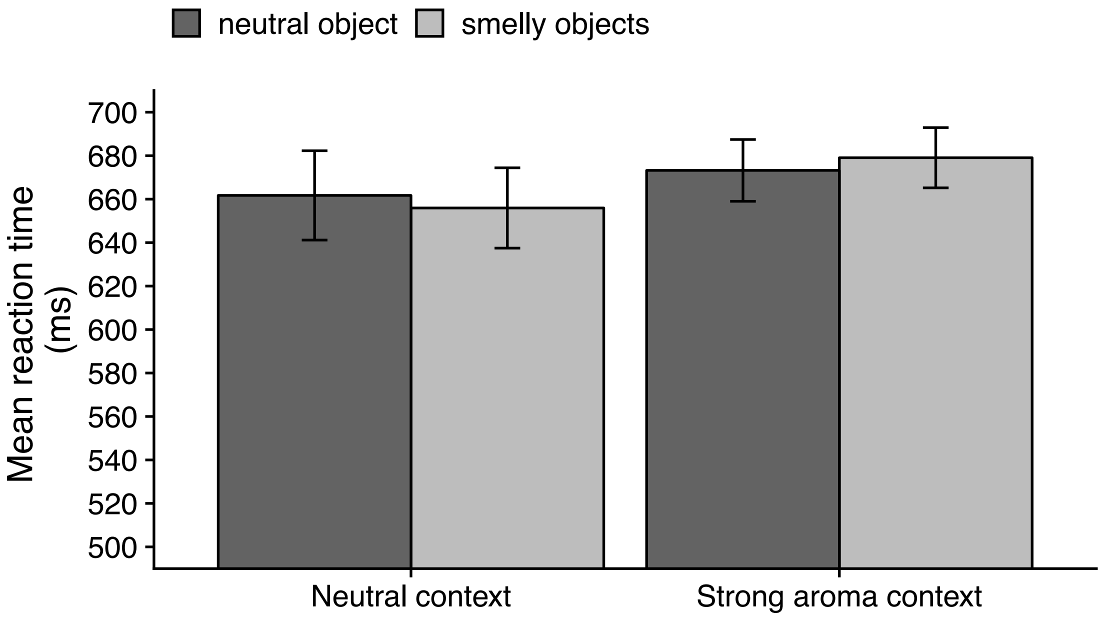


Figure 9. Olfactory experiment semantic task RTs, by participant. Mean reaction time, by participant, as a function of interference condition and object type. Error bars represent standard error of the mean.

By individual rating

The results of another LMER model, (using all the data) to predict olfactory-interference in RTs based on the *continuous* predictor of olfactory experience ratings similarly revealed no main effect of condition (*t*(64) = 0.37, p > .7). There was, however, a significant effect of rating (*t*(2493) = -3.19, p < .005, 95% CI [-5.32 , -1.3]). More importantly, the critical interaction of olfactory experience rating and interference condition was significant ($\chi2(1) = 5.35, p = 0.021$) such that interference (i.e., a relative slowing of response times) increased by 3ms (95% CI [0.43, 5.1]) for each unit increase in olfactory experience rating. For visualisation purposes, for each object name but collapsing over participants, we calculated an overall interference effect by subtracting its average latency in the no-interference condition from its value in the interference condition and then plotted this effect against average olfactory experience ratings for each item. See **Error! Reference source not found.** for an indicative graph.

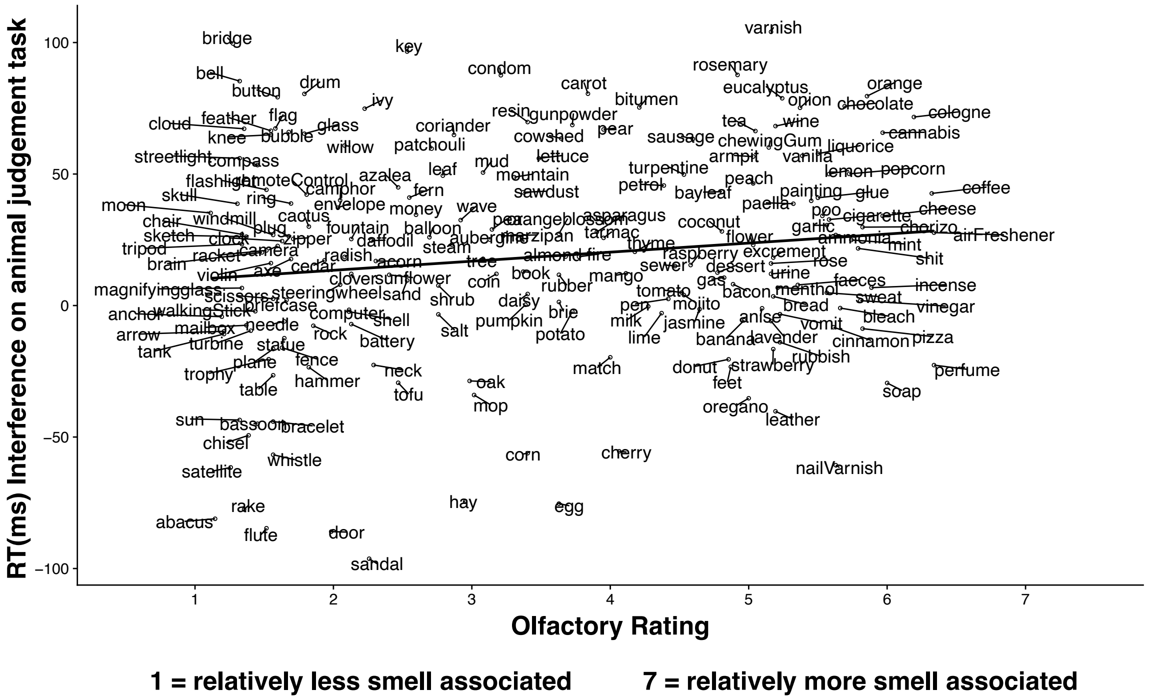


Figure 10. Olfactory experiment semantic task RTs, by item. Scatterplot (with best fitting regression line) showing the relationship between RT interference effect scores (ms) (aggregated by word) and olfactory experience ratings.

3.3.3 Accuracy

By object category

Participants made similar percentage errors on the word judgement in the ambient aroma condition than in the neutral condition (errors ± 1 SD: M = 5.9 ± 3.8 % and M = 6.4 ± 4.3 % respectively). The results of a GLMER model to predict interference to the semantic task (by object category) revealed no main effect of condition (z = -0.94, p > .3) or of object category (z = 0.03, p > .9). The critical interaction of interference by object category was also non-significant ($\chi2(1) = 0$, p > .9).

By individual rating

In a GLMER model to predict interference by individual olfactory ratings, there was no main effect of condition (z = -0.25, p > .8) or of rating (z = -0.66, p > .5). However, there was a significant interaction between rating and condition ($\chi2(1) = 3.94$, p = .047), but the direction of this effect was counter to what we would have predicted—for each unit increase in olfactory rating, interference (i.e., the relative increase in errors) went *down* (OR = 0.93, 95% CI [0.87, 1.00]). We will speculate about this unexpected result below. Overall, our results show, greater response time interference when responding to "smellier" objects than more "neutral" objects as a function of odour context and that this interference scales with individual reports of odour experience.

3.4 Discussion

If, as sensorimotor theories maintain, there is a continuity between perceptual and semantic processing, then accessing the meaning of words which refer to smelly objects (but not neutral objects) should be more difficult in the presence of a strong ambient aroma because the two processes are mutually engaging the same neural resources. Furthermore, the degree of overlap between semantic representations should vary at an individual level depending on a person's lifetime olfactory experience with a given item.

Using an innovative passive olfactory "interference" paradigm, we find evidence that a strong ambient smell *does* make it slightly harder (i.e., slows responses) to think about smelly objects relative to neutral objects. This suggests that that the conceptual representations of smelly objects *do* make use of areas of the brain active when they are experienced, i.e., olfactory brain areas. Furthermore, because the interference we observe scales with ratings of individual participants' olfactory experiences with those objects, this supports the second prediction: that lifetime individual sensory experience should influence how a given conceptual representation is distributed over different sensory brain regions. In this case, that the amount of olfactory experience a person has with an object determines how much interference is observed as a result of competition for neural resources and therefore the degree to which its representation involves the olfactory system.

Unexpectedly, in one analysis (predicting errors based on continuous individual ratings), we observed that smelly items were responded to *more accurately* when there was a strong and incongruent smell in the room than without it. Given the small number of errors that participants made in the experiment, this effect should be interpreted with caution, as it may be less reliable or informative than the response time results, a dependent variable for which the analysis which is much better powered. However, it is possible that the pattern reflects a speed accuracy trade-off, whereby participants took longer to respond, as evidenced by the RT interference, but produced fewer errors as a result (See: Heitz, 2014 for discussion). If true, this finding does not conflict with the predictions of sensorimotor accounts because the presence of a speed accuracy trade-off is consistent with increased cognitive load due to the experimental manipulation between conditions (i.e., the olfactory context and semantic content of the target word). We believe that this increase in cognitive load is most parsimoniously explained by perceptual-semantic multitasking interference. We will explore this intriguing finding in future work.

While one recent study (Speed & Majid, 2018) failed to observe semantic-odour interference using a sequential interference paradigm and concluded therefore that words do not automatically lead to olfactory simulation, our data suggest that olfactory features of objects *are* automatically activated (or simulated) even when participants are simply making animal judgements, a task which does not, in principle, explicitly encourage participants towards accessing olfactory features of words more than other modalities (as opposed to asking them to make explicit odour judgements). We believe this to be because our study, instead of testing whether recall memory for smelly object names could be interfered with by using an "olfactory judgement" task *between* encoding and recall, tested the effect of interference between *online* semantic processing and *continuous* olfactory stimulation. The timing and nature of dual interference tasks fundamentally alters whether/how semantic-perceptual processes interact (Connell & Lynott, 2012). In the first place, we contend that our semantic task (animal judgement) is more "semantic" in that it requires participants to access the distributed semantic representations of the word's referent more than theirs, which involved maintaining a phonological/lexical representation in short term memory. In short, their perceptual "interference task" was sequential while ours was concurrent and concurrent perceptual-semantic tasks more frequently result in mutual interactions i.e., interference. Furthermore, on a methodological level, their experiment involved fewer experimental trials than ours and their dependent variables (predominately recall accuracy) are generally less sensitive than response times.

Another important difference between our findings and others (Cimatti et al., 2016; Speed & Majid, 2018) is that we observe perceptual-semantic interference as a result of 1) a *passive* interfering context which was opaque to participants, and 2) without *overtly* probing olfactory information. First, although the ambient aroma in our interference condition was strong, according to post experiment debriefing: of the 31 participants who were exposed to the strong ambient aroma 24 noticed an odour and on average rated its intensity as 3.4 (on a 1-7 rating) and none identified the odour itself. Furthermore, when asked explicitly about their thoughts on the experimental aims or hypotheses only four mentioned smell in very general terms and none were deemed sufficiently close to understanding the manipulation to warrant exclusion.

Secondly, other work involves making explicit odour judgements on words clearly (and always) associated with odours. In our experiment, however, the semantic task was making animal judgements on a wide variety of single concrete nouns and animal names, which varied widely in their smell associations. Importantly, participants were only asked to make explicit judgements about the olfactory properties of the nouns *after* the main experiment.

On a practical level, the large number of stimuli we selected were intentionally chosen to refer to as diverse a collection of concrete objects from a wide variety of categories as possible and to vary widely in their smell associations. While certain categories of objects are confounded with their olfactory associations (e.g., foods) we intentionally sought to minimise this in our analysis: i.e., in the mixed effects models we used to test our hypotheses we always included random intercepts for participants and items along with random slopes whenever licensed. This random effect structure ensures that parameter estimates are pooled for the effects of experimental participants and individual words and makes us confident that the main effects or interactions we observe are a result of the experimental manipulation rather than the specific subjects or items we sampled or selected.

The flexible nature of concepts is only just beginning to be investigated. The interaction between our individual semantic representations and the context in which we activate them varies continuously. Here, the ambient odour context in which people think about objects subtly effects the conceptual representation activated. The meaning of the word *lemon* is different when you process it in an incense filled church as opposed to an air conditioned and bland office space. These findings are an elegant demonstration that when we talk about “meaning” we may need to bear in mind that no stable representational outcome for an object’s meaning exists, extrapolated from its context.

Our finding that lifetime olfactory experience with objects shapes their neural representations is in line with emerging behavioural findings in other modalities (Chrysikou et al., 2017; Yee, Chrysikou, Hoffman, et al., 2013) and with recent imaging results (e.g., Bellebaum et al., 2013). This central, but less commonly tested prediction of sensorimotor accounts is important, because it moves in the direction of studying the differences between peoples’ concepts rather than their commonalities, and suggest that concepts can change over time as experience changes (Yee, 2017).

In conclusion, the results reported in this chapter support the sensorimotor claim that conceptual and perceptual processing are continuous (as opposed to modular) and therefore mutually interact. They extend this to the olfactory domain. The mere presence of an ambient aroma is sufficient to selectively interfere with thinking about smelly objects (but not neutral objects) even when olfactory information is not explicitly probed. Furthermore, we observe that the interaction between semantic and olfactory processing measurably depends on an individual's immediate context and lifetime experiences.

Finally, notwithstanding the unexpected effect in errors, our results suggest that olfactory sensory areas of the brain are *functionally* related to semantic processing rather than peripheral to it. This important as it converges with imaging evidence (Ghio et al., 2016; González et al., 2006) but bolster their findings against criticisms of their perspicacity (Mahon & Caramazza, 2008). These results are novel because they provide support for sensorimotor accounts of conceptual representation and their experience-based nature, in the relatively less studied modality of olfaction.

Part 2 – Parkinson’s and the manual modality

While, in the first two studies of this thesis I tested visual and olfactory components of object representations, the following chapters report two studies designed to test manual features of object representations. First, I report a behavioural experiment designed to test whether deterioration in people’s motor capacities, due to a motor disease (namely Parkinson’s disease), impacts their ability to think about objects which are frequently associated with motor actions. Second, I report an fMRI study designed to explore the neural correlates of any such deterioration.

Parkinson’s disease

Parkinson’s disease (PD) is a degenerative disease characterised by motor issues including, tremor, rigidity, akinesia (inability to initiate movement) and bradykinesia (slowness of movement). It is caused by degradation of the nigrostriatal pathway which causes dopamine deficiencies in individuals with PD. These deficiencies lead to an imbalance in the motor loop of the brain-based-motor-circuit (including the basal ganglia and thalamus) and dysregulation in frontoparietal areas implicated in voluntary action generation, i.e., primary motor cortex (M1), supplementary motor area (SMA), and pre-motor cortex (pMC) (Rodriguez-Oroz et al., 2009). Specifically, PD has been shown to cause hypo-activation in the preSMA, SMA and M1 and hyper-activation in the ventral-pMC. This pattern of hyper/hypo-activation has been argued to be a form of compensatory activation in individuals with PD (PDs) (Grafton, 2004). Treatment for PD involves prescribing levadopa (LDopa) and/or dopaminergic agonists which, when taken, restore function to the basal ganglia and alleviate motor symptoms, or, in more developed cases, surgical interventions and the placement of electrodes for the purpose of deep brain stimulation (DBS) and restoration of motor function. Aside from motor issues, PDs also exhibit a number of perceptual and cognitive deficiencies. In terms of global cognitive issues, in the later stages of PD development, dementia (Pigott et al., 2015) or mild cognitive impairment (Yarnall et al., 2014) is common alongside cognitive control pathologies (Cools & D’Esposito, 2011). With regards to language, PDs often exhibit speech difficulties e.g., slowness and difficulty to initiate speech and dysarthria (poor articulation of speech) (Smith & Caplan, 2018) and global impairments, as compared to healthy controls, in the lexical retrieval of nouns and verbs (Pell & Monetta, 2008). Interestingly, PDs also seem to have a less keen sense of smell (Doty, 2012) and are even known to have visual hallucinations (Sanchez-Ramos, Ortoll, & Paulson, 1996).

Chapter 4: Parkinson’s, manual experience & object representations – behavioural

4.1 Introduction

While there is strong evidence for motor system involvement in semantically processing actions verbs (e.g., “jump”) (Hauk, Johnsrude, & Pulvermüller, 2004), sensorimotor models also make analogous, but scarcely tested, predictions concerning object concepts (e.g., “typewriter”); i.e., that when people activate the semantic representations of manipulable objects, related motor associations will be automatically activated in service of semantic access. A modicum of neuroimaging evidence supports this. In fMRI, for example, motor areas are activated when seeing pictures or processing the names of manipulable objects (Binder et al., 2009; R. F. Goldberg et al., 2006; Robert F Goldberg et al., 2006; Alex Martin, 2007; Noppeney & Price, 2003) and some studies suggest that detailed knowledge of how objects are manipulated is activated (Boronat et al., 2005; Hargreaves et al., 2012; Rueschemeyer et al., 2010; Yee et al., 2010). Similarly, in EEG, seeing manipulable objects, even where no explicit semantic processing is required, evokes action related potentials (Grafton, Fadiga, Arbib, & Rizzolatti, 1997)

There is also ample psycholinguistic evidence that motor information forms part of the conceptual representations of objects. For example, lexical decisions are sped up when object names are primed by the names of other objects which are similarly manipulated (e.g., typewriter and piano; Myung, Blumstein & Sedivy, 2006) Similarly, for both images, visually presented names and auditory names, physical responses to questions about objects are facilitated if they are made using the specific grip type typically associated with that object (e.g., a clawed hand and a doorknob; Bub et al., 2008; Masson, Bub, & Warren, 2008). The balance of evidence thus suggests that the motor system is involved in representing manipulable objects and that it is recruited to semantically process their names. However, as pointed out throughout this thesis, it is logically possible that both priming effects and observed motor activation in neuroimaging, putatively arising as a response to semantic processing, could result from non-semantic processes (i.e., motor imagery: Jeannerod, 1994) thereby challenging the view that these regions form part of semantic representations themselves (Mahon & Caramazza, 2008).

One approach to showing that the motor system is *functionally* involved in the representations of manipulable objects is to test if interruptions to the brain regions supposedly recruited in support of semantically processing a given word, perhaps as a result of neurological damage to sensory or motor systems, lead to specific semantic impairments in processing that word. Essentially, to test if damage to experience-relevant brain networks selectively impairs associated semantic domains, but spares others (Bak, 2013).

There is some evidence that taxing brain areas (i.e., motor areas) important for the representation of manipulable nouns has a measurable impact on processing those nouns. For example dual task interference paradigms (Bub et al., 2008; Marino et al., 2014; Tucker & Ellis, 2004; Witt, Kemmerer, Linkenauger, & Culham, 2010; Yee, Chrysikou, Hoffman, et al., 2013) and brain stimulation studies (Cattaneo, Devlin, Salvini, Vecchi, & Silvanto, 2010; Gough et al., 2012; Pobric, Jefferies, & Lambon Ralph, 2010) have all provided evidence that motor system occupation/interruption results in corresponding impairments to accessing motor semantics. Similarly, with regards to motor disorders, it has been shown that apraxia (a motor disorder) selectively impairs people's ability to process manipulable objects (Buxbaum & Saffran, 2002; Myung et al., 2010), as do lesions to motor areas (Guido Gainotti, Silveri, Daniel, & Giustolisi, 1995).

Because PD is considered to be primarily a motor disorder, it is often viewed as an informative testing ground for the predictions of sensorimotor accounts. Specifically, PD should selectively affect the motor components of semantic representations. A number of studies to date have demonstrated that action-language (i.e., verbs related to bodily movement) is indeed impaired in PDs (Birba et al., 2017; Cardona et al., 2014; for review see: da Silva, Machado, Cravo, Parente, & Carthery-Goulart, 2014; García & Ibáñez, 2016; Salmazo-Silva et al., 2017) and, generally, these deficiencies have been attributed to disruption of sensorimotor-based semantics in the motor system.

Naming pictures of action verbs (Bertella et al., 2002; Cotelli et al., 2007; Herrera & Cuetos, 2012; Patrice Péran et al., 2009; Rodríguez-Ferreiro, Menéndez, Ribacoba, & Cuetos, 2009), generating verbs related to a particular action (Patrice Péran et al., 2003), making lexical decisions on action verbs (Boulenger et al., 2008) and making semantic judgements on (hand related) verbs associated with speed (Speed, van Dam, Hirath, Vigliocco, & Desai, 2017) are all impaired in PD. Furthermore, making motor responses to manipulable stimuli is modulated in PDs as compared to healthy controls (HCs) (Cardona et al., 2014; Ibáñez et al., 2013), which has been attributed to reduced frontotemporal connectivity and basal ganglia atrophy in PDs (Melloni et al., 2015).

While much of the research concerning action language processing and PD has been related to single words, a few studies have used more natural stimuli such as simple sentences or short texts. One such study looked at the effect of PD on the processing of sentences (Fernandino et al., 2013). They manipulated the motor content of sentences (i.e., the verbs) and compared: literal, figurative-non-idiomatic, and figurative-idiomatic to abstract sentences. They show that sentences involving action content were impaired in PDs as compared to abstract sentences. Another study assessed PDs reading naturalistic texts and found relative impairments on action texts compared to neutral texts (García et al., 2018). Elsewhere, it has been shown that in spontaneous discourse PDs rely less on action-related concepts (García et al., 2016).

In general, PDs have been reported to exhibit a noun and verb processing dissociation (with verbs relatively more impaired; Bertella et al., 2002, but see Cotelli et al., 2007 for evidence of relativly greater noun deficits in PDs vs. HCs). However, many of the studies showing this do so by comparing nouns to verbs, despite inherent differences in their grammatical complexity. Relatively little work controlling for this difference has been conducted exploring whether PD leads to impairments in processing *concrete noun words*. Because sensorimotor theories predict that *semantic action content, rather than grammatical class* is behind language deficits in PD, they predict that concrete nouns should be impaired in a similar way to action verbs as long as motor content is comparably relevant to the nouns' representations (Vigliocco, Vinson, Druks, Barber, & Cappa, 2011). Below I briefly review some studies which have tested noun processing in PDs.

In one behavioural study (Cotelli et al., 2007), PDs (in the ON state of DRT) and HCs named actions and objects which varied in their manipulability. Action naming was impaired in PDs but no differences were found for objects, even when the stimuli were further categorized into more and less manipulable categories (in a post-hoc analysis). Another behavioural study (Bocanegra et al., 2015) showed a clear deficit in PDs compared to HCs for nouns in the pyramids and palm trees test. While the authors did not control for the motor components of the nouns in the test, they theorised that the deficits they observe may be due to the presence of manipulable nouns in the list (65% of their trials involved manipulable objects). However, because both of these experiments were not originally designed (and were therefore underpowered) to test our specific question of whether manipulable nouns are impaired compared to non-manipulable nouns in PDs, caution must be taken interpreting their results.

Two studies comparing PDs treated with STN-DBS (sub-thalamic-nucleus deep brain stimulation) to HCs on processing objects have been done. In one, HCs were faster and more accurate to name both objects and actions than PDs overall and PDs were more accurate and faster to name objects and actions with stimulation compared to without. Importantly however, their stimuli objects varied widely in type and manipulability making their findings uninformative about the specific question of motor content being critical to PD deficits (Silveri et al., 2012).

In the other study (Phillips et al., 2012), early PDs with STN-DBS were faster than controls to name pictures of frequently manipulated objects (but not animals) when undergoing stimulation compared to without it suggesting, in general, that naming manipulable objects involves parts of the motor system influenced by STN-DBS. While these findings are suggestive that motor system interruptions impact the semantic processing of manipulable nouns, the lack of a reported interaction between naming animals and manipulable objects in PDs (ON/OFF DRT) and HCs is of note. Relative differences between groups and stimuli types (accounting for varying baseline response differences between groups) are required to support the sensorimotor predictions described above. Furthermore, the comparison between manipulable objects and animal names is problematic because these categories differ in many ways aside from manipulability (i.e., natural vs. man-made, animate vs. inanimate, etc.) and it remains possible that category differences in stimuli may be influence any category differences.

Finally, another behavioural study looked at the effect of PD on processing the written names or photos of manipulable objects (Buccino et al., 2018). In a go-no-go motor response (i.e., a keypress) paradigm, HCs (both young and age matched to PDs) made slower manual responses to objects which are frequently grasped with the hands compared to infrequently manipulated objects. This effect is interpreted to arise as a result of conflict between accessing the motor components of object representations and using those same regions to initiate keypress motor responses. In contrast, while PD participants performed worse than controls overall, they did not show the same pattern as HCs-- rather, they responded to both classes of objects similarly. The absence of interference for PDs is interpreted as being due to PD causing difficulty accessing the motor components of object representations (which is what presumably causes the resource conflict in HCs), meaning that for PDs there is less interference. This finding is suggestive that PD affects motor components of semantics, but is but is rather indirect in that it is based on making inferences from a *lack* of interference.

4.1.1 Questions

In this chapter I report an experiment designed to test whether, compared to HCs, individuals with motor system impairments (i.e., PDs) have relatively more difficulty accessing the representations of objects strongly associated with motor interaction (i.e., frequently manipulated objects) compared to objects weakly associated with motor interactions (i.e., infrequently manipulated objects). Using an object naming behavioural paradigm, we tested whether PDs show more interference (i.e., more errors/slower responses) to naming more-manual objects like “hammer” than less-manual objects like “airplane” than HCs. Importantly, in this study, action semantics are not confounded with grammatical class because we are comparing nouns with high motor associations to those with low. Furthermore, because we were interested in how, according to sensorimotor accounts, *language* might be impacted by PD, we chose object naming as our task because verbal production of words is a more direct test of these than other dependent variables such as action compatibility effects.

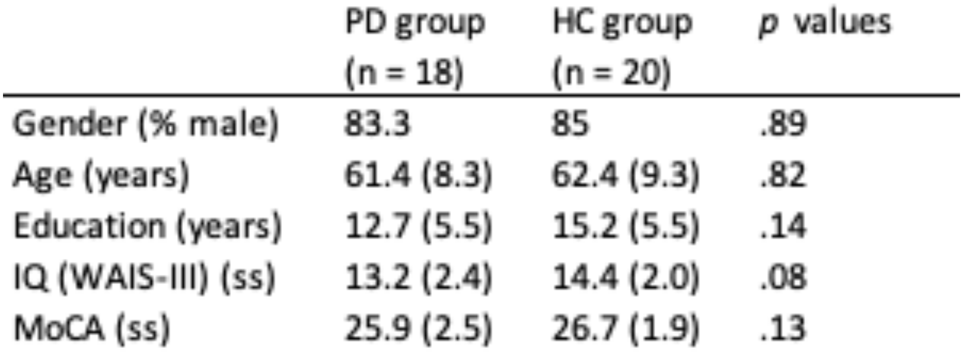
4.1.2 Predictions

If important parts of an object’s distributed semantic representation involve the motor system, then a disease which affects those areas, such as PD should lead to selective relative impairments to accessing those representations. We therefore predict that PDs should experience relatively more difficulty than HCs producing the names of manipulable objects, but no more difficulty than HCs naming non-manipulable objects.

4.2 Methods

4.2.1 Participants

PDs were recruited from the Movement Disorders unit of the Hospital Universitario Donostia (HUD). HCs were recruited from the BCBL participant pool and remunerated for their time. The final study sample consisted of 38 participants: 18 non-demented PDs and 20 HCs. All participants were right handed native Spanish speakers with normal or corrected-to-normal vision. Groups were matched in age, gender, years of education, verbal intelligence quotient and cognitive status. See Table 3 for further information. Exclusion criteria for both groups included: dementia, prior cerebral surgery and impulse control disorders. PDs were diagnosed according to the UK Parkinson's Disease Society Brain Bank criteria by HUD neurologists as being at stage 1-to-3 on the Hoehn & Yahr scale (i.e., mild- to-moderate) and had been diagnosed between 2-to-14 years before testing. PDs were idiopathic and in chronic treatment (i.e., two or more years of Levodopa and/or dopaminergic agonists). None had brain stimulation treatment.



	PD group (n = 18)	HC group (n = 20)	*p* values
Gender (% male)	83.3	85	.89
Age (years)	61.4 (8.3)	62.4 (9.3)	.82
Education (years)	12.7 (5.5)	15.2 (5.5)	.14
IQ (WAIS-III) (ss)	13.2 (2.4)	14.4 (2.0)	.08
MoCA (ss)	25.9 (2.5)	26.7 (1.9)	.13

Table 3. PD behavioural experiment group balancing. Participant demographics and cognitive screening. Standard deviations in parentheses. All ps are from two sample t-tests except for gender which is from a chi-squared proportion test.

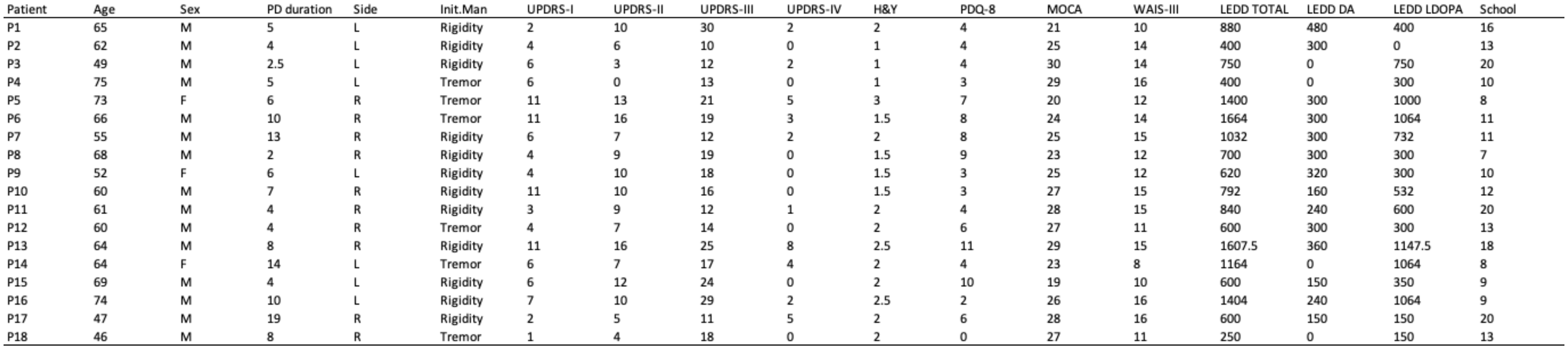
4.2.2 Ethics statement

The study was approved by the Gipuzkoa Clinical Research Ethics Committee and written informed consent in compliance with the BCBL ethics committee and the Helsinki declaration was obtained from all the subjects prior to participation.

4.2.3 Clinical and Neuropsychiatric assessment

Before taking part in the study, all participants underwent assessment for clinically relevant dementia, psychosis, impulsivity, addictions, aphasia, language disorders and depression. Cognitive status was assessed using the Montreal Cognitive Assessment (MoCA) (Nasreddine et al., 2005) and verbal IQ using the WAIS-III vocabulary tool. For PDs, all assessments were performed under the effect of the first dose of habitual anti-Parkinson's medication in the morning.

The following measures were collected on PDs: Parts I to IV of the Unified Parkinson's Disease rating scale (UPDRS) (Goetz et al., 2008), the Hoehn and Yahr staging scale (Hoehn & Yahr, 1967), the Parkinson's Disease Questionnaire (PDQ-8) (Jenkinson, Fitzpatrick, Peto, Greenhall, & Hyman, 1997). Table 4 provides detailed demographic and clinical information. It includes each individual's total levodopa equivalent dose ($\text{LEDD}_{\text{TOTAL}}$), daily levadopa dose ($\text{LEDD}_{\text{LDOPA}}$) and daily levodopa equivalent dose of dopamine agonist (LED_{DA}) (Tomlinson et al., 2010) which provide a converted and standardised measure of anti-Parkinson's medication allowing for comparisons between people on different regimes.



Patient	Age	Sex	PD duration	Side	Init.Man	UPDRS-I	UPDRS-II	UPDRS-III	UPDRS-IV	H&Y	PDQ-8	MOCA	WAIS-III	LEDD TOTAL	LEDD DA	LEDD LDOPA	School
P1	65	M	5	L	Rigidity	2	10	30	2	2	4	21	10	880	480	400	16
P2	62	M	4	L	Rigidity	4	6	10	0	1	4	25	14	400	300	0	13
P3	49	M	2.5	L	Rigidity	6	3	12	2	1	4	30	14	750	0	750	20
P4	75	M	5	L	Tremor	6	0	13	0	1	3	29	16	400	0	300	10
P5	73	F	6	R	Tremor	11	13	21	5	3	7	20	12	1400	300	1000	8
P6	66	M	10	R	Tremor	11	16	19	3	1.5	8	24	14	1664	300	1064	11
P7	55	M	13	R	Rigidity	6	7	12	2	2	8	25	15	1032	300	732	11
P8	68	M	2	R	Rigidity	4	9	19	0	1.5	9	23	12	700	300	300	7
P9	52	F	6	L	Rigidity	4	10	18	0	1.5	3	25	12	620	320	300	10
P10	60	M	7	R	Rigidity	11	10	16	0	1.5	3	27	15	792	160	532	12
P11	61	M	4	R	Rigidity	3	9	12	1	2	4	28	15	840	240	600	20
P12	60	M	4	R	Tremor	4	7	14	0	2	6	27	11	600	300	300	13
P13	64	M	8	R	Rigidity	11	16	25	8	2.5	11	29	15	1607.5	360	1147.5	18
P14	64	F	14	L	Tremor	6	7	17	4	2	4	23	8	1164	0	1064	8
P15	69	M	4	L	Rigidity	6	12	24	0	2	10	19	10	600	150	350	9
P16	74	M	10	L	Rigidity	7	10	29	2	2.5	2	26	16	1404	240	1064	9
P17	47	M	19	R	Rigidity	2	5	11	5	2	6	28	16	600	150	150	20
P18	46	M	8	R	Tremor	1	4	18	0	2	0	27	11	250	0	150	13

Table 4. PD behavioural experiment PD clinical information. ss= standard scores. Yrs = years. Duration = time since diagnosis. Laterality = side (i.e., left or right) first affected. Init.maifestation = initial manifestation (i.e., Rigidity or Tremor).

4.2.4 Stimuli

Experimental stimuli were 179 colour photographs of objects on a white background. We obtained most from the bank of standardised stimuli (BOSS) database (Brodeur, Dionne-Dostie, Montreuil, & Lepage, 2010), but we sourced the images unavailable from there online. The concrete objects included: tools (36), food/plants (28), objects (78) and animals (37). See Table 14 in the appendix for a full list of stimuli names. Because relative image size can have an impact on reaction times (Grèzes, Tucker, Armony, Ellis, & Passingham, 2003) we ensured that any sourced images followed the BOSS conventions. All images were selected such that they were oriented for use by right handers (Creem & Proffitt, 2001). We selected the final stimuli from those which had the highest naming agreement in a pre-study conducted on a group of 20 individuals (M age = 22 years, range = 18-29 years, 10 male) who did not participate in the current study. Each participant saw all of the stimuli once and we arbitrarily allocated participants to one of 10 pseudo-randomised presentation lists in which no more than four items of the same category (i.e., tool, animal etc.,) was presented in succession.

Ratings

We collected ratings of manual experience for the names of the stimuli objects online. Sixty paid participants (M age = 33 years, range = 19-68 years, 20 male), rated lists of half the words according to the following question: “Do you have more experience looking at this or touching it with your hands?” 1 = relatively more experience looking, to 7 = relatively more experience touching. This process resulted in 28 or 29 ratings for each word.

4.2.5 Procedure

Participants were seated in a well-lit cabin and wore a headset with a voice activated microphone to record verbal responses. Two trained experimenters manually noted responses as they were made and we recorded each session using a hand recorder for data retention, and checking purposes. Visual stimuli were presented using Presentation software on a CRT monitor. After 10 practise trials to familiarise participants with the task and to calibrate the voice key, participants saw objects on the screen and named them as quickly and as accurately as they could. We asked that they refrain from making any other noises in the session. Participants saw a fixation cross before each trial began. After 200ms of a blank screen, an image was presented on the screen for 4800ms, or until a response was made. Each trial began when an experimenter saw that the participant was prepared (see Figure 11 for a visual representation). No feedback on accuracy was provided. The experiment lasted around 20 minutes in total. All PDs were tested while in the "ON" phase of LDopa medication.

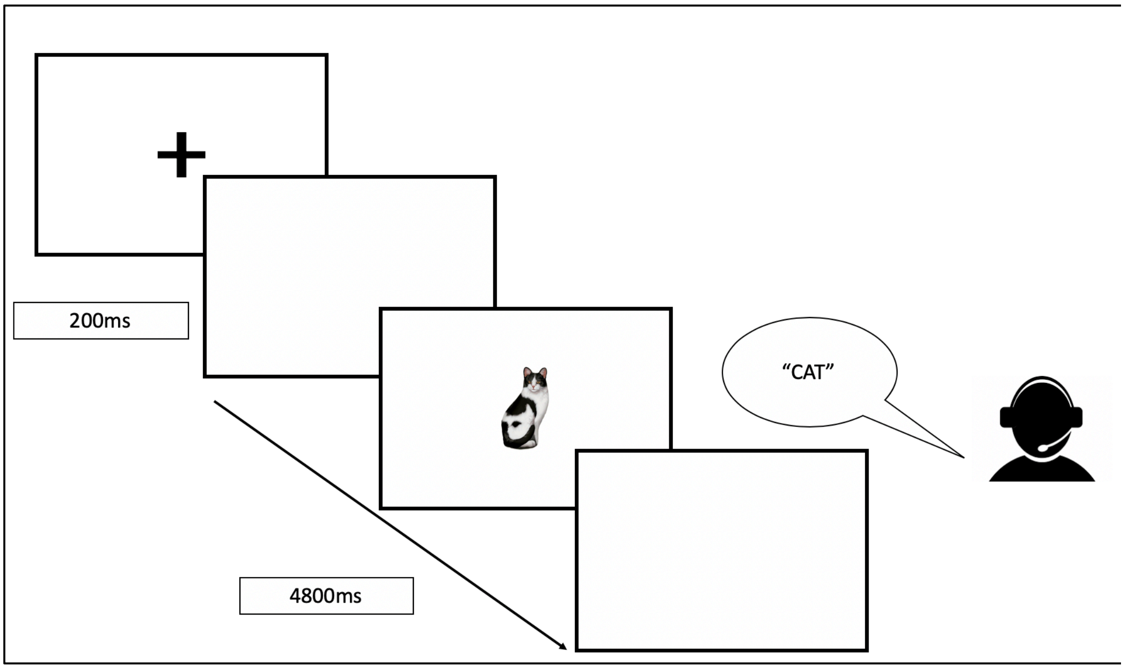


Figure 11.PD behavioural experiment trial structure

4.2.6 Statistical analysis

We performed analyses using the lme4 package (Bates, Maechler, et al., 2015) in the R programming environment (R Core Team, 2018). Response times (RTs) were submitted to linear mixed effects regression models (LMERs) and errors were submitted to generalised linear mixed effects (logistic) regression models (GLMERs). The significance of the effects was assessed using the likelihood-ratio tests (i.e., chi-squared tests of fit) between a model with and one without the critical term. To approximate degrees of freedom and *p* values for individual predictors in the models we used the lmerTest package (Kuznetsova et al., 2017). For analyses we report relevant regression coefficients (either RTs or odds ratios (ORs)) with 95% CIs and t-values (LMER) or z-values (GLMER). As counterbalanced-crossed random effects we always included participant and item as intercepts. We also included random slopes of the fixed effects, by subject and by item, when they: improved the fit of the model, were theoretically motivated, justified by the data and design, computationally converged, and did not lead to underspecified estimates (i.e., random effect correlations of >.8/-.8). We aimed to be as maximal (Barr et al., 2013) as was warranted without sacrificing parsimony (Bates, Kliegl, et al., 2015; Matuschek et al., 2017). As fixed effects we entered object-type (a categorical variable with two levels: less-manual objects (baseline) and more-manual objects and Group (a categorical variable with two levels and HC as baseline) and their interaction. In further analyses we replaced object-type with average experience ratings (a continuous, mean centred variable from 1-7).

A significant critical positive interaction between object-type/manual experience ratings and Group would indicate that PDs are relatively impaired, compared to HCs, at naming objects associated with more manual experience than less manual objects.

We coded responses by hand (both online and offline) to ensure that only correct responses were included in RT analysis. Errors (% errors ± 1SD: 29.81 %, ± 10.61 % in total) include: incorrect names (82.7%), responses made before 100ms and after 4800ms of picture onset (8.6%) and verbal disfluencies or hesitations (i.e., incorrect mic trips) (8.7%). Response times were calculated from the appearance of an object images to the onset of a valid response, they were trimmed, by participant, to ±3SD of the mean (<2%).

4.3 Results

Data Exclusion

We excluded data from two participants (5% of sample), not included in the final sample described in the participants section, because of poor microphone calibration meaning that either no responses were logged (1) or they were logged incorrectly (1).

Following a preliminary analysis, we discarded the data from four stimuli (2% of sample) because they were too hard to name (i.e., accuracy < 3 SDs from the sample mean) (2), or because we did not collect ratings for them (2).

Object condition assignment

Using experience ratings collected online we divided the objects into two conditions: The bottom half of the objects became the relatively-less-manually-experienced-objects (less-manual) condition (M = 2.16, SD = 0.60) and the top half the relatively-more-manually-experienced-objects (more-manual) condition (M = 4.83, SD = 0.82).[9]

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[9] In the visual and olfactory experiments, we used a tercile split. Due to the limited time we had to test each participant, we had fewer items in this study, so in order to maintain sufficient statistical power we used a median split.

4.3.2 Response times

Overall, PDs were not slower to name objects than HCs (RTs ± 1 SE: 1102 ms ± 47 ms and 1122 ms, ± 45 ms respectively). The results of an LMER model to predict manual-interference in RTs based on object category revealed no main effect of object-type ($t(177) = -0.148$, $p > .8$) or group ($t(37) = -0.390$, $p > .6$). Further, the critical interaction between object-type and group was not significant ($\chi2(1) = 0.37$, $p > .5$). See Figure 12 for a visualisation of this comparison and Table 5 for aggregated means. The results of an LMER model to predict manual-interference in RTs based on continuous rating revealed no main effect of rating ($t(46) = -0.88$, $p > .3$) or group ($t(38) = -0.356$, $p > .7$) and no significant critical interaction between rating and group ($\chi2(1) = 0.73$, $p > .3$). See Figure 13 for an approximate visualisation of this effect.

Figure 12. PD behavioural experiment object naming RTs, by participant. Mean Reaction time, by participant, as a function of group and object type. Error bars represent standard error of the mean.

	less-manual-objects		more-manual-objects	
	RT (ms)	Errors (%)	RT (ms)	Errors (%)
Healthy Controls	1079 (39)	29.43 (2.42)	1059 (32)	30.34 (2.12)
Parkinson's Patients	1053 (56)	30.49 (2.89)	1041 (44)	28.98 (2.87)

Table 5. PD behavioural experiment results table. By participant aggregated mean RTs and % Errors for the object naming task by group and object condition. Standard error of the mean is in parentheses.

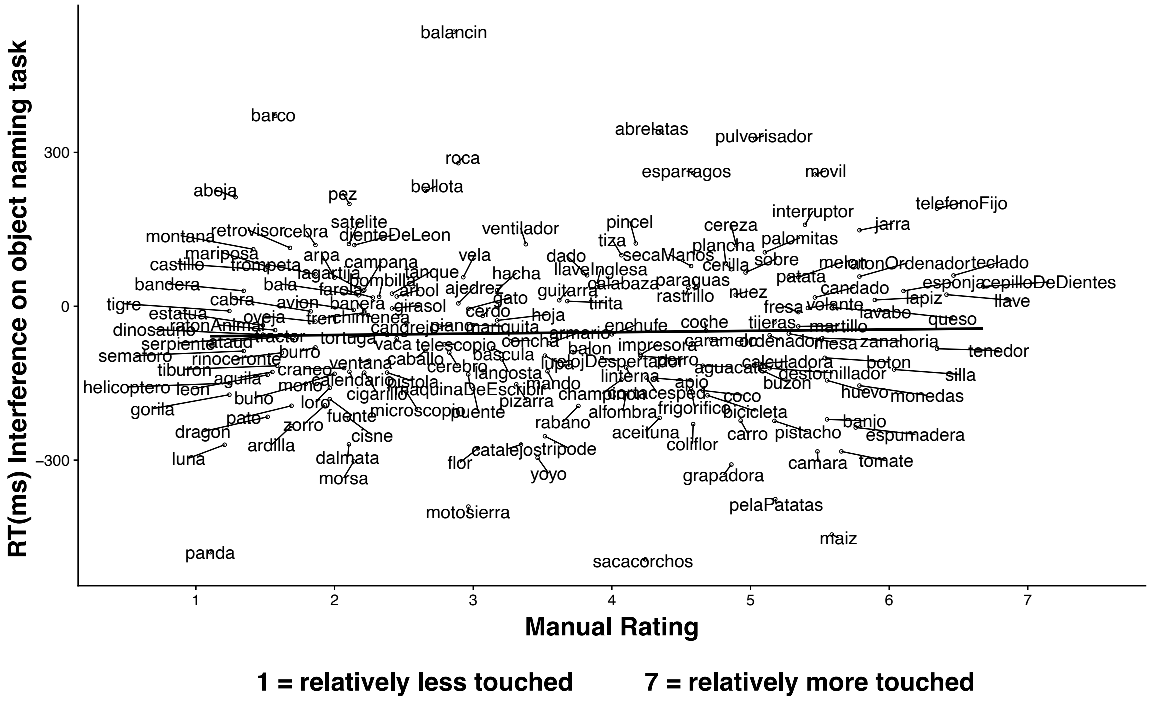

Figure 13. PD behavioural experiment object naming RTs, by item. Scatterplot (with best fitting regression line) showing the relationship between RT interference effect scores (ms) aggregated and manual experience ratings. Interference effect for each object calculated as RT HC – RT PD.

4.3.3 Accuracy

Overall, PDs did not make more errors naming objects than HCs (% errors ± 1SD: 29.73 %, ± 12.08 % and 29.89 % ± 10.06 % respectively). The results of a GLMER model to predict manual-interference in errors based on object category revealed no main effect of object-type (z = -0.191, *p* > .8) or group (*z* = -0.05, *p* > .9) and there was no significant critical interaction between object-type and group ($\chi2(1) = 0.22$, *p* > .2). The results of a GLMER model to predict manual-interference in errors based on rating revealed no main effect of rating (z = -0.87, *p* > .3) or group (*z* = -0.31, *p* > .7) and there was no significant critical interaction between object-type and group ($\chi2(1) = 2.06$, $p > .15$). Our results show no interference either to response times or to accuracy when responding to more manual objects than less manual objects as a result of PD.

4.3.4 Exploratory analysis

Though our sample was small it had enough variability to evaluate if any interference effect could be predicted by individual differences in disease metrics. In order to assess the impact of these we calculated an interference effect, by participant, by subtracting the average RT or % error for manual objects from visual objects. We then tested whether this interference measure scaled in proportion to individuals' age, time since diagnosis of PD, score on the UPDRS-3 scale (a measure of motor skills) and their score on the H&Y scale (a measure of motor fluency). We observed that none of these measure correlate with interference, see Table 6.

	RT		Error	
	r	*p*	*r*	*p*
Age	-0.24	.14	-0.33	.17
PDyrs	0.05	.83	0.16	.52
UPDRS3	-0.08	.73	0.02	.93
HY	-0.15	.53	-0.07	.79

Table 6. PD behavioural experiment correlations of interference effect with factors of interest.

In exploratory mode, following previous studies (Rueschemeyer et al., 2010) we analysed subsets of the manipulable objects (n=94) which required the use of either a fine grip (n=47) or a grasp (n=47) (functional / volumetric manipulability). The results of an LMER model to predict manual-interference in RTs based on grip-type revealed no main effect of grip-type ($t(82) = 0.193$, $p > .8$) or group ($t(38) = -0.015$, $p > .9$) and there was no significant critical interaction between object-type and group ($\chi2(1) = 0.70$, $p > .4$). The results of a GLMER model to predict manual-interference in errors based on grip-type revealed no main effect of grip-type ($z = 0.83$, $p > .4$) or group ($z = 0.67$, $p > .7$) and there was no significant critical interaction between grip-type and group ($\chi2(1) = 0.45$, $p > .5$).

4.4 Discussion

According to sensorimotor accounts, sensory, motor and semantic process are not functionally distinct, but rather overlap, interact and are supported by the same brain areas. If so, accessing the conceptual representations referred to by concrete noun words should engage the brain areas which are engaged when interacting with or experiencing those objects. The behavioural study reported here tested this prediction in PDs and HCs by measuring accuracy and response times to naming photos of objects. Sensorimotor accounts predict that having PD, which is predominately a motor disease, should interfere more with naming frequently manipulated objects relative to infrequently manipulated objects, as compared to HCs. This is because the representations of manipulated objects are predicted to involve motor areas, access to which are disrupted in PD. On the other hand, amodal accounts would predict no differences.

Firstly, we did not observe that PDs were slower or less accurate than HCs in a confrontation naming task overall. That we do not observe such differences in such a large and carefully matched sample challenges some previous work (Bocanegra et al., 2015) and suggests that PD does not necessarily lead to noun impairments compared to HCs. However, contrary to our predictions, we found no evidence that PD makes it *relatively* more difficult for people to name frequently vs. infrequently manipulated objects compared to HCs. Furthermore, exploratory analyses did not suggest a subtler relationship between semantic processing and PD driven by stimuli factors (i.e., by subclassifying objects by manipulability type) or influences of individual differences between people (i.e., age, time since diagnosis or measures of PD severity). At the outset it should be noted that this null result is broadly in line with a number of previous behavioural findings in PDs (Cotelli et al., 2007) showing that they are not impaired on processing manipulable nouns. However, our finding differs from other work (Buccino et al., 2018; Phillips et al., 2012) which has suggested, on the contrary, that such impairments exists. While our null result could, clearly, be interpreted as a challenge to sensorimotor accounts of semantics, we will now discuss a number of issues pertinent to contextualising our results before drawing conclusions from them.

A major limitation to our study is that, for practical reasons, our PDs were in the ON stage of their anti-parkinsonian medication when we tested them. All were being treated with dopamine replacement therapy (DRT), predominately Levadopa (LDopa), which alleviates the motor deficits associated with PD by restoring underactive neuronal activity in primary motor and premotor regions thereby repairing the motor loop through improved connectivity between the cortex and basal ganglia (Haslinger et al., 2001). Aside from movement improvements, some imaging work has shown that DRT increases motor activation during cognitive activities like motor imagery and action processing (P.

Péran et al., 2013). A number of studies have assessed the effect of anti-parkinsonian treatment on action language impairments, generally reporting that semantic deficits in verb processing in PDs are absent or ameliorated due to DRT and/or STN-DBS. For example, in picture naming (Herrera & Cuetos, 2012; Herrera, Cuetos, & Ribacoba, 2012; Silveri et al., 2012), masked priming (Boulenger et al., 2008) and confrontation object naming (Cotelli et al., 2007). Though one study (Cardona et al., 2014) suggests that semantic deficits associated with PD persist even in ON state, at least for "action compatibility" effects.

Because it seems possible that DRT could obscure impairments in semantic processing (normally present in PDs in OFF stage) by "repairing" any access problems to motor aspects of semantic representations, it is possible that our PDs' motor systems were not sufficiently impaired, *at time of testing*, to interfere with the motor representations of manipulable object concepts. If true, the fact that PDs were not relatively more impaired in naming manipulable objects in that state is unsurprising. Future work should explore this topic more fully by varying the DRT state of individuals and comparing people both ON and OFF medication. From the point of view of "fluid" accounts of concepts (Yee, 2017) that impairments are impermanent or contextual would be highly informative about the nature of concepts. This will be discussed further below.

Aside from the DRT concerns above, there is another concern about using PD as model of manual motor impairment. This is because PD is not necessarily a specifically "hand-related" impairment and, in fact, negatively affects very different regions of the body on an individual level. Therefore, it is important to consider whether our PDs can properly be considered as homogenously impaired in their manual capacities. An implicit assumption of the sensorimotor assumptions outlined above. After all, the "body specificity hypothesis" (Daniel Casasanto, 2011), for which there is increasing neuroimaging evidence (Willems, Hagoort, & Casasanto, 2010), states that how people represent objects in the brain is intimately connected with their *personal* physical capacities. In support of this consideration two studies with PDs have shown specific verb deficits (i.e., hand or leg related verbs) to be correlated with corresponding upper vs lower limb PD motor impairments (Nguyen, 2013; Roberts et al., 2017). Examining the data with respect to the type of motor difficulties present in each individual is a sensible approach which may add power to experimental analyses of PD and semantic-motor impairments. Unfortunately, however, the motor assessments we collected were not sufficiently detailed to allow us to take this approach.

On a methodological level, it is worth asking whether our chosen task, object naming, is optimally sensitive for measuring sensorimotor-semantic impairments. Of note is that previous evidence of manipulable noun impairments in PD (Buccino et al., 2018) comes from an action compatibility methodology, which involve a potentially more sensitive dependent variable than verbal production, namely keypress latencies. Overall, it may be that object naming is not always measurably interfered with by motor impairments (Garcea, Dombovy, & Mahon, 2013; Negri et al., 2007; Rosci, Chiesa, Laiacona, & Capitani, 2003). This may be because it is possible to name photographs of without accessing motor aspects of an object's representation especially if, given the visual nature of the task (seeing colour photographs of the objects), visually diagnostic aspects of an object's representation are naturally given primacy. On the other hand, object naming has been successfully used elsewhere to test very similar hypotheses (e.g., Yee, Chrysikou, Hoffman, et al., 2013), and sensorimotor research widely suggests that nouns vary in their motor content and ones rich in motor associations *should* be interfered with (Vigliocco et al., 2011).

As discussed in the visual experimental chapter of this thesis, the stimuli we used are concrete objects which have *relative* as opposed to *absolute* differences in the modality they are most frequently associated with (i.e., "visual" vs. "manual objects"). Because all the objects are *multimodally* experienced (i.e., visually, auditorily etc.), according to sensorimotor accounts their representations extend widely over the cortex. A given object may "load" more onto one modality or another (i.e., computer screens [visual] vs. keyboards [manual]) but their representations should involve other modalities too (you sometimes carry or adjust screens and we often look at keyboards). Given this, it is possible that picture naming might be preserved in PD because it is possible (and even felicitous) for the representations of even highly manipulable objects to be accessed using other (perhaps less "primary") sense modalities (i.e., vision) rather than through activation of motor information. Future work might elect to contrast noun word processing (visually and auditorily) with object naming to see the degree to which semantic access relies on the motor system when the task relevant importance of visual characteristics is lessened. On the other hand, it should be noted that the suggestion that different aspects of representations might be activated depending on the task at hand fits nicely with the main thrust of this thesis; namely the importance of contextual factors to concepts.

A few final comments should be made about the experimental methodology we employed with regards to our null result. For practical reasons (time constraints with the clinical population) we were unable to collect manual experience ratings from the participants themselves. While the group average of ratings collected online are widely used in the field, and can be a good proxy for individual ratings, it is conceivable that, because our ratings were a) collected from a younger population than our experimental sample, and b) collected from healthy individuals, our ratings of experience may less closely reflect the particularities of our older PDs' experiences with objects (e.g., it is possible that PDs, perhaps as a result of their impairments, have less manual experience with objects than HCs). In future studies, experience ratings provided by the participants themselves may reveal more about how *personal* manual experience interacts with motor impairments and the representations of manual objects.

On a theoretical level, another possible explanation for our null effect presents itself. There are (at least) two ways of characterising, from a sensorimotor perspective, the predicted sensorimotor-semantic impairments arising from lesions to "relevant" sensory or motor areas. One is to argue that, when probed, components of impaired representations are either less activated or inaccessible to PDs. Their representations extend over the same regions as when they were healthy and now are relatively diminished. On this first view, impairments should be measurable in tasks such as ours (though not, perhaps if individuals are under DRT). Another possibility is to argue that if representations of objects are experience-based, and over time, an individual's capacities and by extension their experience has *changed*, their representations too should "shift" to more readily reflect their current "understanding" of it. There is some recent behavioural evidence that individuals after a stroke rapidly adapt their representations of manipulable objects to reflect their current situation (Chrysikou et al., 2017). On this conception, it is possible that long term conditions such as PD might, over time, lead to sufficient "representational shift" for any measurable differences at the level of object naming to be ameliorated, as the disease progresses. This possibility could be tested behaviourally by tracking patients longitudinally. However, some suggestion in the literature exists indicating that PDs exhibit fMRI functional connectivity differences, as compared to healthy controls, in processing action language (Abrevaya et al., 2016). It is possible that, while we did not observe any differences *behaviourally*, imaging data may shed some light on subtle neural differences. In the following chapter this possibility will be addressed.

In conclusion, in one behavioural experiment we did not observe either that PDs are impaired on noun processing compared to HCs or their predicted relative impairment of manipulable object representations. However, as discussed above, there were a number of features of our sample and our methodology which make our results complicated to interpret. Firstly, the fact that our PDs were treated with DRT and therefore “motorically-unimpaired” makes it difficult to judge whether PD, in the *absence of treatment*, would lead to relative impairments in naming manipulable objects, as predicted by sensorimotor accounts. Secondly, because of the wide variety of motor impairments that are present in PD, recruiting a sample of participants who are uniformly impaired in fine hand motor control is challenging making PD a suboptimal motor disorder with which to test these predictions. Further concerns revolve around the sensitivity of the object naming task itself (as opposed to action compatibility effects, for example) as well as its potential to encourage people to focus on more visual aspects of representations than less visually based tasks. Therefore, further experimental work, perhaps using linguistic stimuli and certainly with experience ratings from affected individuals themselves, is required to shed light on the relationship between PD and the representation of manipulable objects. This work should attempt to tease apart the effect of Parkinson’s medication on “repairing” conceptual access, as well as exploring the relationship between long term shifts in conceptual representations in individuals who have divergent experience to healthy individuals.

Chapter 5: Parkinson’s, manual experience & object representations – fMRI

5.1 Introduction

As outlined throughout this thesis, according to sensorimotor accounts, important elements of lexicosemantic content are grounded in perceptual and motor brain areas as a result of sensory and motor experience. This means that these accounts predict that the conceptual representations of objects associated with actions should involve parts of the motor system responsible for the procedural knowledge required to perform those actions. In the previous chapter I reported an experiment designed to test these predictions by measuring the effect of a motor disease; Parkinson’s disease (PD), on naming frequently manipulated objects compared to infrequently manipulated objects. While we found no evidence of manipulable-object naming impairments at the *behavioural* level, this may have been because, for practical reasons, the PDs in our sample were all under the effects of dopamine replacement therapy. This medication may have restored the motor loop function at the time of testing in these people, resulting that impairments to action semantics in PDs were either absent or too subtle to be readily detected using a behavioural confrontation naming paradigm. In this chapter I report an fMRI experiment designed to explore at the *neural level* if there are more subtle signatures of long-term changes to semantically processing the names of manipulable objects and accessing their representations due to PD.

Object representations

At least two primary networks and one processing hub are commonly identified in neuroimaging experiments as being involved in processing concrete objects: one is a frontoparietal network, thought to be engaged in service of activating information about how objects are usually manipulated; and the second is an occipitotemporal network commonly implicated in accessing information about their visual properties (for review see: Lewis, 2006; Pulvermüller, 2005; Weisberg et al., 2007). The retrieval of information from these networks, in the service of semantic processing, is thought to be mediated by inferior regions of the prefrontal cortex (PFC) (S. L. Thompson-Schill, D’Esposito, Aguirre, & Farah, 1997). According to sensorimotor accounts, the representation of concrete objects with both visual and motor associations (e.g., “*tools”*) should include areas in *both* the frontoparietal and occipitotemporal network. However, those with fewer motor associations; i.e., those infrequently *manipulated* but frequently *seen* objects (e.g., *"sculptures"*) should *primarily* be sub-served by the latter, occipitotemporal network. Below I briefly summarise relevant findings related to these networks.

In healthy participants, a left lateralised frontoparietal network is involved in *online* object manipulation (i.e., active when actually touching and using objects) and includes areas such as the: pre-motor cortex (pMC), primary motor cortex (M1), primary somatosensory cortex (S1), supplementary motor area (SMA), and parietal cortex (PC). Crucially however, this network is also active when people retrieve semantic information about manipulable objects *offline*, for example when viewing pictures of them (Chao & Martin, 2000), hearing their names (Rueschemeyer et al., 2010) and naming them (Chouinard & Goodale, 2010; Patrice Péran et al., 2010). As is common in other processing streams, the frontoparietal network involves a posterior-anterior gradation of complexity with more posterior regions such as the anterior intraparietal sulcus (aIPS) and the adjacent supramarginal gyrus (SMG) representing more schematic information about manipulable objects (Boronat et al., 2005) and more anterior regions such as the ventral-PMC representing more elaborated motor semantics, such as those associated with complex motor pattern execution (Aziz-Zadeh & Damasio, 2008; Gerlach, Law, & Paulson, 2002; Kan et al., 2006). Because selective stimulation of motor regions (aIPS/SMG and vPMC) with TMS (Ishibashi, Lambon Ralph, Saito, & Pobric, 2011; Pobric et al., 2010), brain lesions (Arévalo, Baldo, & Dronkers, 2012; G Gainotti, 2000; Tranel, Damasio, & Damasio, 1997; Tranel, Kemmerer, Adolphs, Damasio, & Damasio, 2003) and behavioural dual task interference paradigms (Yee, Chrysikou, Hoffman, et al., 2013) selectively interfere with accessing the meaning of manipulable object noun words, the motor regions of the frontoparietal network seem to be *functionally,* as opposed to epiphenomenally, implicated in their representations.

The second network commonly implicated in representing semantic knowledge about concrete objects is the occipitotemporal network. Generally speaking it is related to the representation of visual semantics and includes areas such as ventral-occipitotemporal cortex including the fusiform and lingual gyri and the lateral occipital cortex (LOC: a region sensitive to the visual features of intact, recognisable objects: Grill-Spector et al., 2001). These regions are thought to feed visual properties of objects forward to key semantic areas in posterior temporal and prefrontal cortex (Malach et al., 1995).

Finally, the retrieval and selection of semantic knowledge about concrete objects from both frontoparietal and temporooccipital networks is mediated by the ventrolateral prefrontal cortex (vlPFC) (Alex Martin, 2007; Rissman & Wagner, 2012). One area, the inferior frontal gyrus (IFG) is commonly implicated in the guidance of semantic retrieval and selection of contextually valid representations from information stored over the cortex (Badre & Wagner, 2007; S. L. Thompson-Schill et al., 1997), and is equally active when processing animal names vs tool names (Chouinard & Goodale, 2010). In fact, the IFG (and more specifically: BA44 or opercularis and BA 45 or triangularis) has been suggested as a major semantics hub at which information from distributed cortical networks of object recognition processing come together (Vigliocco et al., 2011). Support for this view comes from studies showing that TMS of the left IFG leads to generalised deficits in semantic processing (Devlin, Matthews, & Rushworth, 2003).

Experience & training

As highlighted throughout this thesis, an under-examined prediction of sensorimotor accounts is that sensorimotor representations develop as a result of *an individual's* sensory and motor experience. There is growing evidence that motor experience with objects alters activation in the frontoparietal network. For example, manual training with novel objects increases activation in the intraparietal sulcus (IPS) and PMC when merely viewing images of them in a scanner (Weisberg et al., 2007). Similarly, objects which are rated as being commonly interacted with lead to increased activation in the anterior-IPS and SMG as compared to objects infrequently interacted with (Hargreaves et al., 2012). Basically, the more people have physically used specific objects such as tools dictates the degree to which vPMC is recruited, with frequently manipulated objects yielding the highest activation (Kan et al., 2006; Oliver et al., 2009).

Parkinson's disease

If personal experience with manipulable objects alters the recruitment of the frontoparietal network, and this is attributed to changes in the conceptual content of their representations, then impairments to this network should selectively interfere with "normally" processing those objects. One way of testing this hypothesis is to measure whether individuals who have developed interruptions in their motor network (such as PDs), show evidence of altered processing pathways for objects typically reliant on the frontoparietal motor network. Such alterations in the frontoparietal network might also be accompanied by compensatory variations in the "typical" involvement of the occipitotemporal network and/or frontal semantic control regions in PDs.

PD leads to interruptions in a frontostriatal network comprised of prefrontal, motor and basal ganglia regions including motor control circuits looping through the SMA from the PMC and M1 areas (Rodriguez-Oroz et al., 2009). The affected frontostriatal network, which significantly overlaps with the frontoparietal network discussed above, is, in healthy individuals, responsible for motor control. Growing evidence of action-language deficits in PDs has been attributed to disruptions in the frontal motor nodes of these networks (Birba et al., 2017). Moreover, frontal networks seem to be a particularly important for action language, as motor disorders which do not involve such disruptions to frontostriatal function (i.e., neuromyelitis optica and acute transverse myelitis) do not lead to comparable action-language deficits (Cardona et al., 2014).

What work has been done with PD to date?

In the previous chapter I reviewed the growing behavioural evidence of motor language disruption in PDs. However, as far as I am aware, to date, only three fMRI studies have been published which report testing sensorimotor hypotheses (primarily concentrating on action verbs) in PDs (Abrevaya et al., 2016; Péran et al., 2013; Péran et al., 2009). I review these briefly below.

Univariate analysis

The first study (Péran et al., 2009) followed previous behavioural work (Péran et al., 2003) suggesting that PDs are impaired at producing verbs compared to naming objects. They tested PDs (N=14) in ON state of DRT without a healthy control (HC) comparison group (this limitation is discussed below). Participants were asked to either name or generate action verbs for 50 black and white line drawings of objects (either biological objects such as foods and animals or manipulable man-made objects such as tools). Behaviourally, in accordance with their predictions, they observed that verb generation was impaired compared to object naming. However, within object naming there were no behavioural differences between manipulable or biological objects. Neuroimaging results for picture naming (collapsing over object types) vs. rest showed activation in occipital lobe, fusiform gyrus and lingual gyrus; suggesting the engagement of the occipitotemporal network related to visual properties of objects (further activation was observed in the SMA and STG). Verb production vs rest activated a similar network, presumably as a result of the trials involving visually processing identical images, but additionally involved a cluster in parietal cortex, suggesting the further involvement of the frontoparietal network. While direct comparison of object naming and verb generation yielded no differences after statistical thresholding, exploratory, uncorrected results ($p < .001$) tentatively suggest higher activation for action naming in the PFC (IFG-opercularis) and anterior cingulate cortex. The authors argued that this may indicate a “non-motor” route developed as an alternative to the frontoparietal for processing action semantics in

PDs. To bolster this claim, they reported a correlation between standardised measures of motor dysfunction and activity in the PFC when generating action verbs suggesting that the more an individual with PD has motor impairments, the more they recruit PFC when generating verbs to describe images.

The second study (Péran et al., 2013) was conducted with a small sample (N=8) but report repeated measures for each participant, both in OFF state of DRT (after a 12hr "washout" period) and in ON state of DRT. Again, no healthy control group was tested and PDs engaged in blocks of verb generation, mental simulation of action and object naming, in response to the same images as above. In line with their previous study, behavioural results showed that participants (irrespective of DRT state) made more errors for verb generation than for object naming and no differences appeared in accuracy between biological and man-made manipulable object types. Imaging results revealed differences for "action semantics" (i.e., both verb generation and mentally simulating an action) compared to object naming: namely, increased activation in the PFC, suggesting increased semantic processing cost. Overall, ON state of DRT led to comparatively higher activation in motor and premotor areas both for producing verbs and mentally simulating actions as compared to naming objects. For object naming, no differences appeared for the same comparisons (i.e., between OFF vs ON state) and no differences appeared between object categories (i.e., between manipulable and biological objects). The authors interpreted these results as suggesting that action semantics recruit motor brain areas in PDs, and that DRT restores function to these regions. Specifically, they argued that DRT influences motor activation not only in motor tasks (e.g., Haslinger et al., 2001) but also in motor imagery tasks and, interestingly, in verbal tasks involving action semantics.

These studies suggest that the behaviourally observed action language impairments in PDs have neural correlates in motor areas. Furthermore, they suggest that as a result of this, PDs develop alternate "non-motor" processing pathways for action language. However, the absence of an HC comparison group in the first study (Patrice Péran et al., 2009) is a limitation. Essentially, their findings show differences *between* different tasks *within* PDs. While the correlation they report between motor impairment and PFC recruitment is highly suggestive, the optimal test of sensorimotor hypotheses would be to show that PDs *differ from* HCs in the way that they process action semantics. On the other hand, the second study comparing PDs in OFF and ON state of DRT (Péran et al., 2013) provides intriguing evidence about the recruitment of motor loop regions in different contexts (i.e., whether in ON or OFF state), however, it does not address how long-term motor capacity changes in PDs (compared to HCs) impacts on how they habitually process action semantics.

Functional connectivity in PD

One way of investigating long-term differences in processing strategy for action semantics in PDs is to carry out functional connectivity (FC) experiments comparing HCs and PDs while they process action language. While whole-brain (univariate) contrasts rely on maximum activation *in a given area* to gain information about its measure, FC methods are sensitive to connections and dynamics *across* the brain as a result of testing long-range correlations of activity during processing. With regards to PD, it is likely that long-term differences in processing capacities, perhaps as a result of motor loop dysfunction, may result in neural reorganisation whereby the brain forges alternate routes for action-semantics processes, which in healthy populations typically involve frontoparietal networks. Such subtle changes in functional circuits may be most readily detected using connectivity analyses methods. One such fMRI study (Abrevaya et al., 2016) tested HCs and PDs by comparing correlated brain activation while they listened to either action verbs (e.g., *"dance"*) or the names of concrete-non-manipulable nouns (e.g., *"house"*). They correlated activity in three seeds to the rest of the brain, each conforming to a prominent node in a network related to: 1) PD dysfunction: the frontostriatal network (seed: putamen), 2) action semantic processing: the frontoparietal network (seed: M1) and 3) semantic processing in general: the occipitotemporal network (seed: superior temporal cortex). They found that the M1 seed was, for action verbs, functionally connected more frontally (i.e., to IFG) in HCs, and more posteriomedially (i.e., to the cingulate) for PDs. In PDs, as might be predicted, the putamen seed and basal ganglia showed less functional coupling both for verbs and nouns, reflecting frontostriatal dysfunction. No differences were observed in the temporal seed. The authors argued that their results show that PDs rely on an altered "non-motor" or "a-modal" route to process action language via medial areas such as the cingulate as opposed to through the "normal" frontoparietal network. This claim is further supported by the finding that the degree of M1 posterior connectivity was correlated with BG atrophy.

Summary

Overall, neuroimaging studies tentatively suggest that PDs differently rely on prominent semantic networks to HCs when processing action semantics. On the other hand, there remain many questions concerning sensorimotor accounts and PD. First, the studies to date have contrasted action verbs and nouns, as a proxy for "action" vs "non-action" concepts (i.e., using grammatical class as maximally diagnostic of action content). However, as explained in the previous chapter, sensorimotor models maintain that *motor experience* associated with a concept (not grammatical class) is what determines action content and therefore nouns which refer to frequently acted upon objects (but not those referring to relatively-more-visually experienced objects) should be represented over motor regions in a similar way to action verbs (Saccuman et al., 2006; Vigliocco et al., 2011). This prediction remains to be tested using neuroimaging in PDs. Secondly, the specifics of "compensatory" non-motor alternate processing routes for action semantics in PDs, like those described above (Abrevaya et al., 2016), remain to be replicated and further explored.

Another possibility is that the occipitotemporal (primarily visual) network will "pick up the slack" when the frontotemporal (primarily motor) network is compromised. Such visuomotor "conceptual compensation" is suggested by eye tracking findings that individuals with aphraxia exhibit not only *impairments* to accessing motor information, but also trends towards *increased sensitivity* to visual aspects of manipulable objects, compared to HCs (Myung et al., 2010). It may be the case that PDs, in a similar fashion, shift *away* from the frontoparietal and *towards* the occipitotemporal networks when processing manipulable object names. A further possibility is that the performance of such "shifts", if they occur, would be mediated by frontal semantic control regions. Such possibilities are ripe for exploration. Finally, the lack of HC groups in the majority of previous studies makes it challenging to draw general conclusions about the long-term implications of motor impairments on processing action language. Therefore, we set out to address these issues.

5.1.2 Questions and predictions

Our primary question is whether, in line with sensorimotor accounts, long-term motor loop dysfunction due to PD results in differences in processing the names of manipulable objects compared to HCs. To our knowledge no studies feature in the literature which have examined the neural correlates of processing the heard names of regularly manipulated (*manual*) vs. regularly seen (*visual*) objects in both PDs *and* HCs using fMRI connectivity analysis methods. Given this, we decided to carry out whole-brain FC analyses from independently functionally localised seeds in the frontoparietal and occipitotemporal semantic networks: specifically, our functionally localised seeds were located in the SMA (which is related to motor control), and LOC (which is sensitive to viewpoint invariant object identity processing), respectively. We hypothesised that the long-term implications of motor loop impairments due to PD would result in functional reorganisation within these networks when processing *manual* nouns compared to HCs.

Primarily, we predict, that when processing the names of *manual* objects, HCs compared to PDs will exhibit increased coactivation of motor areas in the frontoparietal "action" network, suggesting motor-semantics disruptions due to PD. Crucially this effect should differ for *visual* object names, i.e., we do not expect differences for *visual* object names with respect to coactivation in motor regions. Second, given that Abrevaya et al. (2016) observed increased functional connectivity for action verbs beween M1 and a posteriomedial region, we predict that PDs compared to HCs will show similar increased coactivation between frontoparietal motor nodes and more posteromedial (non-motor) regions for *manual* names, suggesting the development of non-motor processing routes for action semantics.

A further, more speculative possibility is that non-motor aspects of the representations of *manual* objects such as their visual properties (which are more reliant on the occipitotemporal network), will become relatively more important for PDs compared to HCs, i.e., PDs will exhibit some *conceptual compensation* in order to process manual objects via "non-action" routes. Therefore, our third (exploratory) prediction is increased "compensatory" coupling between key nodes within the occipitotemporal network in PDs for *manual* nouns. Because such functional reorganisation might be mediated by semantic control areas in the IFG reflecting changes in the control of semantic selection following representational reorganisation in PDs, our fourth (exploratory) prediction is divergent coactivation between HCs and PDs of frontal semantic control areas (e.g., IFG) and the occipitotemporal and frontoparietal seeds.

5.2 Methods

5.2.1 Participants

PDs were recruited from the Movement Disorders unit of the Hospital Universitario Donostia. HCs were recruited from the BCBL participant pool and remunerated for their time. The final study sample consisted of 34 participants: 15 non-demented PDs and 19 HCs. All participants were right handed native Spanish speakers with normal or corrected-to-normal vision. Groups were matched in age, gender, years of education, verbal intelligence quotient and cognitive status (see Table 7 for further information).

Exclusion criteria for both groups included: dementia, prior cerebral surgery and impulse control disorders. PDs were diagnosed according to the UK Parkinson's Disease Society

Brain Bank criteria by HUD neurologists as being at stage 1-to-3 on the Hoehn & Yahr scale (i.e., mild-to-moderate) and had been diagnosed between 2-to-14 years before testing. PDs were idiopathic and in chronic DRT treatment (i.e., two or more years of Levodopa and/or dopaminergic agonists). None had brain stimulation treatment. Testing occurred in the ON stage of anti-parkinsonian medication (i.e., DRT) because this study was conducted at the same time as another study which required participants to be under the effects of treatment.

	PD group (n = 15)	HC group (n = 19)	*p* values
Gender (% male)	86.7	84.2	.8
Age (years)	61.4 (8.3)	63.1 (9.4)	.6
Education (years)	12.7 (5.5)	15.1 (5.5)	.2
IQ (WAIS-III) (ss)	13.2 (2.4)	14.4 (2.1)	.12
MoCA (ss)	25.9 (2.5)	26.5 (1.9)	.4

Table 7. PD fMRI experiment group balancing. Participant demographics and cognitive screening. Standard deviations in parentheses. SS = standard scores. All p's are from two sample t-tests except for gender which is from a chi-squared proportion test.

Patient	Age	Sex	PD duration	Side	Init.Man	UPDRS-I	UPDRS-II	UPDRS-III	UPDRS-IV	H&Y	PDQ-8	MOCA	WAIS-III	LEDD TOTAL	LEDD DA	LEDD LDOPA
P1	65	M	5	L	R	2	10	30	2	2	4	21	10	880	480	400
P2	62	M	4	L	R	4	6	10	0	1	4	25	14	400	300	0
P3	49	M	2.5	L	R	6	3	12	2	1	4	30	14	750	0	750
P4	75	M	5	L	T	6	0	13	0	1	3	29	16	400	0	300
P6	66	M	10	R	T	11	16	19	3	1.5	8	24	14	1664	300	1064
P7	55	M	13	R	R	6	7	12	2	2	8	25	15	1032	300	732
P8	68	M	2	R	R	4	9	19	0	1.5	9	23	12	700	300	300
P9	52	F	6	L	R	4	10	18	0	1.5	3	25	12	620	320	300
P10	60	M	7	R	R	11	10	16	0	1.5	3	27	15	792	160	532
P11	61	M	4	R	R	3	9	12	1	2	4	28	15	840	240	600
P12	60	M	4	R	T	4	7	14	0	2	6	27	11	600	300	300
P13	64	M	8	R	R	11	16	25	8	2.5	11	29	15	1607.5	360	1147.5
P14	64	F	14	L	T	6	7	17	4	2	4	23	8	1164	0	1064
P16	74	M	10	L	R	7	10	29	2	2.5	2	26	16	1404	240	1064
P18	46	M	8	R	T	1	4	18	0	2	0	27	11	250	0	150

Table 8. PD fMRI experiment PD clinical information. PD's clinical information. ss= standard scores. Yrs = years. Duration = time since diagnosis. Laterality = side (i.e., left or right) first affected. Init.maifestation = initial manifestation (i.e., Rigidity or Tremor).

5.2.2 Ethics statement

The study was approved by the Gipuzkoa Clinical Research Ethics Committee and written informed consent in compliance with the BCBL ethics committee and the Helsinki declaration was obtained from all the subjects prior to participation.

5.2.3 Clinical and Neuropsychiatric assessment

Before taking part in the study, all participants underwent assessment for clinically relevant dementia, psychosis, impulsivity, addictions, aphasia, language disorders and depression. Cognitive status was assessed using the Montreal Cognitive Assessment (MoCA) (Nasreddine et al., 2005) and verbal IQ using the WAIS-III vocabulary tool. For PDs, all assessments were performed under the effect of the first dose of habitual anti-parkinson's (i.e., DRT) medication in the morning. The following measures were collected on PDs: Parts I to IV of the Unified Parkinson's Disease rating scale (UPDRS) (Goetz et al., 2008), the Hoehn and Yahr staging scale (Hoehn & Yahr, 1967), the Parkinson's Disease Questionnaire (PDQ-8) (Jenkinson et al., 1997). Table 8 provides detailed demographic and clinical information. It includes individuals' total levodopa equivalent dose ($\mathrm{LEDD}_{\mathrm{TOTAL}}$), daily levadopa dose ($\mathrm{LEDD}_{\mathrm{LDOPA}}$) and daily levodopa equivalent dose of dopamine agonist ($\mathrm{LED}_{\mathrm{DA}}$) (Tomlinson et al., 2010) which provide a converted and standardised measure of anti-Parkinson's medication allowing for comparisons between people on different regimes.

5.2.4 fMRI paradigms

The stimulation protocol consisted of three tasks: manual localiser, visual localiser and main functional word processing task:

Manual Localiser

We used a finger tapping functional localiser for motor regions. Specifically, areas of the brain related with fine movement of the fingers (Drobyshevsky, Baumann, & Schneider, 2006). The localiser conformed to a blocked design and included eight 12s activation blocks with eight 16s rest-fixation periods between them to allow the hemodynamic response function to return to baseline. During activation blocks participants were instructed to sequentially touch the fingertips of one hand to the tip of their thumb starting from their index finger and progressing to their pinkie finger and back to their index finger at a self-paced comfortable rate. The hand to use (i.e., right or left) and for how long was indicated to participants with arrows on the screen. For the purpose of the study we were interested in the contrast *right & left > rest-fixation* to localise manual motor cortex in the frontoparietal network.

Visual Localiser

We used a functional localiser for the visual cortex (Hindy, Solomon, Altmann, & Thompson-Schill, 2015). Subjects were presented with 1) five 18s activation blocks presenting 18 objects on a white background and 2) five 18s activation blocks of scrambled images of the same objects. Scrambled images were generated by separating the images into a 60*60 grid and randomly permuting the sections (except for a weighting to preserve centre coherence). The localiser conformed to a block design and included the presentation of an 18s rest-fixation period between each of the 10 activation blocks to allow the hemodynamic response to return to baseline. Within each activation block, each of the images were presented on the screen for 490ms, followed by a 490ms ISI. During the activation blocks, the participants had to detect item repetitions (i.e., 1-back) and press a button when an item was repeated. Only 2% of the items were repeated along the entire functional localiser. For the purpose of the study we were interested in the contrast *objects > scrambled* to localise late visual cortex areas related to whole object processing in the occipitotemporal network.

Main functional word processing task

Stimuli selection

In a previous normative study, we collected online ratings of manual experience for the names of the stimuli objects. Sixty paid participants rated a preliminary list of words (to prevent fatigue, each participant rated only half the N words) according to the following question: “Do you have more experience looking at this or touching it with your hands?” 1 = relatively more experience looking, to 7 = relatively more experience touching. This process resulted in 28 or 29 ratings for each word.

Based on this normative study, 40 object names were selected as referring to relatively-less-manually-experienced (*visual*) objects (e.g., *“windmill”*) and 40 to relatively-more-manually-experienced (*manual*) objects (e.g., *“pencil”).* Using the SOS stimuli optimisation tool (Armstrong et al., 2012) stimuli were distributed so that, within each condition: the amount of relative manual experience associated with the objects varied uniformly, but that between conditions, it differed maximally, while remaining balanced for log-frequency, word duration, and number of syllables. See Table 15 in the appendix for a full list of word stimuli and Table 9 for balancing comparisons.

	visual	manual	*p* values
Rating	2.54 (0.69)	5.48 (0.54)	.00
Log frequency	0.74 (0.54)	0.92 (0.53)	.16
Duration (seconds)	0.91 (0.17)	0.87 (0.17)	.36
Syllables	3.08 (0.76)	2.88 (0.88)	.28

Table 9. PD fMRI experiment stimuli balancing, by condition. Standard deviation in parentheses. All ps are from two sample t-tests.

For catch trials, sixty well-known brand names (e.g., *"Ford"*) were chosen as being widely representative of different types of companies and products and extremely recognisable to participants. To ensure this, a separate group of twenty healthy participants were recruited and asked to identify the brands. They correctly recognised the brands 88.75% of the time (SD=8.67). All the words were recorded by a female native Spanish speaker with a local accent. Recordings were equalised in sampling rate and amplitude-modulation and trimmed so that word onset was at the beginning of each file. Eleven pseudo-randomised counterbalance lists of stimuli presentation order were created and randomly assigned to participants. Participants heard each word once over the course of the experiment.

Task

The main functional word processing go/no-go task conformed to a fast-event-related-design wherein participants heard single words and were instructed to press a button when they heard a brand name. Importantly, the brand name identification task was orthogonal to our experimental manipulation: experience of manipulating objects. So as to maximise our efficiency of estimating participants' blood-oxygen-level-dependent (BOLD) responses, the order of presentation of experimental conditions (i.e., *visual* object words, *manual* object words or brand name catch trials) and the inter-trial intervals (jitter fixation) for each functional run were determined by using the Optseq-II algorithm (Dale, 1999). See Figure 14. The task lasted approximately 16 minutes. Interspersed among the 80 *visual* and *manual* items of interest and the 60 brands there were 160 words included as part of a separate study that is not part of this thesis.

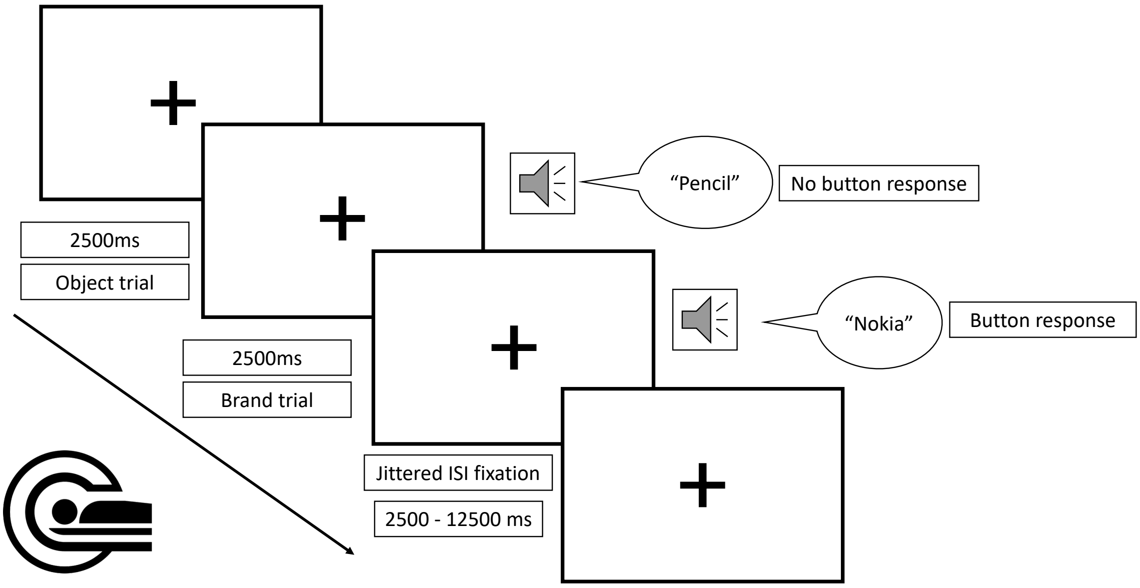

Figure 14. PD fMRI experiment structure. Main functional word task run schematic

5.2.5 MRI data acquisition procedure

Scanning was conducted in the morning when PDs´ cognitive functions have been shown to be optimal (Bruguerolle & Simon, 2002) and PDs were under the effects of their usual DRT medication. Before entering the scanner, participants were familiarised with the two localisers and the main functional word processing tasks. In scanner, due to variability in hearing ability in some participants and scanner noise, we ensured participants were able to clearly hear and repeat back a practise word list before experimental scanning began. Data were obtained at the Basque Center on Cognition, Brain and Language (BCBL) 3T Siemens Magnetom TIM Trio MRI scanner (Siemens Medical Solutions, Erlangen, Germany) using a 32-channel array head coil. Visual stimuli were presented using Presentation software (Version 18.0, Neurobehavioral Systems, Inc., Berkeley, CA, www.neurobs.com) by way of a head-coil-mounted mirror and a rear-projection video display (Panasonic SXGA+ 7000). Auditory stimuli presentation involved S14 insert earphones (Sensimetrics) in ear, MRI compatible, pneumatic, noise cancelling headphones. Responses were collected using 4-button optical response pads (Current Designs). Additional snugly-fitting headphones (MR Confon, Magdeburg, Germany) were used to dampen background scanner noise and to enable communication with experimenters. To limit head movement, the area between participants’ heads and the coil was padded with foam and participants were asked to remain as still as possible. Radio frequency (RF) pulses were time locked to the start of each functional run using a synchronisation box (NordicNeuroLab SyncBox).

Imaging Parameters

High-resolution structural T1-weighted images were acquired with a MPRAGE sequence with TR = 2530ms, TE = 2.97ms, inversion time = 1100ms, FA = 7°, FoV = 256x256mm, 176 slices and voxel size = 1mm^3. Functional echo-planar images (EPI) for the word task were acquired in two separate runs using a gradient-echo echo-planar pulse sequence with the following acquisition parameters: TR = 2500ms, time echo (TE) = 28ms, 41 contiguous 3mm^3 axial slices, 10% inter-slice gap, flip angle (FA) = 90°, field of view (FoV) = 192 x 192mm. In total 225 volumes were collected per functional run but to allow for T1-equilibration effect, four volumes were discarded from the start and four from the end of the run. For the localisers the same EPI sequence was used except for a TR of 3000ms. For the visual localiser 128 volumes were collected and for the manual localiser 83 volumes were collected. Four volumes were removed from the start and four from the end of those runs respectively.

Imaging Pre-processing

Standard pre-processing routines and analyses were carried out using statistical parametric mapping (SPM8) software (Wellcome Department of Cognitive Neurology, London). Images were corrected for differences in timing of slice acquisition and were re-aligned to the first volume by means of rigid-body transformation. Then, functional images were spatially smoothed using a 4-mm full width at half-maximum (FWHM) isotropic Gaussian kernel. Next, motion parameters obtained from realignment were used to inform a volume repair procedure (ArtRepair; Stanford Psychiatric Neuroimaging Laboratory) that identified bad volumes on the basis of within-scan movement (i.e., scan-to-scan motion exceeding 0.5mm) and signal fluctuations (i.e., variation in global intensity exceeding 1.3%), and then corrected bad signal values via linear interpolation between the nearest non-outliers time points (Mazaika, Hoeft, Glover, & Reiss, 2009). We ensured that not more than 20% of the total volumes were corrected/interpolated in any participant. Three subjects, not included in the sample described in the participants section above (2 HCs & 1 PDs), were excluded due to excessive motion/signal fluctuation i.e., having either more than 20% to-be-repaired functional volumes or drifts over 3mm in any of the functional runs. After volume repair, structural and functional volumes were co-registered and spatially normalized to T1 and echo-planar imaging templates, respectively. The normalization algorithm used a 12-parameter affine transformation together with a non-linear transformation involving cosine basis functions. During normalization, the volumes were sampled to 3-mm^3 voxels. Templates were based on the MNI305 stereotaxic space (Cocosco, Kollokian, Kwan, Pike, & Evans, 1997). Then, functional volumes were spatially smoothed with a 7-mm FWHM isotropic Gaussian kernel. Finally, a 128 sec high-pass filter was used to eliminate contamination from slow drift of signals. Brain coordinates are reported in Montreal Neurological Institute (MNI) atlas space (Cocosco et al., 1997).

fMRI Statistical Analysis

Statistical analyses were performed on individual participants' data using the general linear model (GLM). The fMRI time series data were modelled by a series of impulses convolved with a canonical haemodynamic response function (HRF). Motion parameters for translation (i.e., x, y, z) and rotation (i.e., yaw, pitch, roll) were used as covariates of non-interest in the GLM. Trials were modelled as events, time-locked to the onset of each word. The functions resulting from *visual* object and *manual* object conditions were used as covariates in a GLM designed to examine neural changes restricted to the two task conditions and rest-fixation periods in whole-brain contrasts and functional connectivity analyses.

The least-squares parameter estimates of the effect for each study condition were used in whole-brain pairwise contrasts whereby contrast images, computed on a participant-by-participant basis were submitted to group analysis. At the group level, whole-brain contrasts between conditions were computed by performing one-sample *t*-tests on these images, treating participants as a random effect. The standard statistical threshold for whole-brain maps involving all participants and contrasting experimental conditions (i.e., *visual*/*manual* object words > *rest-fixation* in the main word processing task, *right & left* > *rest-fixation* in the manual localiser and *objects* > *scrambled* in the visual localiser) was a voxel-wise corrected false discovery rate (FDR) set at $q < .01$. See Figure 15 for a visualisation of the whole-brain contrasts.

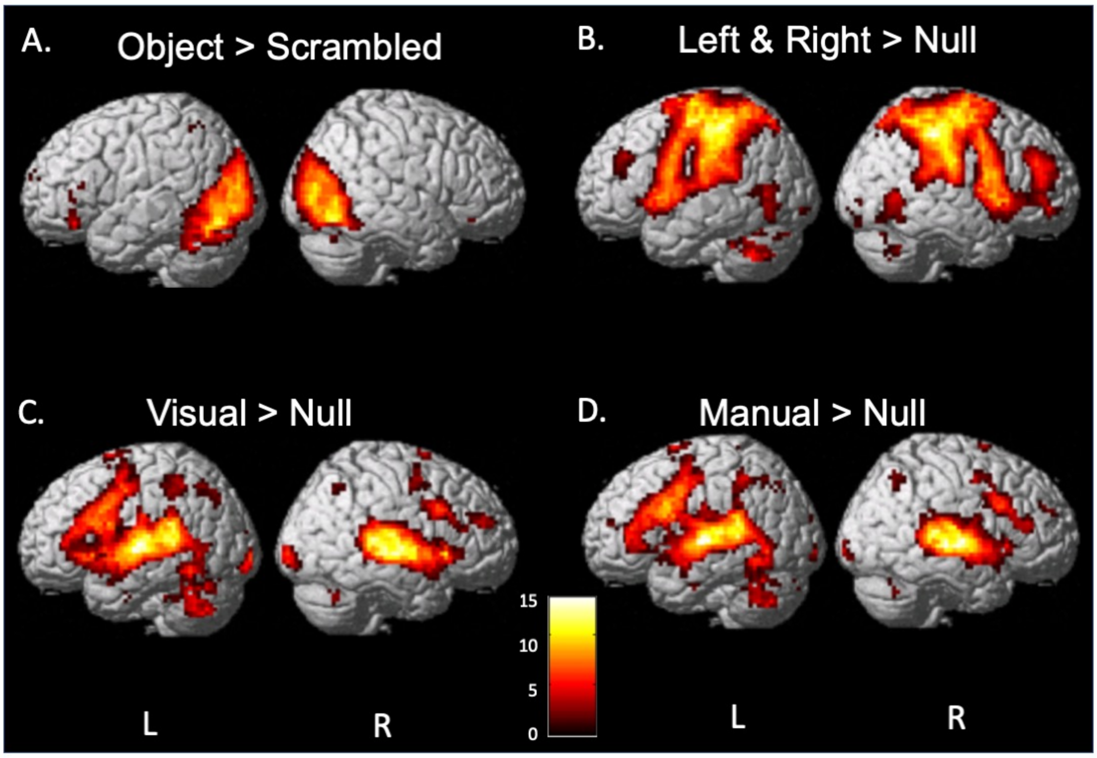

Figure 15. PD fMRI experiment whole-brain contrasts. Brain renderings showing activation in whole- brain contrasts across all subjects at a statistical threshold of q < .01 FDR voxel-wise corrected for multiple comparisons. A) Visual localiser. B) Manual localiser. C) Main functional word-processing task– Visual objects. D) Main functional word-processing task – Manual objects.

Data from the two functional localisers were analysed in order to independently functionally determine seeds in the frontoparietal and occipitotemporal networks for use in connectivity analyses. Seed region of interest (ROI) creation was achieved with the MARSBAR toolbox for use with SPM8 (Brett, Anton, Valabregue, & Poline, 2002) and resulted in 5mm-radius spheres centred at the global maxima of active voxels identified from whole-brain contrasts across all participants at a threshold of $q < .01$, FDR corrected voxel-wise. The *right & left > rest-fixation* contrast of data from the manual localiser resulted in a global maximum in SMA [-3, -4, 55]. *objects > scrambled* contrast of the visual localiser yielded a global maximum in LOC [-45, -76, -14]. See Figure 17 for visualisations of seed ROIs.

We assessed FC via the beta correlation method (Rissman, Gazzaley, & D'Esposito, 2004) implemented in SPM8 with custom Matlab scripts. The canonical HRF in SPM was fit to each occurrence of each condition and the resulting parameter estimates (i.e., beta values) were sorted according to the study conditions to produce condition-specific beta series for each voxel. In these analyses the beta series associated with each functionally localised seed were correlated with voxels across the whole brain to create beta correlation images for each subject. Group-level two-sample t-tests were performed on the resulting subject *manual* object-words > *rest-fixation* or *visual* object-words > *rest-fixation* contrast images for the SMA and LOC seeds respectively for the comparisons HC > PD (q < .01, cluster-wise-FDR corrected). Since the correlation coefficient is inherently restricted to range from −1 to +1, an arc-hyperbolic tangent transform was applied to these beta-series correlation values (*r*-values) to make its null hypothesis sampling distribution approach that of the normal distribution to allow for statistical inference based on the correlation magnitudes.

5.3 Results

5.3.1 Main functional word processing task – Behavioural

Accuracy was high on the main functional word processing go/no-go brand name recognition task (HC accuracy M = 85%, SD = 14%, PD M = 78%, SD = 25%) indicating that participants were concentrating on the words they were hearing. Accuracy did not differ between the groups: two-tailed-two-sample-$t(32)=1.07$, $p>.29$, 95% CI[- 6.5, 21.1].

5.3.2 Test for gray-matter structural differences between groups

To examine potential between-group differences in gray matter at the structural level that could determine functional differences, we used participants' T1-weighted images to run Freesurfer's (Fischl, 2012) mri_glmfit on gray-matter volume, cortical thickness and surface area. These analyses revealed no significant between-group differences.

5.3.3 Univariate whole-brain analysis

In order to test for differences in functional activation that might contribute to functional connectivity differences, we conducted a series of whole-brain functional contrasts (see Figure 2). For PDs and HCs separately, we contrasted: *manual* > *rest-fixation, visual* > *rest-fixation* and *manual* >/< *visual*. No differences were observed which survived statistical thresholding using appropriate multiple comparison corrections. Similarly, second level comparisons (i.e., the interactions) showed no significant differences between PD-*visual* > *rest-fixation* vs HC-*visual* > *rest-fixation* or PD-*manual* > *rest-fixation* vs HC-*manual* > *rest-fixation*. These analyses suggest that potential differences in functional connectivity may not be determined by differential regional engagement between conditions, nor between groups.

5.3.4 Functional connectivity

In order to check the overall patterns of functional connectivity for each group when processing object names which contribute to the group comparisons reported below, we visualised whole-brain FC from the functionally defined seeds (LOC & SMA) for all words combined: i.e., *visual & manual > rest-fixation* in PDs and HCs separately (see Figure 16). The results visualised are those that survived cluster-wise FWE correction for multiple comparisons ($p < .01$). While overall patterns of connectivity are in line with expectations, in general, PDs show less FC than HCs in all conditions, which is probably due to more variability within the PD sample. This may have some bearing on the interpretation of the main findings reported below and will be further considered in the general discussion.

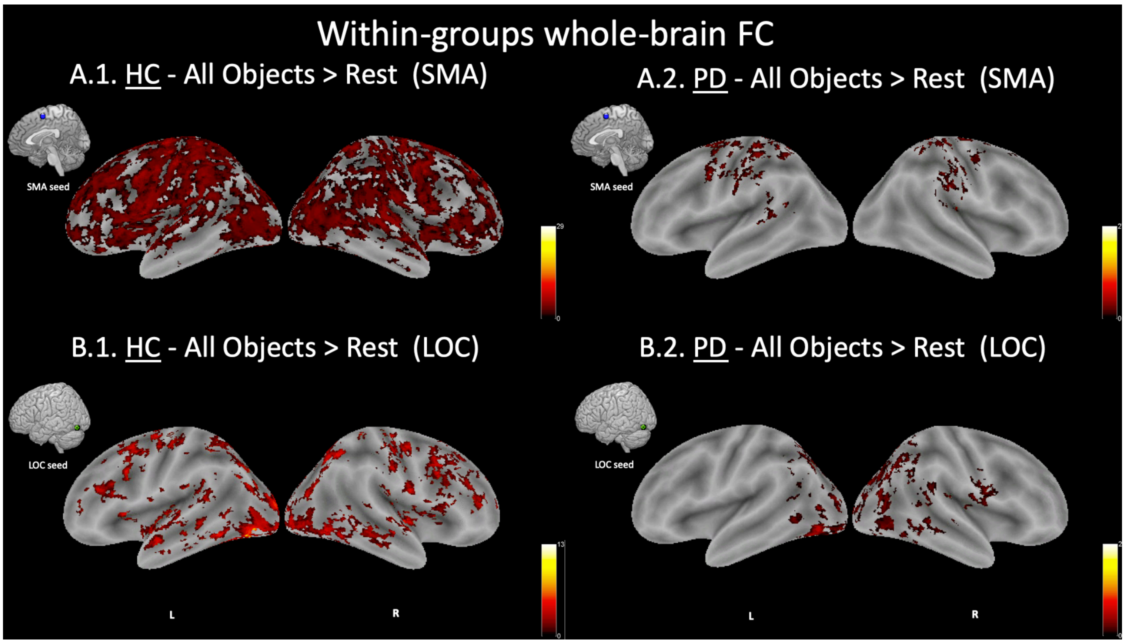

Figure 16. PD fMRI experiment overall whole-brain FC. Whole-brain FC from functionally defined seeds for all-objects (i.e., manual & visual > rest-fixation) (p < .01, FWE cluster-wise corrected for multiple comparisons). Panel A: the frontoparietal (SMA) seed for 1) HCs, 2) PDs. Panel B: the occipitotemporal (LOC) seed for 1) HCs, 2) PDs.

In order to test our main hypotheses, we examined *dissimilarities* between PDs and HCs in functional coupling between the manually localised seed in the frontoparietal network (SMA) and the visually localised seed in the occipitotemporal network (LOC) and all other voxels in the brain, for *manual* object-words > *rest-fixation* and *visual* object-words

> *rest-fixation* conditions respectively. The results reported here are those that survived cluster-wise FWE correction for multiple comparisons ($p < .01$). See Figure 17 for a visualisation of these results and Table 10 for cluster information.

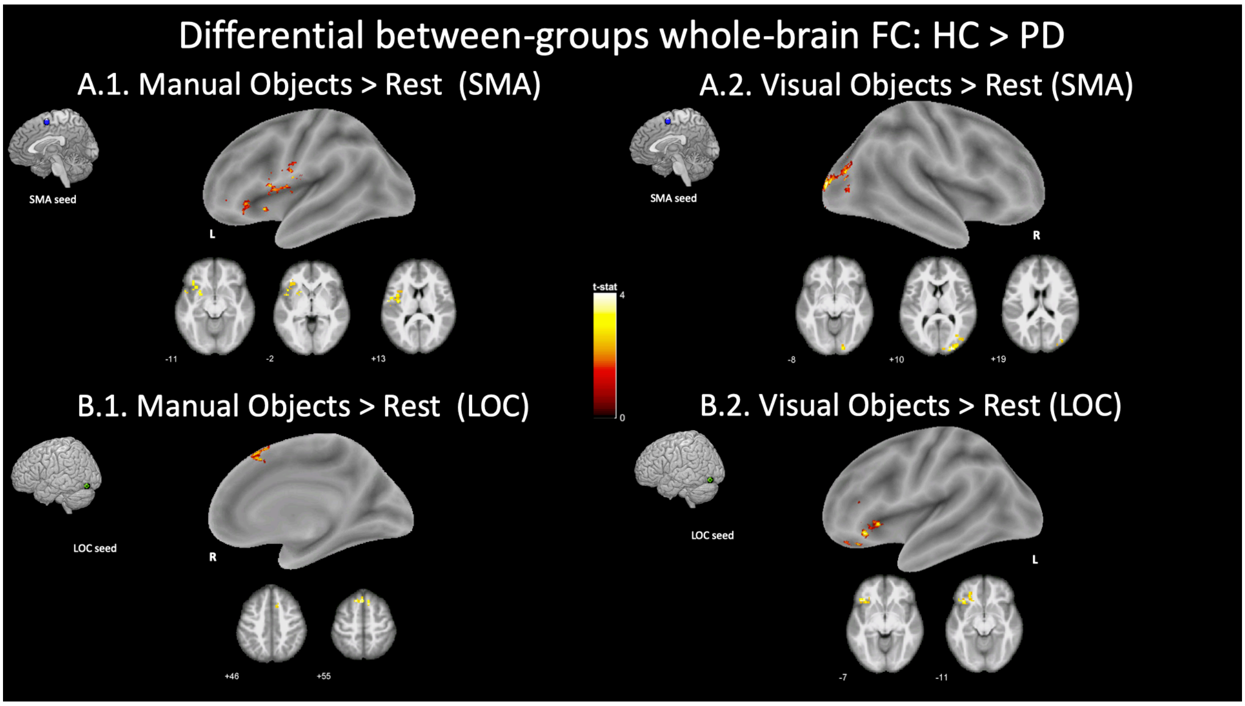

Figure 17. PD fMRI experiment whole-brain FC contrasts. FC differences between PDs and HCs. Colours indicate clusters where connectivity with a seed was significantly higher (p < .01, FWE cluster-wise corrected at for multiple comparisons) for HCs than PDs. Panel A: the frontoparietal (SMA) seed when processing 1) manual object-names 2) visual object-names. Panel B: the occipitotemporal (LOC) seed for 1) manual-object names 2) visual-object names.

Condition	Network seed	Brain areas	Cluster extent	Voxels	*t* value	Coordinates		
						x	y	z
Manual objects	Frontoparietal seed (SMA)	L IFG Triangularis	89	27	3.9	-39	35	-2
		L IFG Orbitalis		15	3.2	-39	29	-11
		L Insula		16	3.6	-27	11	-14
		L Temporal Pole		5	3.2	-48	17	-17
		L Putamen		9	2.8	-24	11	-5
		L IFG Opercularis	74	15	4.1	-39	5	10
		L Rolandic Operculum		23	3.9	-60	-7	13
		L Precentral gyrus		25	2.5	-54	-4	19
		L Postcentral gyrus		18	3.0	-51	-13	19
		L Temporal pole		8	3.0	-54	11	-11
	Occipitotemporal seed (LOC)	R SMA	80	28	3.92	12	20	46
		L medial SFG		33	3.7	-6	26	55
Visual objects	Frontoparietal seed (SMA)	R Cuneus	116	10	4.24	24	-97	10
		R Middle Occipital gyrus		61	3.6	39	-82	19
		R Lingual		9	3.4	15	-97	-8
	Occipitotemporal seed (LOC)	L IFG Orbitalis	89	45	4.22	-39	26	-11
		L Insula		20	2.7	-30	26	-7

Table 10. PD fMRI experiment whole-brain FC cluster information. HC > PD. p < .01, FWE-cluster wise.

We first describe results from analyses using the frontoparietal network seed (SMA) established from the manual functional localiser: With respect to processing nouns referring to *manual* objects, in HCs, as our primary hypothesis predicts, there was higher functional coactivation compared to PDs between the seed in the frontoparietal network and two closely distributed clusters: one in ventral motor areas (*t*=4.05, voxels=74, maxima=[-39, 5, 10]) and another in frontal semantic control regions / basal ganglia (*t*=3.86, voxels= 89, maxima=[-39, 35, -2]) (see: Figure 17, panel A.1). With respect to processing nouns referring to *visual* objects, in HCs, as expected, there was no appreciable increase compared to PDs in functional coactivation between the frontoparietal SMA seed and other motor areas. However, there was an unexpected increase in functional coupling in one cluster in right posterior visual regions (*t*=4.24, voxels=116, [24, -97, 10]) (see Figure 17, panel A.2.). Crucially, the fact that *manual* object names result in changes in motor region connectivity but *visual* object names do not, is consistent with sensorimotor theories. We will elaborate on this point in the discussion

We now turn to results from the analyses using the occipitotemporal network seed (LOC) established from the visual functional localiser: Contrary to our predictions, for HCs, relative to PDs, processing *manual* object words involved more functional coupling between the (LOC) seed in the occipitotemporal network and a cluster in dorsomedial motor areas (SMA and SFG) (*t*=3.9, voxels=80, [12, 20, 46]) (see Figure 17, panel B.1). This result suggests that visual and motor information about *manual* objects may be more tightly coupled for HCs than PDs. This finding runs counter to our exploratory hypothesis that there would be increased (compensatory) functional coactivation of occipitotemporal regions in PDs when processing *manual* object words. With respect to *visual* object words, HCs show higher connectivity between the (LOC) seed in the occipitotemporal network and one cluster in frontal semantic control regions (LIFG orbitalis) (t=4.22, voxels=89, [-39, 26, -11]) (see Figure 17, panel B.2.) indicating that for HCs there is relatively more functional connectivity from areas in the occipitotemporal network and semantic control regions when processing *visual*-object names.

5.4 Discussion

Sensorimotor accounts predict that changes in the availability of sensory or motor brain areas to language processing should lead to interrupted access to semantic information which is putatively represented in those areas. Furthermore, if such areas are less well integrated to semantic processing over extended periods of time (i.e., months or years) then it is likely that changes in the routine exploitation of their neural real estate, in service of semantics, should occur in a process called “representational shift” or “conceptual compensation” (Gallese, 2009). For example, prolonged degradation in motor system function (such as that arising from PD) should result in the motor components of *manual* object representations being down-regulated when they are accessed, and may be accompanied with compensatory up-regulation of non-motor areas. Therefore, in this study we evaluated the neural underpinnings of semantic processing in PDs and HCs by comparing FC in key semantic networks while they were processing the names of frequently-manipulated (*manual*) and infrequently-manipulated (*visual*) objects. Overall, our findings provide support for sensorimotor accounts in that motor brain regions are involved in processing the names of manipulable objects, a novel finding. However, we observe no evidence of experienced-based conceptual compensation in PDs for processing action semantics via non-motor/amodal routes.

In line with our first prediction, we observed significant FC differences between PDs and HCs in the way that they coactivate key semantic networks in the brain when processing *manual* nouns. Of particular interest is the finding that HCs coactivate a node in the frontoparietal network and ventral motor regions more than PDs for *manual* objects. This suggests that the frontoparietal (action) network is involved in processing the names of manipulable objects. Further, the fact that PDs and HCs did *not* exhibit coactivation differences in this network for *visual* objects suggests that its coactivation is semantically driven, i.e., attributable to differences in the *manual experience* associated with different categories of objects.

However, contrary to our second prediction we did not observe higher FC for PDs than HCs between the frontoparietal seed and posteromedial regions, meaning that we did not replicate one suggested compensatory “amodal” processing route for action language (Abrevaya et al., 2016).

With regards to our third (exploratory) prediction, we did not observe increased FC within the occipitotemporal network for PDs than HCs when processing *manual* nouns, which might have suggested another route for conceptual compensation; i.e., increased reliance on visual aspects of objects’ representations instead of motor aspects, via the occipitotemporal stream.

We observed mixed evidence of our fourth (exploratory) prediction; i.e., variations in FC between frontal semantic control regions (IFG) and the frontoparietal and occipitotemporal networks which interact with group and word type. We observed higher SMA-IFG FC for HCs when processing *manual* but not *visual* object names which may suggest that the importance of the motor system for processing action language has been “downgraded” in PDs relative to HCs and that this is IFG controlled. On the other hand, we did not observe stronger LOC-IFG FC for PDs for *manual* object names, which might have been suggestive of PDs “upgrading” the importance of the occipitotemporal stream to process them. Finally, for *visual* object names, we did not observe FC differences between HCs and PDs between SMA-IFG. This could be interpreted in line with the view that with respect to *visual* items, PDs and HCs should not differ in their reliance on the frontoparietal (action) network. On the other hand, we did see tighter FC for HCs than PDs between LOC-IFG suggesting that differences may exist.

Similar to previous FC work with PDs (Abrevaya et al., 2016) we observe relatively greater frontoparietal connectivity in HCs (compared to PDs) between our SMA seed and IFG and motor areas for action language but no differences (in either group) in connectivity in the occipitotemporal network. However, in contrast we did not see any compensatory PD > HC FC differences in the cingulate for action language.

Overall, FC within the networks involved when processing *manual* and *visual* object names differed between HCs and PDs, with action language involving less coactivation of motor regions in PDs than HCs. Because the atypical coactivation of regions in the frontoparietal network in PDs is particular to *manual* as opposed to *visual* objects it seems to be semantically driven, and best attributed to differences in the *manual experience* associated with *manual* and *visual* objects i.e., the semantic content of their representations, in line with sensorimotor accounts.

Considerations and limitations

Given that the analyses pursued here were specifically intended to examine potential differences in coactivation between the different groups, it might be asked if the differences in PDs we observe arise as a result of structural damage to their brains or an overall inability to co-activate relevant brain regions. While we presume that there are structural differences between the brains of the PDs and the HCs that we tested, several factors lead us to believe that these differences are unlikely to be the sole cause of the functional connectivity differences that we observed. First, although it is certainly possible that baseline differences in co-activation in general influence our results, our finding that when processing *manual*, but not *visual* object words, PDs showed less coactivation with other portions of the motor network, suggests that semantic processing interacts with any such limit on co-activation and mitigates these concerns. Further, our grey matter comparisons show that there are no structural alterations in grey matter in PDs vs. HCs, therefore, it is not the case that the affected regions are structurally affected, but that the areas in the networks are differently coactivated during processing. Finally, we did observe lower whole-brain FC when processing nouns in PDs compared to HCs, which is likely due to more variation in FC.

Another consideration concerning this study (as outlined in the previous chapter) is that our participants were all in ON state of DRT at time of testing and therefore were not experiencing motor system dysfunction. We tested patients ON DRT for two reasons: first, this is common practice when measuring PDs in MRI scanners, because it helps to reduce head motion artefacts, and second it was not practically possible for us to manipulate their medication regime because they were participating in further studies at the same time which *required* DRT. Although being in the ON state of DRT could certainly have influenced our ability to detect differences in FC, we believed that our tests might still reveal differences arising from long-term, experience-based alterations in the functional dynamics of network recruitment during semantic processing.

Second, from a sensorimotor perspective, it is likely that in populations for whom medical intervention can restore function to relevant sensory or motor areas, (such as PD with DRT therapy), a gradual shift away from reliance on motor areas when processing manual objects is more likely than catastrophic semantic deficits. With this in mind, it is unsurprising (and in line with previous work: Péran et al., 2013; Péran et al., 2009) that activation analyses with appropriate statistical thresholding did not reveal differences between PD and HC groups in processing *manual* words.[10] That connectivity analysis *did*, suggests it may be a more sensitive method of measuring long-term experience-driven representational-shift. Furthermore, because this situation creates a more challenging scenario to test sensorimotor theories, the fact that we do see selective recruitment of different circuits in spite of what might be partially "normalised" motor loop function makes our findings all the more intriguing.

Another consideration concerns study design. Due to time limitations we were obliged to keep the task short and therefore we tested using relatively few trials. Future studies should seek to increase statistical power by including more items. Similarly, while on the one hand our smaller sample reflects the fact that we were limited in the number of PDs we had access to, on the other hand our sample is comparable to published research in the field.

It should be noted that the analytical strategy adopted in this experiment was largely determined by the conservative nature of our mixed effects. The strongest test of our hypothesis would be to test the interactions of group and object category; however, for power reasons our data do not permit reliable inferences to be drawn based on these contrasts. Nonetheless, the differences we observe in whole-brain FC are both theoretically interesting and statistically reliable.

Conclusions

In conclusion, in this chapter we provide neuroimaging evidence that differences in people's motor capacities shape the brain networks they activate when processing frequently handled objects. While we did not observe impairments to processing the names of manipulable objects at the behavioural level (see Chapter 4:) we observe divergence at the neural level. The findings reported here support sensorimotor accounts of conceptual representation and suggest that an individual's lifetime experience (i.e., their context) shapes their understanding of the objects that they have experience of.

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[10] While our primary interest was FC it is interesting to compare our activation results to previous studies. As in our results, the Perán study (2009) did not observe differences between action naming and object naming with appropriate statistical thresholding. However, in exploratory analyses ($p < .001$ uncorrected) they observed higher activation in PDs for Verbs > Objects in PFC and ACC, which they refer to as a "non-motor". Similarly, we also observe uncorrected differences in activation for PDs *manual* > *visual* in the SFG (bilaterally) and left ACC. No differences were observed in HCs.

Chapter 6: General Discussion

6.1 Introduction

The overarching goal of the current thesis was to extend our knowledge about the nature of long-term conceptual representations of concrete objects in semantic memory. These representations not only underlie the meaning of noun words but also include and "ground" perceptual and action related knowledge about their referents. In a break from current orthodoxy, the work reported here sought to provide evidence that concepts are best considered as both grounded in sensorimotor systems and contextually sensitive. There were three main experimental objectives in this thesis: First, to test predictions of sensorimotor accounts of sematic processing – specifically that functionally important parts of the conceptual representations of concrete objects are represented over widely distributed modality specific regions of the brain, active during perceptual or motor experience with them. Second, to examine whether, as a result of this, semantic and online sensorimotor processing are mutually interdependent and functionally interact. Finally, to interpret my findings in the light of an as-yet relatively understudied prediction of sensorimotor accounts: namely that the content of multimodal semantic representations varies as a result of context; here defined as both immediate context and personal context i.e., an individual's personal history of experiences with objects over their lifetime. These predictions are incompatible with amodal accounts which maintain that the representational format of concepts and semantic processing is amodal, functionally distinct from sensory and motor processing, and that the core contents of conceptual representations are reliably reproduced units of meaning that are infrangible and contextually inert. To this end we ran four experiments, using behavioural-psycholinguistic and neuroimaging techniques in healthy and clinical populations. Below I present a brief overview of relevant findings.

6.2 Part 1 summary – Visual and olfactory modalities

The first experimental chapter in this thesis demonstrated that occupying the visual system by engaging in a visual task and concurrently making semantic judgements on object names resulted in mutual interference to both processes. Crucially, interference to both tasks was relatively greater for words referring to objects with which particular individuals had accrued more lifetime visual experience than those more frequently manipulated. The second experimental chapter extended our visual findings into the olfactory modality. We demonstrated that if the olfactory system is occupied with a strong odour while participants make semantic judgements on the names of objects, then it interferes more with understanding the names of frequently smelled objects like “garlic” than more neutral words like “hammer”. Furthermore, we observed that interference scales in proportion to the amount of lifetime olfactory experience people have with the objects. Both chapters show that online perceptual processing can be influenced by language comprehension, that lifetime sensory experience shapes the representational structure of object concepts, and that the outcome of semantic processing differs depending on an interaction of personal experience and people’s immediate perceptual context.

6.3 Part 2 summary – Parkinson’s and the manual modality

The second half of the thesis shifted to testing sensorimotor predictions in the manual domain. Experimental chapter three reports a behavioural experiment in which we tested whether motor system degradation due to Parkinson’s disease lead to impairments in naming manipulable objects compared to healthy controls. Contrary to our predications, we found no behavioural evidence of semantic-motor impairments. However, because the PDs were under the effects of their anti-parkinsonian medication (i.e., their motor loop function had been restored) at time of testing, this null result is difficult to interpret. It may be the case that PD does not lead to impairments in processing concepts for manipulable objects, but it may also be the case that treatment status interacts with any such impairments. If so, it is worth noting that this would be in line with the thrust of this thesis, namely that context is key in understanding concepts, in this case, treatment context might lead to variations in conceptual content. With this in mind, in experimental chapter 4 we report an fMRI experiment designed to explore if, at the neural level, motor impairments due to PD interact with the networks involved in semantically processing the names of manipulable objects. In line with our predictions we observed semantically-influenced connectivity differences between HCs and PDs when processing the names of manipulable-objects specifically. In particular, we observed relatively decreased functional connectivity for manipulable object names for PDs in brain networks associated with acting on objects. This pattern of results is suggestive of subtle variations in the processing of manipulable objects due to a motor disorder, in line with sensorimotor predictions. The fact that we do not observe effects in the behavioural study but see differences in the fMRI study might be for a number of reasons. First, fMRI measures can be more sensitive than accuracy or reaction-time measures to subtle differences in the processes underlying task performance and the functional connectivity methods we employ are able to capture theoretically relevant long-term differences in processing strategies. Secondly, because participants had motor-loop-function restored (as a result of DRT) in both experiments it is likely that motor components of manipulable objects were not impaired at time-of-testing, however, Parkinson's is a chronic illness which involves frequent periods of motor system impairments (e.g., between doses). Over time it is likely that such impairments lead to gradual shifts in reliance on the motor system when accessing representations. That our findings are observed in functional-connectivity measures, and we didn't observe differences in activation analyses supports this view. Further research is needed to explore these issues more fully.

6.3.1 Holistic summary

The results of my experiments, viewed as a whole, lend support to sensorimotor accounts of conceptual representation. First, the fact that tasks that modulate activity within visual and olfactory brain areas can selectively interfere with accessing object representations that are putatively reliant on those same areas, suggests that these processes share neural resources. Second, such functional interplay between semantic and sensory/perception processes strongly suggests that semantic knowledge has a variegated and multimodal representational format and not a unitary amodal code. Third, that individual lifetime olfactory and visual experience predicts the degree of interference shows that individual context has a meaningful impact on a concept's representation. Finally, while on the one hand, we did not observe behavioural differences in the way PDs access the representations of manipulable objects, this may be due to their treatment context. On the other hand, the neuroimaging evidence we report suggests that changes in people's motor capacities *does* lead to measurable alterations in the way that they process action semantics.

6.4 Theoretical implications

Overall, our findings suggest that functionally relevant aspects of semantic representations are not "amodal" in nature. Rather, following cognitive linguistics (Lakoff, 1987), they support sensorimotor accounts which provide a biologically plausible description of semantics with no clear distinction between action, perception and semantic processing, in which language is brain-based and semantic memory is not a separate module of cognition from perception and action.

Our results in the visual and olfactory modalities complement previous neuroimaging evidence showing that content-specific sensory and motor areas are engaged when processing the names of concrete objects (e.g., Alex Martin, 2007) and behavioural studies demonstrating measurable interactions between perceptual contexts and semantic processes (e.g., Yee, Chrysikou, Hoffman, et al., 2013). That individual experience modulates semantic-perceptual interference (as shown in our visual and olfactory experiments) also aligns with studies showing that personal experience shapes conceptual representations both as a result of expertise (e.g., I Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999), as a result of training (Bellebaum et al., 2013) and over the lifetime (Chrysikou et al., 2017). The fMRI results in PDs we report similarly suggest that long-term impairments in people's sensory or motor capacities shape how people process object names. While we did not observe behavioural evidence that having PD affects semantic processing of action related objects, this might have been because of DRT status and could be interpreted as evidence of contextual variation in conceptual processing. Overall, our results are in line with more recent accounts of "fluid" concepts which deny that conceptual representations are bounded and reliably reproduced units of meaning, but rather a context-dependent process. Considering conceptual knowledge in this way hints that the content of an elicited conceptual representation at a particular moment in time differs from the content of a similarly elicited representation at another moment, that content depends on the dynamical interplay of what else the brain is busy doing at the same time as accessing a representation and the nature and amount of people's long-term sensory or motor experience with a concept's referent (e.g., D Casasanto & Lupyan, 2015; Connell & Lynott, 2014; Spivey, 2008; Yee, 2017).

6.5 Strengths

The work reported in this thesis is novel and noteworthy in a number of ways. First, our results were obtained from three sensory domains; i.e., visual, manual and (the largely neglected) olfactory domain. That we observe similar patterns across different modalities, using novel paradigms, strengthens our conclusions considerably. Second, our finding that dual-task interference in the olfactory and visual domains scaled with individual lifetime experience is of particular note. Many studies testing similar hypotheses make use of experience ratings averaged over participants, or obtained from ratings studies or corpora. In contrast, we show our effects at the individual level. Third, our dual task interference methodologies are non-correlational demonstrations of a functional relationship between sensory and semantic processing and therefore free from the criticism, often levelled at neuroimaging evidence, that activation in sensory or motor areas is unrelated to semantic processing, i.e., downstream, epiphenomenal or spreading activation. Forth, the neuroimaging evidence we do report in experimental chapter 4 improves on previous work because it includes a HC group and therefore is informative about differences in semantic processing due to PD. It also employs functional connectivity methods which may provide a more informative window into questions of conceptual compensation and shift due to long-term changes in people's capacities than activation approaches. Finally, a great deal of work into sensorimotor hypotheses concentrates on studying verbs as canonical examples of "action" semantics, but here, we examined an underexplored prediction of sensorimotor theories, - everyday concrete objects with which people have varying experience in many domains.

6.6 Limitations

Of course, there are a number of limitations to the evidence reported here which are worth consideration. First, in the visual and olfactory modalities we do not show that the selective perceptual-semantic interference we observe (to frequently-seen or frequently-touched stimuli respectively) disappears for the *same stimuli* in a *different context,* such as an interference task or ambient context designed to tax or occupy a modality which is *not* though to underlie their representations (e.g., an auditory task), but appears for other items which *are* reliant on the newly taxed modality for their representation (e.g., musical instruments). Showing such a double-dissociation would allow us to make the strongest claim about a functional relationship between the visual and olfactory modality and frequently seen or smelled objects respectively (and in the above example, the auditory modality), we do not see its absence as critically problematic for our conclusions for a couple of reasons. First, in the case of the visual chapter, the experiment itself can be considered as following on from a previous experiment (Yee, Chrysikou, Hoffman, et al., 2013) which successfully showed that a manual task selectively interfered with processing the names of frequently-manipulated objects. Furthermore, follow up work recently published by our group (Davis et al., n.d.) reports a double dissociation between visual and manual modalities. In the case of olfactory interference, we are running another study incorporating a control interference task. However, while we can't rule out that a non-olfactory interfering context would have caused a similar selective relative interference effect only to smelly objects, our findings are, in our view, most parsimoniously explained as supporting sensorimotor predictions.

Another concern might be the small effects that we observe. On the one hand, while they are of the same order as previous research, it must be acknowledged that participants were not rendered unable to conceive of, for example; *"the moon"* while performing our visual task, nor incapable of identifying, e.g., a lemon while in a smelly room. As suggested throughout the thesis, this is not too damning a criticism when the redundancy of sensorimotor representations is considered; all of the concrete objects that we used as stimuli are commonly experienced multimodally; i.e., smelt, touched, heard and tasted, so their representations should extend over a variety of sensory or motor modalities. If one source of representational knowledge is interrupted, it should still be possible to activate enough of a representation to perform the task. In fact, our recent publication (Davis et al., n.d.) was conceptually similar to the visual experiments reported here, but included primarily things with which we have virtually no visual experience e.g. "thunder", and report similar results to those reported here. Given that we used less "extreme" stimuli it might be argued that this reduced the likelihood that we would have observed an effect and that we did is noteworthy.

6.7 Future directions

There are a number of promising avenues for future study which arise out of the work reported here. For example, the boundary conditions of the contextual effects that we observe should be carefully explored and demarcated which could be achieved by parametrically manipulating the difficulty or nature of the interference tasks/contexts and observing any resultant changes. Second, it would be interesting to explore whether different types of experience affect the representations people have of objects. For example, if perceptual simulations, which arise as a result of reading descriptions of objects or mental rehearsal, are comparable to direct perceptual experience or whether the representations arising from such "experience by proxy" is differently reliant on sensorimotor areas or less susceptible to interference than that which was perceptually gained (e.g., Edmiston & Lupyan, 2017; cf: Günther, Dudschig, & Kaup, 2018). Finally, a question that the implications of context-sensitive sensorimotor models raise is that of interpersonal agreement. If the conceptual representations of objects reflect everybody's personal experience, how might such agreement be possible? It is likely that to the extent that experiences are the same, which they often are, we can communicate well enough (if not perfectly), and to the extent that they differ, we may have communication difficulties. Such possibilities are ripe for further exploration.

6.8 Final conclusions

Taken together the experiments presented in this thesis provide evidence that the content and format of the conceptual representations of objects is multimodal and grounded in sensory and motor brain systems. They also suggest that people's lifetime sensory and motor experience with objects shapes their representations. Therefore, contrary to amodal accounts, there is functional overlap between sensorimotor and semantic processing, such that sensory, motor and semantic processes mutually interact with context (at many levels) such that each time a noun is processed its representational outcome and content varies dynamically. This suggests that exploring the relationship between concepts and context is both necessary and vital in order to properly understand semantic representations.

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Appendix

Abstract				Concrete			
Spanish	English	Spanish	English	Spanish	English	Spanish	English
abandono	abandonment	infancia	childhood	llave	key	rábano	radish
aceptación	acceptance	infinito	infinite	lápiz	pencil	cincel	chisel
adaptación	adaptation	influencia	influence	bolígrafo	pen	furgoneta	van
admiración	admiration	innovación	innovation	peine	comb	tofu	tofu
afición	hobby	instinto	instinct	tenedor	fork	ola	wave
alianza	alliance	intención	intention	cuchara	spoon	ábaco	abacus
alivio	relief	interacción	interaction	tijeras	scissors	ventilador	fan
alma	soul	interés	interest	taza	cup	piano	piano
amargura	bitterness	intimidad	privacy	cuchillo	knife	microscopio	microscope
amor	love	júbilo	joy	pañuelo	handkerchief	rosa	rose
angustia	anguish	lealtad	loyalty	esponja	sponge	hámster	hamster
ansia	craving	lejanía	remoteness	colchón	mattress	caballo	horse
apocalipsis	apocalypse	lentitud	slowness	teléfono	telephone	langosta	lobster
aprobación	approval	libertad	freedom	palomitas	popcorn	trébol	clover
armonía	harmony	limitación	limitation	mesa	table	hacha	axe
atracción	attraction	locura	madness	cremallera	zipper	valla	fence
aura	aura	logro	achievement	auriculares	earphone	pizarra	whiteboard
autonomía	autonomy	maestría	mastery	escoba	broom	cangrejo	crab
blasfemia	blasphemy	maldad	evil	patata	potato	telescopio	telescope
bondad	goodness	mejora	improvement	calculadora	calculator	conejo	rabbit
brutalidad	brutality	melancolía	melancholia	manzana	apple	ratón	mouse
cansancio	fatigue	memoria	memory	bicicleta	bicycle	trofeo	trophy
caos	chaos	miedo	fear	volante	steering-wheel	cordero	lamb
caridad	charity	miseria	misery	cinturón	belt	violín	violin
cariño	fondness	misterio	mystery	grapadora	stapler	dálmata	dalmatian
categoría	category	mitología	mythology	plátano	banana	arbusto	shrub
cautela	caution	molestia	annoyance	huevo	egg	motosierra	chainsaw
certeza	certainty	monotonía	monotony	cazo	ladle	candelabro	chandelier
coherencia	coherence	moralidad	morality	linterna	flashlight	tortuga	turtle
cohesión	cohesion	nobleza	nobility	tiza	chalk	pino	pine-tree
compasión	compassion	noción	notion	zanahoria	carrot	hormiga	ant
complicidad	complicity	nostalgia	nostalgia	puerta	door	burbuja	bubble
comprensión	understanding	obligación	obligation	cacahuete	peanut	trombón	trombone
concepto	concept	obsesión	obsession	batidora	blender	motor	engine
conciencia	awareness	ocio	leisure	cebolla	onion	acordeón	accordion
conexión	connection	optimismo	optimism	destornillador	screwdriver	arpa	harp
confianza	trust	orgullo	pride	aceituna	olive	bala	bullet
consecuencia	consequence	paciencia	patience	cámara	camera	girasol	sunflower
conspiración	conspiracy	paradoja	paradox	mechero	lighter	burro	donkey
continuidad	continuity	parentesco	relationship	sacacorchos	corkscrew	proyector	projector
coraje	courage	pasión	passion	lavabo	sink	bisturí	scalpel
cortesía	courtesy	pasividad	passivity	tomate	tomato	rana	frog
creencia	belief	paz	peace	lechuga	lettuce	trompeta	trumpet
criterio	criterion	pena	pain	cajero	cash-machine	sauce	willow-tree
crueldad	cruelty	penitencia	penance	fresa	strawberry	pistola	gun
culpa	guilt	pensamiento	thought	libro	book	hiedra	ivy
cultura	culture	pérdida	lost	uvas	grape	montaña	mountain
curioso	curiosity	persecución	persecution	limón	lemon	tulipán	tulip
debilidad	weakness	personalidad	personality	pistacho	pistachio	cabra	goat
decadencia	decadence	perspectiva	perspective	cereza	cherry	puente	bridge
dedicación	dedication	pesadilla	nightmare	cerilla	match	cactus	cactus
degradación	degradation	pesar	sorrow	ordenador	computer	bandera	flag
dependencia	dependence	pesimismo	pessimism	pincel	paintbrush	grillo	cricket
depresión	depression	petición	demand	melón	cantaloupe	tuba	tuba
desafío	challenge	piedad	piety	champiñón	mushroom	vaca	cow
desaparición	disappearance	plenitud	fullness	bañera	bathtub	cigarra	cricket
desencanto	disenchantment	preocupación	concern	raqueta	racket	cerebro	brain
deseo	wish	prioridad	priority	portátil	laptop	loro	parrot
desgracia	misfortune	privilegio	privilege	flauta	flute	ardilla	squirrel
devoción	devotion	proposición	proposition	albaricoque	apricot	lagarto	lizard
dicha	saying	prosperidad	prosperity	martillo	hammer	saxofón	saxophone
dificultad	difficulty	prudencia	prudence	espátula	spatula	antena	aerial
dignidad	dignity	realidad	reality	inodoro	toilet	bomba	bomb
discrepancia	discrepancy	recelo	suspicion	maletín	briefcase	pato	duck
diversión	fun	reflexión	reflection	tambor	drum	ganso	goose
eficacia	effectiveness	reglamento	regulation	impresora	printer	calavera	skull
elogio	praise	resurrección	resurrection	frambuesa	raspberry	avión	airplane
emoción	emotion	ritual	ritual	mango	mango	ancla	anchor
énfasis	emphasis	romance	romance	hoja	leaf	mariposa	butterfly
engaño	scam	sabiduría	wisdom	navaja	razor	mono	monkey
enigma	enigma	sacrificio	sacrifice	maiz	corn	serpiente	snake
ente	entity	seguridad	security	lupa	magnifying-glass	cisne	swan
envidia	envy	sentimiento	feeling	pepinillo	pickle	molino	windmill
escasez	shortage	seriedad	seriousness	espárragos	asparagus	mapache	raccoon
escepticismo	skepticism	socialismo	socialism	gatito	kitten	estatua	statue
esfuerzo	effort	soledad	loneliness	rastrillo	rake	paloma	pigeon
estabilidad	stability	sospecha	suspicion	aguacate	avocado	televisión	television
estrategia	strategy	sufrimiento	suffering	fuente	fountain	morsa	walrus
euforia	euphoria	superioridad	superiority	rompecabezas	jigsaw-puzzle	tanque	tank
excelencia	excellence	talento	talent	persianas	blind	dragón	dragon
excepción	exception	tendencia	trend	gato	cat	búho	owl
excitación	excitement	tentación	temptation	estufa	stove	zorro	fox
exilio	exile	ternura	tenderness	buzón	mailbox	tigre	tiger
experiencia	experience	tiranía	tyranny	prismáticos	binoculars	cuervo	crow
explotación	exploitation	tolerancia	tolerance	coco	coconut	dinosaurio	dinosaur
éxtasis	ecstasy	trance	trance	coliflor	cauliflower	ataúd	coffin
fama	fame	tranquilidad	tranquility	calabaza	pumpkin	rinoceronte	rhinoceros
fantasía	fantasy	utopía	utopia	cachorro	puppy	panda	panda
fealdad	ugliness	validez	validity	concha	seashell	semáforo	traffic-light
fidelidad	fidelity	valoración	assessment	guitarra	guitar	satélite	satellite
frustración	frustration	velocidad	speed	trípode	tripod	águila	eagle
gratitud	gratitude	venganza	revenge	clavija	plug	helicóptero	helicopter
habilidad	ability	ventaja	advantage	balancín	seesaw	cebra	zebra
histeria	hysteria	verdad	truth	bate	bat	gorila	gorilla
honradez	honesty	vergüenza	shame	estantería	bookcase	tiburón	shark
humor	humor	vicio	vice	alfombra	carpet	león	lion
idea	idea	victoria	victory	bellota	acorn	nube	cloud
importancia	importance	virtud	virtue	apio	celery	luna	moon
impotencia	impotence	vocación	vocation	árbol	tree		
impresión	impression	voluntad	will	escaleras	stairs		

Table 11. Visual experiment 1 stimuli

Abstract		Concrete					
Spanish	English	Spanish	English	Spanish	English	Spanish	English
abandono	abandonment	bolígrafo	pen	tambor	drum	tortuga	turtle
alivio	relief	llave	key	lupa	magnifying glass	saxofón	saxophone
alma	soul	lápiz	pencil	rastrillo	rake	pino	pine tree
amor	love	tenedor	fork	pepinillo	pickle	antena	aerial
apocalipsis	apocalypse	peine	comb	calabaza	pumpkin	helecho	fern
aura	aura	taza	cup	navaja	razor	roble	oak
cansancio	fatigue	cremallera	zipper	maiz	corn	burro	donkey
caos	chaos	esponja	sponge	perro	dog	grillo	cricket
cariño	fondness	cuchillo	knife	cachorro	puppy	chimenea	chimney
cautela	caution	escoba	broom	aguacate	avocado	bala	bullet
certeza	certainty	cazo	ladle	bate	bat	bomba	bomb
concepto	concept	pañuelo	handkerchief	coliflor	cauliflower	cerebro	brain
coraje	courage	bicicleta	bicycle	clavija	plug	hormiga	ant
criterio	criterion	cuchara	spoon	alfombra	carpet	trombón	trombone
culpa	guilt	manzana	apple	gatito	kitten	trompeta	trumpet
cultura	culture	tijeras	scissors	fuente	fountain	calavera	skull
desafío	challenge	linterna	flashlight	estantería	bookcase	farola	streelight
desdicha	misery	calculadora	calculator	concha	seashell	canario	canary
desencanto	disenchantment	colchón	mattress	microscopio	microscope	avión	airplane
deseo	wish	volante	steering wheel	persianas	blind	pato	duck
dicha	saying	plátano	banana	guitarra	guitar	cactus	cactus
elogio	praise	auriculares	earphone	coco	coconut	ancla	anchor
énfasis	emphasis	cacahuete	peanut	cincel	chisel	rottweiler	rottweiler
engaño	scam	teléfono	telephone	ábaco	abacus	vaca	cow
enigma	enigma	palomitas	popcorn	gato	cat	cerdo	pig
escasez	shortage	patata	potato	hierba	grass	cigarra	cricket
esfuerzo	effort	grapadora	stapler	escaleras	stairs	lagarto	lizard
exilio	exile	aceituna	olive	piano	piano	girasol	sunflower
éxtasis	ecstasy	cinturón	belt	apio	celery	motor	engine
extrañeza	strangeness	cámara	camera	estufa	stove	sauce	willow tree
fama	fame	huevo	egg	rábano	radish	estatua	statue
gratitud	gratitude	puerta	door	hacha	axe	hiedra	ivy
humor	humor	raqueta	racket	trofeo	trophy	ortiga	nettle
idea	idea	sacacorchos	corkscrew	bisturí	scalpel	serpiente	snake
infinito	infinite	cerilla	match	tofu	tofu	tanque	tank
júbilo	joy	pincel	paintbrush	furgoneta	van	cabra	goat
lentitud	slowness	tomate	tomato	cobayo	guineapig	rana	frog
locura	madness	melón	cantaloupe	margarita	daisy	bandera	flag
logro	achievement	mesa	table	bellota	acorn	dinosaurio	dinosaur
mejora	improvement	tiza	chalk	flor	flower	loro	parrot
metafísica	metaphysics	pistacho	pistachio	terrier	terrier	oveja	sheep
miedo	fear	mopa	mop	pizarra	whiteboard	ataúd	coffin
misterio	mystery	cebolla	onion	motosierra	chainsaw	mapache	raccoon
nobleza	nobility	lavabo	sink	rosa	rose	montaña	mountain
ocio	leisure	lechuga	lettuce	violín	violin	paloma	pigeon
orgullo	pride	libro	book	ventilador	fan	televisión	television
parentesco	relationship	fresa	strawberry	telescopio	telescope	zorro	fox
paz	peace	mechero	lighter	candelabro	chandelier	araña	spider
pena	pain	ordenador	computer	hámster	hamster	cucaracha	cockroach
pérdida	lost	uvas	grape	langosta	lobster	mariposa	butterfly
perspectiva	perspective	zanahoria	carrot	arbusto	shrub	búho	owl
plenitud	fullness	destornillador	screwdriver	mariquita	ladybird	ganso	goose
privilegio	privilege	bañera	bathtub	árbol	tree	panda	panda
recelo	suspicion	champiñón	mushroom	caballo	horse	satélite	satellite
reglamento	regulation	limón	lemon	conejo	rabbit	cuervo	crow
ritual	ritual	maletín	briefcase	trébol	clover	molino	windmill
romance	romance	portátil	laptop	valla	fence	morsa	walrus
sacrificio	sacrifice	albaricoque	apricot	cordero	lamb	águila	eagle
sospecha	suspicion	martillo	hammer	pistola	gun	mono	monkey
talento	talent	flauta	flute	acordeón	accordion	ardilla	squirrel
ternura	tenderness	cereza	cherry	cedro	cedar	tiburón	shark
trance	trance	cajero	cash machine	tuba	tuba	helicóptero	helicopter
validez	validity	espárragos	asparagus	narciso	daffodil	semáforo	traffic light
venganza	revenge	espátula	spatula	proyector	projector	cebra	zebra
ventaja	advantage	impresora	printer	puente	bridge	cisne	swan
vergüenza	shame	buzón	mailbox	ratón	mouse	gorila	gorilla
vicio	vice	hoja	leaf	cangrejo	crab	tigre	tiger
virtud	virtue	mango	mango	orquídea	orchid	rinoceronte	rhinoceros
		frambuesa	raspberry	tulipán	tulip	león	lion
		inodoro	toilet	arpa	harp	luna	moon

Table 12. Visual experiment 2 stimuli

Animals				Objects				Adjectives	
Spanish	English	Spanish	English	Spanish	English	Spanish	English	Spanish	English
abeja	bee	hiena	hyena	aguja	needle	fregona	mop	afilado	sharp
aguaviva	jellyfish	hipopótamo	hippo	pulsera	bracelet	condón	condom	peligroso	dangerous
águila	eagle	hormiga	ant	bandera	flag	asfalto	tarmac	frágil	delicate
albatros	albatross	hurón	ferret	flecha	arrow	rotulador	pen	rápido	fast
alce	elk	iguana	iguana	nube	cloud	resina	resin	valioso	valuable
almejas	clam	jabalí	boar	reloj	clock	azalea	azalea	silbido	whistling
anaconda	anaconda	jirafa	giraffe	sol	sun	cerilla	match	ruidoso	noisy
anguila	eel	koala	koala	anillo	ring	pólvora	gunpowder	agrio	sour
araña	spider	lagarto	lizard	trípode	tripod	goma	rubber	robusto	sturdy
ardilla	squirrel	langosta	lobster	estatua	statue	pies	feet	dulce	sweet
armadillo	armadillo	larva	maggot	molino	windmill	fuego	fire	pesado	heavy
armiño	stoat	lémur	lemur	calavera	skull	serrín	sawdust	liso	smooth
asno	ass	león	lion	lupa	magnifying glass	almendra	almond	suave	soft
atún	tuna	leopardo	leopard	enchufe	plug	ginebra	ginger	sólido	solid
avestruz	ostrich	libélula	dragonfly	farola	streetlight	brie	brie	arrugado	wrinkled
avispa	wasp	liebre	hare	linterna	flashlight	sándalo	sandal	radiante	bright
babuino	baboon	lince	lynx	luna	moon	mazapán	marzipan	curvo	curved
bacalao	cod	lirón	mouse	cactus	cactus	establo	cowshed	llano	flat
ballena	whale	llama	llama	hacha	axe	tomillo	thyme	grasiento	greasy
bicho	beetle	lobo	wolf	maletín	briefcase	pachulí	patchouli	redondo	round
bisonte	bison	loro	parrot	pluma	feather	betún	bitumen		
bogavante	lobster	mamut	mammoth	silla	chair	pasto	hay		
buey	ox	manatí	seacow	volante	steering wheel	mojito	mojito		
búfalo	buffalo	mandril	mandrill	ábaco	abacus	espárragos	asparagus		
búho	owl	mangosta	mongoose	botón	button	azahar	orangeblossom		
buitre	vulture	mantis	mantis	buzón	mailbox	plátano	banana		
burro	donkey	mapache	raccoon	croquis	sketch	chicle	chewingGum		
caballo	horse	mariposa	butterfly	mesa	table	lejía	bleach		
cabra	goat	mariquita	ladybird	puente	bridge	cereza	cherry		
cacatúa	cockatoo	marmota	groundhog	satélite	satellite	lima	lime		
cachalote	spermWhale	medusa	jellyfish	silbato	whistle	tomate	tomato		
cachorro	puppy	mofeta	skunk	trofeo	trophy	regaliz	liquorice		
caimán	alligator	mono	monkey	brújula	compass	pera	pear		
calamar	squid	morsa	walrus	cincel	chisel	aguarrás	turpentine		
camaleón	chameleon	mosca	fly	martillo	hammer	laurel	bayleaf		
camello	camel	mosquito	mosquito	rastrillo	rake	churro	donut		
canario	canary	mula	mule	avión	plane	panceta	bacon		
cangrejo	crab	murciélago	bat	campana	bell	huevo	egg		
canguro	kangaroo	musaraña	shrew	flauta	flute	melocotón	peach		
caniche	poodle	nutria	otter	ordenador	computer	coco	coconut		
caracol	snail	ñu	gnu	mando	remoteControl	pintura	painting		
carnero	ram	okapi	okapi	cuello	neck	sobaco	armpit		
castor	beaver	orangután	orangutan	sobre	envelope	salchichón	sausage		
cebra	zebra	orca	orca	tambor	drum	ambientador	airFreshener		
cebú	zebu	oruga	caterpillar	tanque	tank	ananas	pineapple		
cerdo	pig	oso	bear	raqueta	racket	cloaca	sewer		
chacal	jackal	ostra	oyster	cremallera	zipper	frambuesa	raspberry		
chimpancé	chimpanzee	oveja	sheep	pila	battery	esmalte	nail varnish		
chinchilla	chinchilla	pájaro	bird	puerta	door	cuero	leather		
ciempiés	centipede	paloma	pigeon	llave	key	fresa	strawberry		
ciervo	deer	panda	panda	piedra	rock	cilantro	coriander		
cigarra	cicada	pangolín	pangolin	tijeras	scissors	pegamento	glue		
cigüeña	stork	pantera	panther	valla	fence	té	tea		
cisne	swan	papión	baboon	vaso	glass	anís	anise		
cobaya	guineapig	pato	duck	ancla	anchor	colonia	cologne		
cobra	cobra	pavo	turkey	bastón	walkingStick	paella	paella		
cocodrilo	crocodile	pelicano	pelican	cámara	camera	alcanfor	camphor		
codorníz	quail	perdiz	partridge	fagot	bassoon	rosa	rose		
colibrí	hummingbird	perezoso	sloth	burbuja	bubble	barniz	varnish		
comadreja	weasel	perro	dog	cerebro	brain	romero	rosemary		
conejo	rabbit	petirrojo	robin	rodilla	knee	heces	faeces		
cordero	lamb	pingüino	penguin	turbina	turbine	jazmín	jasmine		
cotorra	parrot	piojo	louse	trébol	clover	limón	lemon		
cucaracha	cockroach	piraña	piranha	fuente	fountain	orina	urine		
cuervo	crow	polilla	moth	violín	violin	menta	mint		
dálmata	dalmatian	pollito	chick	globo	balloon	petróleo	petrol		
delfín	dolphin	poni	pony	concha	shell	vino	wine		
dinosaurio	dinosaur	pulpo	octopus	montaña	mountain	mierda	shit		
dodo	dodo	puma	puma	arena	sand	eucalipto	eucalyptus		
dromedario	camel	rana	frog	hoja	leaf	vómito	vomit		
elefante	elephant	rata	rat	bellota	acorn	marihuana	cannabis		
emú	emu	ratón	mouse	helecho	fern	sudor	sweat		
erizo	hedgehog	reno	reindeer	hiedra	ivy	chorizo	chorizo		
escarabajo	beetle	rinoceronte	rhinoceros	sal	salt	vinagre	vinegar		
escorpión	scorpion	rottweiler	rottweiler	roble	oak	basura	rubbish		
faisán	pheasant	ruiseñor	nightingale	girasol	sunflower	caca	poo		
flamenco	flamingo	salamandra	salamander	moneda	coin	lavanda	lavender		
foca	seal	saltamontes	grasshopper	libro	book	canela	cinnamon		
gacela	gazelle	sapo	toad	barro	mud	mango	mango		
gallina	hen	sardina	sardine	berenjena	aubergine	orégano	oregano		
gallo	cockerel	serpiente	snake	ola	wave	amoniaco	ammonia		
gamba	prawn	suricato	meercat	tofu	tofu	vainilla	vanilla		
ganso	goose	tapir	tapir	arbusto	shrub	queso	cheese		
garceta	egret	tejón	badger	vapor	steam	flor	flower		
garrapata	tick	terrier	terrier	árbol	tree	pan	bread		
garza	heron	tiburón	shark	dinero	money	palomitas	popcorn		
gatito	kitten	tigre	tiger	sauce	willow	chocolate	chocolate		
gato	cat	topo	mole	lechuga	lettuce	atún	tuna		
gaviota	seagull	toro	bull	rábano	radish	excremento	excrement		
geco	gecko	tortuga	turtle	narciso	daffodil	mentol	menthol		
gibón	gibbon	tritón	newt	maíz	corn	naranja	orange		
gorila	gorilla	trucha	trout	ternera	beef	jabón	soap		
gorrión	sparrow	tucán	toucan	zanahoria	carrot	pizza	pizza		
grillo	cricket	ualabí	wallaby	margarita	daisy	incienso	incense		
grulla	crane	urraca	magpie	cedro	cedar	ajo	garlic		
guepardo	cheetah	vaca	cow	calabaza	pumpkin	cigarrillo	cigarette		
gusano	worm	víbora	viper	guisante	pea	gas	gas		
halcón	falcon	yegua	mare	leche	milk	café	coffee		
hámster	hamster	zarigüeya	opossum	patata	potato	cebolla	onion		
hipocampo	seahorse	zorro	fox	postre	dessert	perfume	perfume		

Table 13. Olfactory experiment stimuli

Spanish	English	Spanish	English
cepillo_de_dientes	toothbrush	ventilador	fan
cuchilla	knife	piano	piano
tenedor	fork	guitarra	guitar
teléfono	phone	báscula	scales
esponja	sponge	catalejos	binoculars
teclado	keyboard	hacha	axe
llave	key	cincel	chisel
lápiz	pencil	vela	candle
ratón_(ordenador)	computer mouse	motosierra	chainsaw
silla	chair	bellota	acorn
queso	cheese	balancín	see-saw
huevo	egg	ábaco	abacus
bañera	bath	pizarra	blackboard
espumadera	spatula	telescopio	telescope
zanahoria	carrot	cerdo	pig
jarra	pitcher	ajedrez	chess
tomate	tomato	maquina_de_escribir	typewriter
maíz	corn	langosta	lobster
candado	padlock	árbol	tree
monedas	coins	cerebro	brain
fresa	strawberry	flor	flower
martillo	hammer	microscopio	microscope
tijeras	scissors	puente	bridge
mesa	table	roca	rock
botón	button	mariquita	ladybug
pela_patatas	potato peeler	cangrejo	crab
calculadora	calculator	pistola	gun
billete	ticket	bala	bullet
interruptor	switch	girasol	sunflower
cámera	Camera	arpa	harp
móvil	mobile	craneo	skull
lavabo	sink	morsa	walrus
palomitas	popcorn	tanque	tank
melón	cantaloupe	bombilla	light bulb
destornillador	screwdriver	campana	bell
grapadora	stapler	cigarillo	cigarette
patata	potato	avión	airplane
volante	steering wheel	caballo	horse
buzón	mailbox	loro	parrot
plancha	griddle	tren	train
pulverisador	spray	burro	donkey
ordenador	computer	diente_de_Leon	dandelion
sobre	envelope	banjo	banjo
cereza	cherry	ventana	window
pistacho	pistachio	farola	streetlight
nuez	nut	chimenea	chimney
aguacate	avocado	tortuga	tortoise
coco	coconut	satélite	satelite
coche	car	zorro	fox
apio	celery	cisne	swan
pomo	knob	cabra	goat
bicicleta	bicycle	pez	fish
caramelo	candy	dálmata	dalmation
coliflor	cauliflower	trompeta	trumpet
pasa_purés	masher	oveja	sheep
aceituna	olive	vaca	cow
espárragos	asparagus	calendario	calendar
seca manos	hand dryer	cebra	zebra
rastrillo	rake	búho	owl
carro	trolley	dragón	dragon
pincel	paintbrush	lagartija	lizard
abrechapas	bottle opener	fuente	fountain
paraguas	umbrella	ardilla	squirrel
cerilla	match	tractor	tractor
cortacésped	mower	mono	monkey
alfombra	carpet	tiburón	shark
sacacorchos	corkscrew	ataúd	coffin
frigorífico	refrigerator	dinosaurio	dinosaur
linterna	torch	rinoceronte	rhino
impresora	printer	tigre	tiger
llave_inglesa	wrench	castillo	castle
perro	dog	gorila	gorilla
tiza	chalk	ratón_(animal)	rat
calabaza	pumpkin	bandera	flag
champiñón	mushroom	mariposa	butterfly
reloj_(despertador)	alarm clock	alarma_de_incendios	fire alarm
enchufe	plug	panda	panda
rábano	radish	águila	eagle
tirita	band aid	barco	boat
balón	ball	montaña	mountain
dado	dice	retrovisor	rearview mirror
trípode	tripod	estatua	statue
hoja	leaf	semáforo	traffic light
gato	cat	león	lion
mando	remote	pato	duck
molinillo_de_pimiento	pepper grinder	serpiente	snake
concha	shell	helicóptero	helicopter
lupa	magnifying glass	luna	moon
yoyo	yo-yo	abeja	bee
armario	closet		

Table 14. PD behavioural experiment stimuli(picture names).

Object Names				Brands	
Visual Objects		Manual Objects			
Spanish	English	Spanish	English	Name	Product
candelabro	chandelier	bolígrafo	pen	iberia	airline
trofeo	trophy	cuchillo	knife	lufthansa	airline
valla	fence	lápiz	pencil	ryanair	airline
árbol	tree	cuchara	spoon	duracell	batteries
furgoneta	van	teléfono	telephone	visa	bank
arbusto	shrub	peine	comb	BMW	cars
violín	violin	taza	cup	ferrari	cars
antena	aerial	puerta	door	ford	cars
bisturí	scalpel	manzana	apple	mercedes	cars
motor	engine	escoba	broom	mitsubishi	cars
monóculo	monocle	pañuelo	handkerchief	porsche	cars
narciso	daffodil	plátano	banana	renault	cars
trombón	trombone	cámara	camera	seat	cars
saxofón	saxophone	libro	book	bershka	clothes
acordeón	accordion	lechuga	lettuce	cartier	clothes
bomba	bomb	espátula	spatula	levis	clothes
hámster	hamster	cinturón	belt	prada	clothes
tuba	tuba	cebolla	onion	zara	clothes
cobayo	guinea pig	melón	cantaloupe	amazon	computing
televisión	television	maletín	briefcase	microsoft	computing
ancla	anchor	portátil	laptop	colgate	cosmetics
molino	windmill	margarita	daisy	kleenex	cosmetics
avión	airplane	cremallera	zipper	neutrogena	cosmetics
hormiga	ant	maíz	corn	sanex	cosmetics
araña	spider	cacahuete	peanut	tampax	cosmetics
ratón	mouse	pepinillo	pickle	endesa	energy
paloma	pigeon	auriculares	earphone	iberdrola	energy
canario	canary	hierba	grass	bimbo	food
ganso	goose	champiñón	mushroom	colacao	food
rana	frog	rábano	radish	dominos	food
cactus	cactus	estufa	stove	fanta	food
lagarto	lizard	alicates	pliers	heineken	food
montaña	mountain	espárragos	asparagus	kas	food
cuervo	crow	buzón	mailbox	kelloggs	food
paracaídas	parachute	cachorro	puppy	lays	food
satélite	satellite	gatito	kitten	nestle	food
helicóptero	helicopter	navaja	razor	pringles	food
semáforo	stoplight	escaleras	stairs	repsol	fuel
águila	eagle	cajero	cash point	ikea	furniture
león	lion	mechero	lighter	correos	mail
				disney	media
				yamaha	mixed
				movistar	phone
				telefonica	phone
				vodaphone	phone
				gillette	razors
				macdonalds	restaurant
				starbucks	restaurant
				nasa	space travel
				alcampo	supermarket
				Eroski	supermarket
				mercadona	supermarket
				fagor	technology
				honda	technology
				nokia	technology
				panasonic	technology
				samsung	technology
				sony	technology
				toyota	technology
				renfe	train

Table 15. PD fMRI experiment word stimuli