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UNIVERSITY OF
PLYMOUTH

**An Electrophysiological Investigation of
Embodied Language Processing**

by

Isabel Marijana Feven-Parsons

A thesis submitted to the University of Plymouth
in partial fulfilment for the degree of

Doctor of Philosophy

School of Psychology

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Author's Declaration

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award without the prior agreement of the Doctoral College Quality Sub-Committee.

Work submitted for this research degree at the University of Plymouth has not formed part of any other degree either at the University of Plymouth or another establishment.

A programme of advanced study was undertaken. Relevant scientific seminars and conferences were attended, in which work was presented and several papers prepared for publication.

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An Electrophysiological Investigation of Embodied Language Processing

Isabel Marijana Feven-Parsons

How we draw meaning from strings of letters is one of the most popular topics under discussion in cognitive science. Traditional theories posited that words represent amodal symbols and meaning is derived through their relationship to other amodal symbols (Galetzka, 2017). The problem with this cognitivist approach is that it was unclear how these symbols came to have meaning, known as the “grounding problem” (Harnad, 1990; Searle, 1980). Theories of embodied cognition were developed in an attempt to resolve this issue (Barsalou, 1999; Glenberg & Robertson, 1999). For example, the Indexical Hypothesis proposed that nouns are indexed to mental representations (such as mental pictures) of the objects they refer to (Glenberg & Robertson, 1999). Subsequently, when a noun is processed, the affordances (behavioural possibilities) of the referent object are made available (e.g., a mug affords being grasped by its handle). According to the Indexical Hypothesis, access to these affordances is crucial for noun comprehension (Glenberg & Gallese, 2012; Glenberg & Robertson, 1999). More recent theories of language comprehension posit that both amodal and embodied representations contribute to understanding (Barsalou, Santos, Simmons & Wilson, 2008; Louwerse, 2007; 2018; Louwerse & Jeuniaux, 2008). The present thesis discusses experiments using event-related potentials (ERPs), measured while participants read object names, in order to explore the timing of access to information related to these embodied representations of the referent objects. The first experiment revealed that

the earliest information related to object affordance was available from 175 ms, soon after retrieval of lexical and semantic information begins (around 160 ms; Hauk, Coutout, Holden & Chen, 2012). Our second study revealed that functionally manipulable objects have a richer semantic representation, compared to objects that are graspable based purely on their geometric properties. Semantic processing of functionally manipulable objects incorporates knowledge about the actions associated with object use, perceptual information related to the object, and the specific motor programs necessary for manually manipulating the object. Actions associated with the use of functionally manipulable objects were accessed from as early as 190 ms. Affordances based on the geometric properties of an object were available from 224 ms and reflected pattern-matching between semantic information about the object’s size and shape, accessed from processing the object name, with proprioceptive information provided by the participant’s body, about the size and shape of the object they were holding during the experiment. Pulvermüller (1999) argued that sensorimotor representations of language are developed during our personal experiences in the world, through Hebbian learning. The findings of our final experiment supported this argument, indicating that the conceptual representation of objects, and the actions associated with their use, were developed during the participants’ previous experience of using the object.

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1. General Introduction

1.1 Where do words get their meaning?

How we draw meaning from strings of letters is one of the most popular topics under discussion in cognitive science. Traditional cognitive theories of language comprehension posited that conceptual meaning arose from the manipulation of abstract symbols, with the human mind working much like a computer (Galetzka, 2017). This computational processing was thought to occur independently from the perceptual and motor brain systems (Dove, 2016). However, the problem with the cognitivist approach to understanding language is that it was unclear how these symbols came to have meaning, otherwise known as the “grounding problem” (Galetzka, 2017; Harnad, 1990). Searle (1980) illustrated this with his description of a hypothetical situation in which he was given a set of Chinese symbols; he did not have any knowledge of Chinese symbols so to him they were meaningless. He then received two new sets of Chinese characters along with rules for how to correlate these with the first set, and instructions on how to give back specific characters in response. To onlookers, the answers were indistinguishable from a native speaker of Chinese. However, he did not understand any of the symbols he was receiving or responding with; he could only identify them by their shapes. Searle concluded that the manipulation of symbols alone could not bring about understanding; these symbols needed to be grounded in meaning.

To overcome this problem, theories of embodied cognition were introduced. According to theories of language embodiment, the meaning of a sentence or word is derived by reactivating the sensorimotor areas of the brain

associated with the actual items or events being described (Barsalou, 1999; Barsalou et al., 2008; Caligiore & Fischer, 2013; Glenberg & Robertson, 2000; Kaschak et al., 2005; Pecher & Zwaan, 2005). Over the last couple of decades, there has been an accumulation of evidence from behavioural and neuroimaging studies in support for embodied language theories. For example, research shows how reading action sentences primes the motor system for performing those actions, which facilitates the execution of motor responses that are related to the sentence action (Zwaan & Taylor, 2006). Sensibility judgements are made quicker when the action described in the stimulus sentence is congruent with the physical action required to make the response (Borreggine & Kaschak, 2006; Glenberg & Kaschak, 2002; Zwaan & Taylor, 2006). In one study, participants were quicker to judge whether the sentence “turning up the volume” made sense when responding with a clockwise manual rotation, compared to an anti-clockwise rotation; whereas “opening the water bottle” was responded to quicker with an anti-clockwise rotation (Zwaan & Taylor, 2006). Further evidence comes from the finding that action-sentence compatibility effects (ACE; Glenberg & Kaschak, 2002) are specific to the effector used to perform the action. Participants were quicker to respond to the sentence “swallow the pill” when making a verbal response and to “kick the ball” when responding with a foot pedal (Borghi & Scorolli, 2009; Scorolli & Borghi, 2007). This is also backed by electrophysiological and neuroimaging studies showing that reading or hearing action words activates areas of the motor cortex associated with the effector used to execute those actions (Hauk, Shtyrov & Pulvermüller, 2008; Pulvermüller, Härle & Hummel, 2001; Pulvermüller, Lutzenberger & Preissl, 1999; Shtyrov, Hauk & Pulvermüller, 2004). The word “kick”, for example, elicits motor activity associated with the execution of leg movements (Hauk & Pulvermüller, 2004).

A major turning point for theories of embodied cognition was the discovery of mirror neurons (Dove, 2016; Gallese & Cuccio, 2018). Mirror neurons are located in the premotor cortex and are activated both during the execution of a purposeful act and also when observing another individual carrying out that same action (Rizzolatti, 2005). Mirror neurons have been found in Broca's area (a region of the frontal lobe associated with language processing; Fogassi & Ferrari, 2007) and are thought to be responsible for the integration of sensorimotor experience in language processing (Rizzolatti & Arbib, 1998; 2012). This discovery gave rise to the neural exploitation hypothesis (Gallese, 2008), which asserts that social cognition, such as language is grounded via the mechanisms that originally evolved to integrate sensory and motor knowledge. Gallese and Cuccio (2018) provided evidence from patients with Parkinson's disease (PD), a neurodegenerative disorder mainly affecting the motor system. These patients were found to have specific deficits in understanding action words. Gallese and Cuccio (2018) contended that this might be related to a damaged mirror neuron system. Rizzolatti and Umiltà (2013) also found brain cells in the ventral premotor cortex of monkeys, that fire when a motor action is executed and when presented with an object affording that action, e.g., initiating a power-grip action and viewing an object that could be grasped with a power-grip. These are called canonical neurons and have also been found in the human brain (Grèzes, Armony, Rowe & Passingham, 2003). It is thought that canonical neurons may be responsible for the integration of sensorimotor activity when processing the names of objects, just as processing action words is thought to be underpinned by mirror neuron activity (Buccino, Colagè, Gobbi & Bonaccorso, 2016; Carota, Moseley & Pulvermüller, 2012; Gallese & Cuccio, 2018; Marino, Gough, Gallese, Riggio & Buccino, 2013).

Many question the necessity of sensorimotor activity for understanding words (Galetzka, 2017). However, there is evidence to suggest it is a fundamental component of linguistic comprehension. For instance, a double dissociation was found for brain-injured patients' performance during a lexical decision task. Lesions to the right frontal lobe (an area associated with the planning and execution of motor actions) led to severe impairments in recognition of action verbs, and right temporo-occipital lesions resulted in severe difficulty with processing nouns with strong visual associations (Neininger & Pulvermüller, 2003). Similar results have been found in studies using transcranial magnetic stimulation (TMS). TMS is a non-invasive procedure that temporarily disrupts information processing in a particular brain region, by directing a strong magnetic current to the corresponding area of the scalp (Sliwinska, Vitello & Devlin, 2014). When TMS was applied over the motor cortex, participants' identification of action-related words was impaired (Innocenti, De Stefani, Sestito & Gentilucci, 2014; Pulvermüller, Hauk, Nikulin & Ilmoniemi, 2005; Repetto, Colombo, Cipresso & Riva, 2013; Vukovic, Feurra, Shpektor, Myachykov & Shtyrov, 2017). Furthermore, brain lesions in the hand area of the motor cortex affect processing of tool names (Dreyer et al., 2015).

Others have argued that sensorimotor brain activity is merely a by-product of linguistic processing and not necessary for understanding language (Binder & Desai, 2011; Kemmerer, Miller, MacPherson & Tranel, 2013; Mahon, 2015; Mahon & Caramazza, 2005; 2008). One study found that patients with apraxia (a motor disorder caused by brain damage) could still recognise tools, despite being unable to perform the appropriate actions on them (Mahon & Caramazza, 2005). For this reason, Mahon (2015) argues that motor activity cannot be central to conceptual processing and instead reflects spreading activation to sensorimotor areas, after amodal processing of the linguistic unit.

Providing further support for this argument, in a semantic similarity judgement task, patients with PD were slower to differentiate between action and non-action words, but were just as accurate as control subjects (Kemmerer et al., 2013). This suggests that motor activity plays a facilitative role rather than being vital for comprehension. It is thought that semantic impairments such as those seen in semantic dementia, are more strongly associated with damage to the temporal lobes (Jefferies & Lambon Ralph, 2006). When repetitive TMS (rTMS) was applied to the left posterior middle temporal gyrus (lpMTG; gyrus located on the temporal lobe), it resulted in syntactic difficulties with processing action verbs (Papeo et al., 2014). Although there was reduced primary motor cortex activation, the authors argue that amodal representations are processed first, in lpMTG, which then leads to the activation of motor areas.

Dove (2016) discusses several issues that research looking at abstract word processing poses for theories of language embodiment. Abstract concepts refer to thoughts or ideas that have no physical existence and therefore it is argued that they cannot be grounded in direct experience. In accordance with this argument, sensorimotor activity is often found in response to concrete words but not present during abstract word processing (e.g., Dalla Volta, Fabbri-Destro, Gentilucci & Avanzini, 2014). Applying TMS over the motor cortex has even been found to facilitate the processing of abstract words (Vukovic, Feurra, Shpektor, Myachykov & Shtyrov, 2017). Wang, Conder, Blitzer & Shinkareva (2010) conducted a meta-analysis which found that abstract concepts are processed in areas of the brain associated with more amodal conceptual processing, whereas concrete concepts are processed in more perceptual regions of the brain. Studies have shown a processing advantage for concrete words compared to abstract words, due to their higher imageability (Wattenmaker & Shoben, 1987). Furthermore, words referring to objects that a

person can more easily physically interact with (high body-object interaction or BOI) are processed more efficiently than words referring to objects with a low BOI rating (Siakaluk et al., 2008; Wellsby, Siakaluk, Owen & Pexman, 2011).

Again, this supports the idea that grounding words in sensorimotor experience has a facilitative effect on processing. However, given that abstract words do not appear to be linked to sensorimotor processing, this suggests that it is not necessary for all language to be embodied in order to be understood.

Nevertheless, some studies show that processing abstract words (such as “justice” or “opportunity”) involves areas of the brain linked to emotional processing (Dreyer et al., 2015; Kousta, Vigliocco, Vinson, Andrews & Del Campo, 2011; Kousta, Vinson & Vigliocco, 2009; Newcombe, Campbell, Siakaluk & Pexman, 2012). This might indicate that abstract words are grounded in emotional, rather than sensorimotor, experience.

These discoveries have led to the development of alternative theories of comprehension which attempt to explain the role of sensorimotor representations, while taking into account the involvement of amodal linguistic processing (Barsalou, Santos, Simmons & Wilson, 2008; Dove, 2016; Galetzka, 2017; Louwerse, 2011). These include hub-and-spoke theories, convergence zones, distributional hybrid models and dual-code theories.

Hub-and-spoke theories. Hub-and-spoke theories propose that semantic processing takes place in a single amodal hub (located in the anterior temporal lobes; ATL) which integrates modality-specific information from other areas of the brain, such as perceptual, somatosensory or motor knowledge, to form concepts (Chow et al., 2014; Ralph, Sage, Jones & Mayberry, 2010). This idea comes from the finding that damage to the ATL leads to semantic dementia, which is marked by impaired semantic memory for many different concepts (Lambon Ralph & Patterson, 2008). Furthermore, higher level

representations of object features were found to activate ATL in a fMRI study, which the authors suggest reflects neural coding of higher-order representations of concepts (Coutanche & Thompson-Schill, 2014).

Convergence zones. In contrast, Damasio (1989) proposed the existence of convergence zones located adjacent to sensorimotor areas. Research with brain-damaged individuals showed that entities from different semantic categories (people, animals, tools) were processed in partially distinct areas of the brain (Tranel, Damasio & Damasio, 1997). A review by Binder & Desai (2011) found that several areas throughout the temporal and parietal lobe are involved in the convergence of multimodal information. Binder & Desai argue that these brain areas allow for the abstraction of conceptual knowledge away from sensorimotor experience, optimising language processing.

Distributional hybrid models. The Symbol Interdependency Hypothesis (Louwrese, 2007; 2011; 2018; Louwrese & Jeuniaux, 2008; 2010) is a hybrid theory combining distributional network accounts of semantic processing with embodied theories. Comprehension can be achieved through the relationship between amodal linguistic symbols via computational processing (symbolic route) or by a deeper form of processing through symbol grounding (embodied route; Louwrese & Jeuniaux, 2008). Furthermore, Louwrese (2011) proposes that language itself also encodes embodied information. This theory can explain how individuals with PD, or brain damage to sensorimotor areas, are still able to access sensorimotor information from amodal symbols. Research shows how models combining both language-based distributional data with experiential representations can explain the findings from behavioural tasks better than distributional models or embodied theories alone (Andrew, Vigliocco & Vinson, 2009).

Dual code theories. Dual-code theories also take the perspective that linguistic processing involves two routes. Language and situated simulation (LASS) theory proposes that there are two primary systems involved in linguistic processing: a linguistic system and a simulation system (Barsalou, Santos, Simmons & Wilson, 2008). When we read linguistic content, both systems become activated immediately. The linguistic system reaches peak activation quicker due to encoding specificity, that is, the information is received linguistically through whichever form (spoken word, written word, braille) and therefore follows that linguistic processing is activated more rapidly. When the word is recognised, associated linguistic forms are generated through the process of word association. As this is the simplest form of word processing, it is possible for word association tasks (e.g., cat, fur, pet) and many other conceptual tasks to be solved through superficial heuristic strategies, using statistical information related to the word form. During recognition of the word, associated simulations involving information from perceptual and motor areas are also activated; these are the deep semantic representations of concepts. The two systems interact continually through processing linguistic stimuli. Linguistic processing will involve each of these systems to varying extents; sometimes utilising the linguistic system more and other times the simulation system. The simulation system takes effect when necessary, and research shows that simulations can be generated very early during linguistic processing, from 160 ms after word-presentation (Mollo, Pulvermüller & Hauk, 2016).

1.2 Focus of the thesis

The majority of the embodied language literature has focused on the sensorimotor activity involved in processing action words and sentences.

However, it is also thought that processing the name of an object recruits sensorimotor brain activity associated with the referent's form and function, such as its action affordances (Bub & Masson, 2012). Affordances are the behavioural possibilities provided by the environment and are detected automatically by the visual system, regardless of the organism's intention to act (Gibson, 1979). The term "affordance" was first coined by Gibson (1979), to refer to the direct perception of actions that could be performed on an object based on its size, shape, and the materials it is made of. For instance, a mug affords being grasped by its handle (Withagen, de Poel, Araújo & Pepping, 2012). The Indexical Hypothesis proposes that nouns are indexed to mental representations (such as mental pictures) of the objects they refer to (Glenberg & Robertson, 1999). Subsequently, when a noun is processed, the affordances of the referent object are made available. According to the Indexical Hypothesis, accessing the affordances of the referent object is crucial for noun comprehension (Glenberg & Gallese, 2012; Glenberg & Robertson, 1999). A number of behavioural studies support the idea that affordances are retrieved during object name processing (Barbieri, Buonocore, Bernardis, Dalla Volta & Gentilucci, 2007; Bub & Masson, 2012; Bub, Masson & Cree, 2008; Gentilucci & Gangitano, 1998; Glover & Dixon, 2002; Glover, Rosenbaum, Graham & Dixon, 2004; Marino, Gough, Gallese, Riggio & Buccino, 2013; Myung, Blumstein & Sedivy, 2006; Tucker & Ellis, 2004). Participants are quicker to make categorical judgements when responding with a hand-grip that would be used to interact with the referent object (Tucker & Ellis, 2004; Experiment 3). For example, precision grip responses (pinch with finger and thumb) are made quicker when indicating that the word "grape" refers to a natural object, compared to "banana", whereas the opposite effect is found when responses are made using a power-grip (grasping with the whole hand). Furthermore, reading the name of a

manipulable object activates areas of the premotor cortex which are also involved in action word processing (Grabowski, Damasio & Damasio, 1998). It is thought that the linguistically-evoked affordances activate similar neural activity to the execution of the associated actions (Bub, Masson & Cree, 2008; Tucker & Ellis, 2004).

There seems to be little doubt that linguistic representations of actions and affordances can generate motor activity, but it is unclear what, if any, role this activity plays in language comprehension (Chatterjee, 2010; Dove, 2009, 2011, 2016; Mahon & Caramazza, 2008). As aforementioned, Mahon and Caramazza (2008) argue that the sensorimotor activity reflects spreading activation from amodal conceptual representations and is merely an epiphenomenal process, such as mental imagery. For this reason, it is essential to understand when, and by implication what stage of processing, language perception makes use of embodied representations. If they are fundamental to the conceptual representations of objects, we would expect them to be available early on during semantic processing. In the experiments described in this thesis, event-related potentials (ERPs) were used to explore the timing of activation of different types of embodied representations during object name reading. In light of the results of these experiments, this thesis will attempt to address the following five questions.

1.3 When are affordances activated during object name reading?

The first experiment (Chapter 2) examines the timing of affordance activation during object name reading. In this experiment, ERPs were used to investigate the precise timing of affordance priming, compared to semantic priming, in a semantic decision task. To prime affordances we presented pairs of

words referring to objects that afford being picked up using the same hand gesture; i.e., picked up using a power-grip (cucumber-hammer) or grasped with a precision grip (tweezers-grape). For the semantic priming condition, objects were either both manmade (tweezers-drill) or both natural (potato-pea). We hypothesised that, if affordances are an essential aspect of semantic processing of object names, then we should see a priming effect in response times (as is found for semantic priming; Lucas, 2000) and early brain activation related to the affordances in the ERP data. Furthermore, we compared the ERPs for both the affordance priming and semantic priming conditions to see if affordance generation comes before more general semantic category processing, as asserted in Glenberg and Robertson's (1999) Indexical Hypothesis. Early activation of affordances would suggest that they are not the result of a post-lexical epiphenomenon resulting from spreading activation, as Mahon & Caramazza (2008) argue.

1.4 Is the significance of affordance-activation dependent on the amount of manual manipulation associated with the use of an object?

Affordances are thought to be more significant to the conceptual processing of nouns referring to objects that are functionally manipulable, compared to objects that are only graspable based on their geometric features, i.e., shape and size (Bub & Masson, 2006). There are two theories about how affordance-related motor activity differs between these two types of object. One approach is that it is a quantitative difference; objects with a higher BOI rating require more motor activity during object name processing (Siakaluk et al., 2008; Wellsby et al., 2011). An alternative argument is that there is a qualitative difference between the two (Buxbaum and Kalénine, 2010). Regarding visual

objects, Buxbaum and Kalénine discuss two types of affordance, structure-based affordances are affordances related to grasping an object to pick it up depending on its shape and size, whereas function-based affordances are related to the grasp adopted during use of the object. According to Buxbaum and Kalénine, these two different types of affordance are activated in two separate brain systems: function-based and structure-based. If it is a quantitative difference, we would expect both types of affordance to be activated in a similar brain region, with greater amplitude of brain activity related to functional affordances. If it is a qualitative difference pertaining to the significance of the affordance to linguistic processing, we might expect earlier activation of affordances for functional objects (Bub, Masson & Cree, 2008; Bub & Masson, 2012). To investigate these two theories, we used ERPs to explore the specific timing and general location of brain activity related to each of these types of affordance during noun processing (Chapter 3; Experiment 1). In this thesis, we refer to structure-based or geometric affordances as volumetric affordances, and function-based or learnt affordances as functional affordances, in accordance with the terminology used by Bub and Masson (2006).

1.5 Is the significance of affordance-activation dependent on the semantic category an object belongs to?

A second study (Chapter 3; Experiment 2) explored whether affordance activation also differs for objects depending on the semantic category they belong to. Gough et al. (2012) found greater activation of the motor system when reading nouns referring to tools, compared to words referring to natural objects. Manmade items are thought to be more associated with their function, whereas natural items are more associated with their perceptual features (Farah & McClelland, 1991; Ferri, Riggio, Gallese & Costantini, 2011; Gainotti, Spinelli,

Scaricamazza & Marra, 2013). For example, a chisel and a screwdriver can be a similar size, yet have very different functions, whereas a banana and a grape share the same function, to be eaten, but differ in terms of size, shape and colour. In this study, we used ERPs to look at the timing of affordance-activation when reading the names of manmade and natural objects. We were interested to see whether the affordance-related ERP activity for natural objects is similar to that observed for volumetric affordances in Experiment 1. If so, this would suggest that it is not the semantic category that determines whether motor affordance is essential, rather it is the extent to which any object, regardless of whether it is manmade or natural, is associated with a motor affordance. Furthermore, this adds weight to the argument that volumetric and functional affordances are qualitatively different.

In addition to this, we examined whether affordances are activated at an earlier stage of linguistic processing, i.e., at the lexical level. If we find affordance-activation merely from deciding whether a letter string is a word or not, without a focus on the meaning of that word, then it is less likely that they reflect post-semantic spreading activation.

1.6 When are the actions associated with a functionally manipulable object accessed during object name reading?

The first experiment in Chapter 4 investigated when, during object name reading, we access information about the actions associated with the object, and when we access information related to the object itself. In this study, we used denominal verbs, i.e., words that refer both to the name of an object and the associated action (e.g., hammer, drill; Clark & Clark, 1979). To access information about the action related to the object, we correlated the ERP activity measured when reading the object names, with how often those words

are used as verbs in the English language (verb frequency). Similarly, to find out when information about the object is processed, we correlated the ERP activity with how often the word is used as a noun (noun frequency).

Previous research suggests that action words activate the motor cortex somatotopically, during the earliest stage of semantic processing, from as early as 150 ms after stimulus presentation (Mollo, Pulvermüller & Hauk, 2016). Also, Amsel (2011) found function and visual motion features activated from 100 ms during object name reading. Nouns, on the other hand, are processed more often in visual or other perceptual areas of the brain (Pulvermüller, Lutzenberger & Preissl, 1999). Visual features associated with an object were found to be activated from around 300 ms after reading its name (Amsel, 2011). We, therefore, predict that the actions associated with the object will be accessed first during noun processing, followed by information about the object. This would reinforce the idea that motor activity related to functionally manipulable objects is processed during very early semantic processing and is important for understanding functionally manipulable objects.

1.7 When do we activate the motor programs associated with object manipulation during object name reading?

We also used ERPs to find out the precise timing of access to manipulability information related to functionally manipulable objects (Chapter 4). We were interested to see whether the object affordances we saw activated in chapters 2 and 3, associated with these complex manipulations or whether manipulability is processed with the actions related to functionally manipulable objects (seen in the verb frequency ERP covariate). Alternatively, these more complex manual motor programs may be activated later on, post-semantic processing, during mental simulation of object use.

Previous findings suggest that manipulation features are activated from visual object and object names from around 200–300 ms (Madan, Chen & Singhal, 2016; Myung et al. 2006). Bub, Masson & Cree (2008) found a priming effect for functional affordances after being presented with the name of an object for 300 ms. However, these studies looked at manipulation features, rather than a complete manipulation motor program. Therefore these basic manipulation features may be activated before more complex motor simulations. Research has shown that information about the function of an object is activated earlier than details about how to manipulate the object (Collette, Bonnotte, Jacquemont, Kalénine & Bartolo & 2016), positing that manipulability should be activated later than the action related to the functional use of the object (question in section 1.6).

1.8 Is our conceptual representation of an object linked to our experience of using it and seeing another person using the object?

It is thought that sensorimotor representations of language are developed during our personal experiences in the world, via Hebbian learning (Pulvermüller, 1999). Neuroimaging studies looking at mirror neuron activation show that the more experience an individual has of executing particular actions, the greater the motor cortex activation when observing those actions (Calvo-Merino, Glaser, Grèzes, Passingham & Haggard, 2005; Cannon et al., 2014). Mirror neuron mechanisms also appear to be involved during action-related language processing (Beilock, Lyons, Mattarella-Micke, Nusbaum & Small, 2008). Beilock et al. (2008) found that the more experience participants had of executing a particular action, the greater their understanding of sentences describing those actions. Ice hockey players understood sentences describing

actions performed in an ice hockey match better than people who watched ice hockey but had no experience of playing (fans). However, fans showed a superior understanding of the sentences compared to novices, who had no experience of performing or watching those actions. fMRI showed that action-sentence comprehension was related to the level of activation in the premotor cortex; ice hockey players showed greatest premotor cortex activation, followed by observers, and novices showed the least activation of these brain areas.

It is argued that nouns become associated with the perceptual and motor brain activity related to our experience of the referent objects in the real world (Barsalou, 2008; Glenberg & Robertson, 2000). If the grounding of concepts takes place through direct sensorimotor experience, then it should be related to how much experience one has had with those particular objects. The amount of experience someone has had with an object, such as a tie or a pair of tweezers, will differ between individuals. For example, someone who enjoys baking will have had ample experience of using a sieve, compared to others who may have had little, or no, experience. Perceptual areas of the brain are also activated in response to objects for which participants have had substantial experience of using (Hoenig et al., 2011). A fMRI study found that when experienced musicians were presented with images of musical instruments, there was greater activation of auditory association cortex and other areas of the brain that would be active when hearing musical sounds, compared to non-musical laypersons (Hoenig et al., 2011).

In Chapter 4, we correlated the ERPs measured during object name reading with participants' ratings of how frequently they had used the referent objects and how often they had seen others using them. We predicted that the more frequently a participant has used an object, the greater the sensorimotor activity becomes associated with the object concept. We also expect that a

participant's experience of observing another using an object will be associated with the semantic representation of the object's concept. However, based on the findings discussed above, we predicted that direct experience of object use will show greater association with the object concept than observation of use.

2. Electrophysiological Study of Action-Affordance Priming Between Object Names

The work in this section is based on published work (Feven-Parsons, I.M. & Goslin, J., 2018).

2.1 Chapter Abstract

If our central representation of an object is defined through embodied experience, we might expect access to action affordances to be privileged over more abstract concepts. We used event-related potentials to examine the relative time course of access to affordances. Written object names were primed with the name of an object sharing the same affordance as the target (e.g., precision-grip: “grape” primed by “tweezers”) or the same taxonomic category (e.g., fruit: “grape” primed by “apple”). N200 latencies, related to go/nogo semantic category decisions on target words, revealed no difference in facilitation provided by affordance and semantic priming. However, separate analyses of ERPs for go and nogo trials showed that semantic priming led to earlier activation during go trials (~430 ms), and affordance priming led to earlier activation during nogo trials (~180 ms). While affordances appear to be peripheral to the conceptual representation of objects, they do lead to direct motor preparation.

2.2 Introduction

It is important to understand when, and by implication what stage of processing, language perception makes use of embodied representations. If they are fundamental to the conceptual representations of objects it might be expected that they would be available in advance of more abstract information.

This kind of temporal information can be difficult to ascertain with behavioural experiments but is particularly well suited to the ERP technique. Amsel, Urbach and Kutas (2013) used this technique to determine the temporal order of access to abstract and motor-related semantic information when presented with the names of objects. Using a go/nogo task they compared the temporal onset of the N200 component when participants were asked to make a judgment on whether objects were graspable or non-graspable, or whether they were living or non-living. The N200 is a negative going component resulting from the subtraction of go from nogo trials and is thought to provide an indication about when sufficient information has become available to allow a participant to make or withhold their response (Augustin, Defranceschi, Fuchs, Carbon & Hutzler, 2011). Amsel et al. (2013) found that the onset of the N200 related to a living/non-living judgment was at around 160 ms after stimulus presentation, compared to 300 ms for the graspable/non-graspable judgment. The relatively late access to grasp-related affordances prompted the authors to conclude that they did not play a crucial role in the conceptual representation of objects.

Although the results provided by Amsel et al. (2013) seem relatively clear, they are based upon the assumption that the participant has direct access to the information relevant to this explicit decision. However, affordances are generally considered to be processed automatically as a component of object representation that provides implicit facilitation of a wide range of responses (Barbieri et al., 2007; Glover et al., 2004; Marino et al., 2013; Myung et al., 2006; Pulvermüller, Shtyrov & Ilmoniemi, 2005; Tucker & Ellis, 2004). For example, Glover et al. (2004) found that when participants went to grasp a wooden block, the aperture of their grip was larger when they read a word referring to a large object than a small object. Another study found that when participants heard the names of objects they spent longer looking toward

pictures of objects that shared similar manipulation features with the named object than those that did not, with affordance-related looking occurring as early as 300 ms (Myung et al., 2006; Experiment 2). As it has been established that affordance modulates behaviour without the awareness of the participant, it is possible that the earliest access to this property may not be revealed through explicit questioning.

In our study we wanted to capture the implicit effects of affordance in an ERP study similar to that of Amsel et al. (2013). However, instead of comparing the N200 related to different explicit judgment decisions, i.e., those based on semantic and affordance information, we examined how the N200 related to the same semantic decision would be modulated by priming. Semantic priming effects are well established in the literature (Lucas, 2000), with priming found to improve both the accuracy and reaction times in lexical decision tasks (Meyer & Schvaneveldt, 1971). This facilitation is also found when the prime is masked (e.g., Forster & Davis, 1984), that is when presented for a very short duration (50–60 ms), usually sandwiched between two visually obscuring forward and backward masks. This is designed to allow the investigation of the prime-target relationship without the awareness of the participant, so preventing the use of explicit response strategies. Studies using the ERP technique have shown that semantically related prime-target pairs elicit a smaller N400 than semantically unrelated prime-target pairs (Deacon, Hewitt, Yang & Nagata, 2000; Kutas & Federmeier, 2011). This is thought to reflect the greater ease in which the target is integrated into the semantic context provided by the prime (Borovsky, Elman & Kutas, 2012). In most studies the semantic relatedness between prime and target is determined by semantic category norms, such as those of Battig and Montague (1969), which largely shared a taxonomic relationship (e.g., steel and iron being “types of metal”). There are few studies that have examined the

relationship between objects formed by a shared affordance. In one such study by Myung et al. (2006), auditory prime and target words either shared similar manipulation features (e.g., “piano” and “typewriter”) or not (e.g., “piano” and “blanket”). This study showed that shared affordances facilitated reaction times, but did not provide any direct comparison with the facilitation provided by taxonomic semantic priming.

Here we have used the masked priming paradigm to compare the relative differences in priming between written prime-target word pairs that are related either through taxonomy (e.g., “grape” and “banana” are both fruit) or affordance (e.g., “hammer” and “carrot” are both manipulated using a power-grip). Both of these related priming conditions were also compared to a baseline condition, where the prime did not share the same taxonomy or affordance with the target (e.g., mushroom-drill). These word pairs were used in a go/nogo task to evoke an N200 component related to a speeded natural/manmade decision on the target words. An estimate of the temporal onset of affordance and general semantic information was provided through a comparison of the N200 between the three priming conditions. If the sensorimotor activity associated with affordances is fundamental to object representation, then we would hypothesise that the facilitation provided by the priming of affordances should occur earlier than that of semantic priming. Conversely, if affordances are produced as part of a post-lexical mental simulation of object use or accessed via an amodal process of spreading activation we would expect that the temporal onset of this information should occur after semantic processing.

2.3 Method

2.3.1 Participants

Sixty native monolingual English speakers gave informed, written consent to participate in the experiment and were paid £12 for their participation. The data from 9 participants was discarded due to excessive electroencephalography (EEG) and electrooculography (EOG; eye movements) artefacts (less than 66% of recorded trials available for analysis). The remaining 51 participants (32 female) were aged between 18 and 32 ($M = 21.76$). All participants were right-handed (as assessed with the Edinburgh Handedness Inventory; Oldfield, 1971), reported having normal or corrected-to-normal vision and had no history of neurological impairment.

2.3.2 Stimuli

The critical stimuli consisted of 32 different concrete nouns (taken from the CELEX database; Baayan, Piepenbrock & Gulikers, 1995) referring to manually manipulable objects. Sixteen of the nouns were used as prime words (3–10 letters in length) and 16 were used as the target words (3–6 letters in length). Half of the prime words referred to natural objects and half referred to manmade objects. Within each of those categories, half were the names of objects affording a power-grip (e.g., “hammer” or “carrot”) and half were names of objects affording a precision-grip (“scalpel” or “grape”). The target words were a different set of 16 nouns that were also equally divided between these four categories (manmade power-grip; manmade precision-grip; natural power-grip; natural precision-grip).

Each prime word was paired with each target word so that there were 256 prime-target pairs. There were three conditions: (a) semantic (when the prime and target referred to objects that were taxonomically related but did not afford

the same grip e.g., “strawberry-banana” or “potato-pea”); (b) affordance (when the prime and target referred to objects that afforded the same hand grip but were not taxonomically related e.g., “tweezers-lentil” or “orange-axe”); or (c) neutral (when the prime and target referred to objects that were neither semantically related nor afforded the same grip e.g., “fig-hammer” or “scalpel-apple”; see Appendix A for a full list of the stimuli). There were 64 different prime-target pairs in each condition. The remaining prime-target pairs were used as filler stimuli.

2.3.3 Procedure

Participants were presented the stimuli on a cathode ray tube (CRT) monitor (30.5cm height by 40.5cm width; 100Hz refresh rate) positioned at eye level one metre from the participant in a quiet dimly-lit booth. Stimuli were presented using E-Prime 2.0 (Schneider & Zuccoloto, 2007), with responses collected using an E-Prime button box.

The sequence of each trial was as follows. At the beginning of each trial, a fixation point, “ + ”, appeared at the centre of the screen for 600–800 ms. The fixation point was followed by a forward mask (#####) for 100 ms. This was followed by a prime word presented for 40 ms and then a backward mask (#####) for 40 ms. The target was then presented for up to 2000 ms or until the participant responded. At the end of each trial a blink symbol, “ (–) (–) ”, was displayed for 1500 ms, giving the participant the opportunity to blink if necessary (see Figure 1 for example stimuli and an illustration of the experimental sequence). The participants were asked to avoid making eye movements or blinks until the blink symbol was displayed in order to reduce contamination of the EEG data. All text was displayed in the Courier New typeface in black on a white background. Participants responded to the target words using the index finger of their left hand. This was to make the response as

unrelated to the object affordance as possible because the participants were all right-handed and would therefore usually pick up the objects with their right hand. A go/nogo paradigm in two between-participants response conditions was adopted whereby half of the participants were required to respond only to natural stimuli and to withhold responses to manmade stimuli. The other half were required only to respond to manmade stimuli and to withhold a response when they saw natural stimuli. Participants were instructed to indicate as quickly and accurately as possible whether the word referred to the semantic category to which they had been assigned (i.e., natural or manmade).

A sequence of 18 practice trials (using separate stimuli that were not used in the main experiment) was completed by each participant and could be repeated if necessary. After this each of the 256 prime-target word pairs were presented three times in three seamless blocks, resulting in 576 critical trials and 192 filler trials. Trials with slow (> 1200 ms) or incorrect responses were excluded from further analysis (1% of trials). Trials were presented continuously with participants being provided with a rest period after every 90 trials.

2.3.4 EEG recording

BrainVision Recorder (Version 1.10, Brain Products GmbH) was used to collect the scalp voltages from 61 Ag/AgCl active electrodes (actiCAP, Brain Products, Gilching, Germany). The sensors were arranged in the International 10–20 configuration and secured in place on the participant's scalp by an elastic cap. An additional two sensors were positioned below and adjacent to the participant's right eye to monitor eye movements. Segments of EEG data containing eye movement or blink artefacts were not included in later analyses. All scalp electrode impedance measurements were kept below $20k\Omega$. The EEG signals were amplified by a BrainAmp MR Plus amplifier (Brain Products).

	Neutral	Affordance	Semantic
Prime	spanner	tweezers	strawberry
Target	lentil	pea	apple

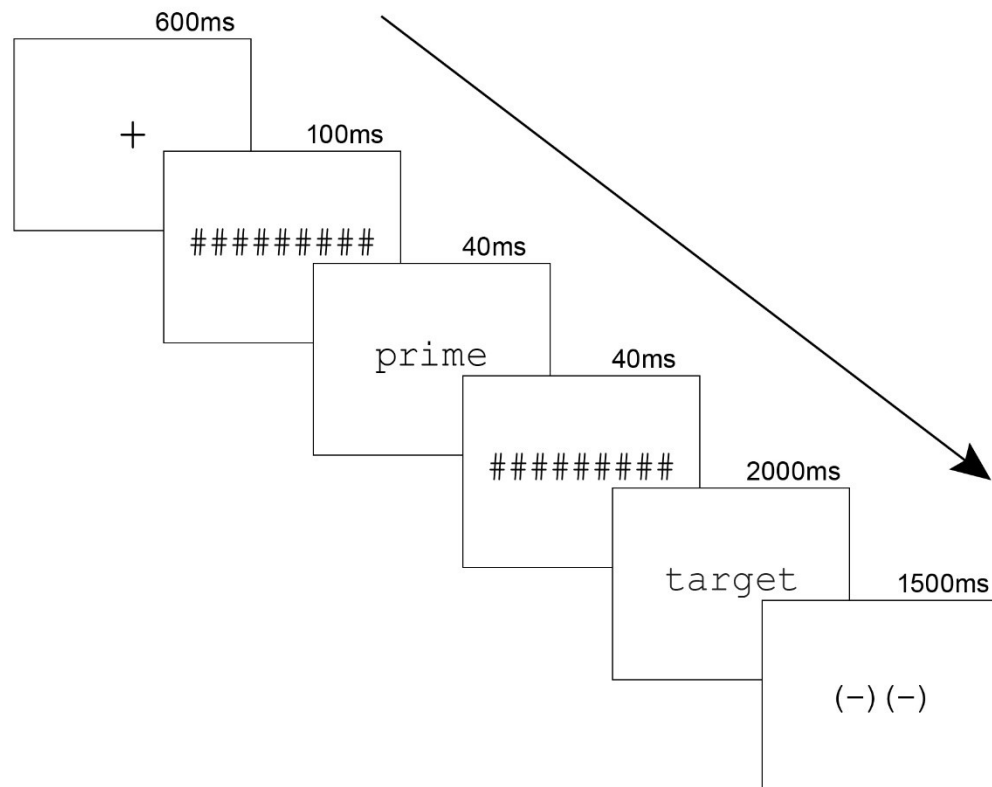


Figure 1. Example of stimuli presented in the experiment (a) and an illustration of the experimental sequence (b).

2.3.5 EEG analyses

Vision Analyser (Version 2.0, Brain Products GmbH) was used to process the data. EEG was sampled at a rate of 250Hz and filtered offline with a band-pass filter of 0.1–40Hz (with a roll-off slope of 12 dB/oct) and subjected to a 50Hz notch filter. The EEG recordings were segmented into 1000 ms epochs, spanning from 200 ms before the onset of the target word until 800 ms afterwards. Separate ERPs were generated for the same set of target word stimuli presented in three different priming conditions (semantic, affordance and neutral priming). Baseline correction was performed using the average EEG activity between -200 ms and 0 ms. The electrodes were referenced to the left mastoid electrode and then re-referenced offline to the average of the left and right mastoid data. The central anterior-frontal electrode (AFz) was used as the ground. Segments containing artefacts were rejected from analyses and participants with less than two-thirds of their segments intact after artefact removal were excluded from the analyses. Inaccurate responses were discarded, as were trials with reaction times 2.5 standard deviations above or below the mean, or outside the 200 to 1200 ms time window.

To calculate the N200, the go data was subtracted from the nogo data for each condition (Amsel et al., 2013; Schmitt, Münte & Kutas, 2000). Comparisons between conditions were conducted across all electrodes and post zero-point sample points using pairwise analyses based upon the cluster randomisation technique of Maris and Oostenveld (2007), to avoid multiple comparisons. In this technique, two-sided *t*-tests were carried out comparing each electrode-time sample pair between two of the tested conditions (e.g., affordance and semantic priming). Those samples with a *t*-value above significance threshold ($p < .05$) were clustered together in terms of temporal and spatial adjacency. Only clusters of eight or more samples were considered

for analysis. For each of the remaining clusters, a summed t -value was calculated as a total of all individual t -values from all of the individual comparisons. Analysis thereafter was based on these clusters rather than the individual data points. In the second step of this procedure, the interval occupied by the cluster with the largest cluster-level t -value was selected. Each of the original paired sample t -tests that were used to generate this cluster were repeated, but with the data items of each pair randomly assigned between the two conditions. This was performed 1000 times to generate a Monte Carlo distribution of summed t -values corresponding to the null hypothesis. The final Monte Carlo p -value was calculated as the proportion of 1000 summed t -values in the random distribution that exceeded the observed cluster-level t statistic.

2.4 Results

2.4.1 Behavioural Results

Accuracy data. The average proportion of correct responses across all conditions was found to be 99.44%. An analysis of variance (ANOVA) was conducted comparing accuracy between the 3 conditions (semantic, affordance, neutral), 2 response types (go, nogo) and 2 categories (manmade, natural). There were no significant effects, $ps > .1$.

Reaction times. An ANOVA was conducted comparing the 3 conditions (semantic, affordance, neutral) and 2 categories (manmade, natural). A significant main effect of condition was found, $F(3, 147) = 9.89, p < .0001$, with participants responding significantly quicker on the semantic primed trials ($M = 572.38$ ms, $SD = 90.78$) compared to the affordance trials ($M = 587.97$ ms, $SD = 90.78$; $F(1, 49) = 11.39, p < .01$), and the neutral trials ($M = 587.88$ ms, $SD = 90.84$; $F(1, 49) = 10.94, p < .01$). Reaction times for the affordance and neutral trials did not differ significantly from each other, $F(1, 49) = .031, p > .5$. A

significant effect of category was also found $F(1, 49) = 4.22, p < .05$, with responses to natural object targets ($M = 552.76$ ms, $SD = 95.63$) being significantly faster than responses to manmade object targets ($M = 601.76$ ms, $SD = 77.08$). There was no significant interaction between condition and target category, $F(3, 147) = 1.50, p > .1$.

2.4.2 Electrophysiological Results

N200 analyses: Comparison to baseline. The N200 was calculated by subtracting ERPs for go trials from those of nogo trials for the three priming conditions. For each condition, independent t -tests were used to compare the voltage of the N200 to a baseline of zero across all temporal samples and active electrodes. These multiple comparisons were then corrected using the previously described cluster randomisation procedure. Significant clusters are listed in Table 1 and scalp maps illustrating the location of activity are shown in Figure 2. This indicates that the information contingent to the semantic decision task (natural vs. manmade categorisation) was available from 280 ms after target word onset when it was primed with a neutral word, after 252 ms when primed with the name of an object with a similar micro-affordance, and 208 ms when primed with a semantically related word.

Table 1

Summary of significant clusters for the N200 of the semantic, affordance, and neutral conditions compared to baseline.

Condition	No. of clusters	Name of cluster	Polarity	Duration	<i>P</i> -value
Semantic	1	cS	Negative	208–800 ms	$p < .001$
Affordance	1	cA	Negative	252–800 ms	$p < .001$
Neutral	1	cN	Negative	280–800 ms	$p < .001$

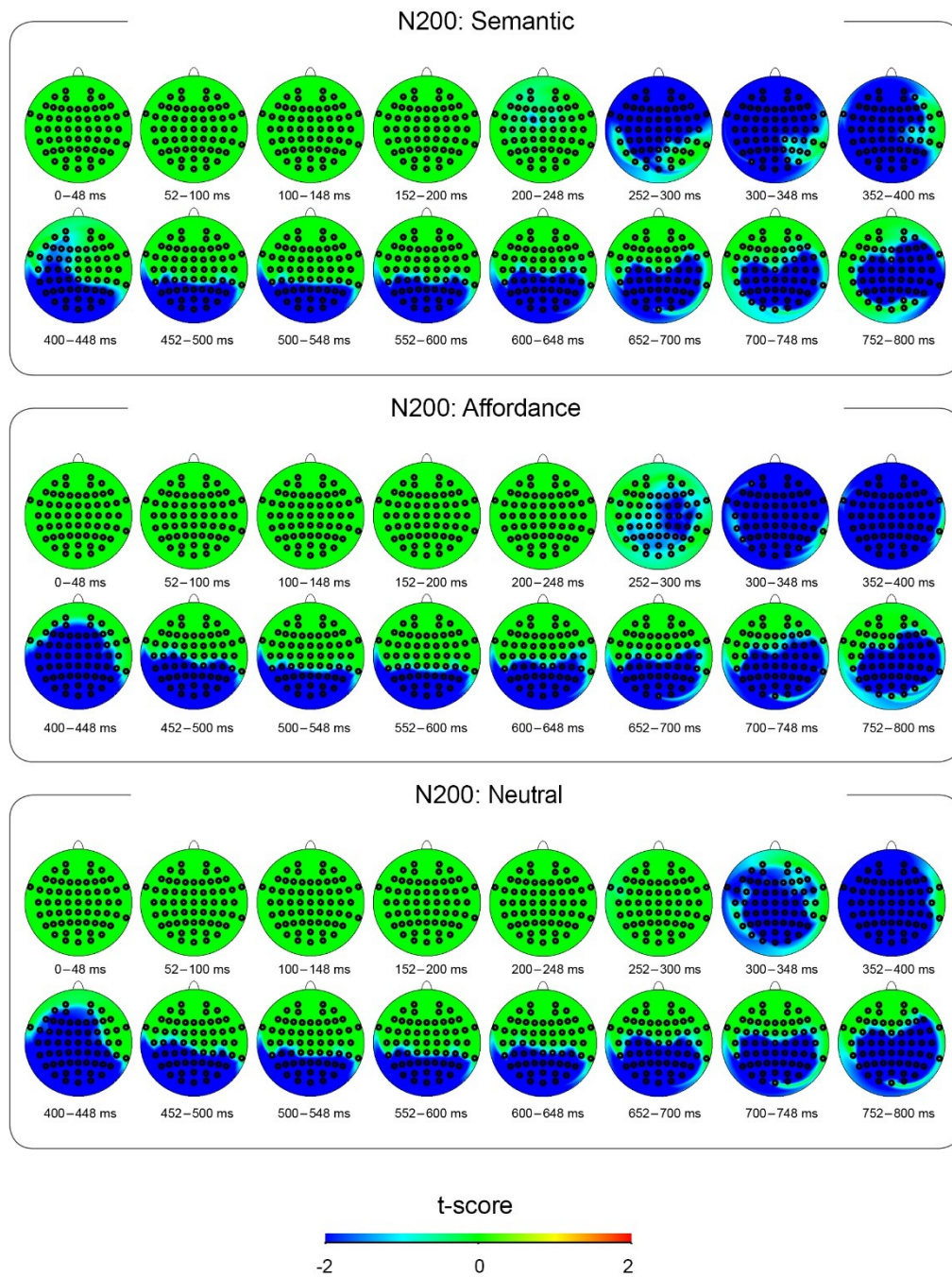


Figure 2. Scalp maps showing t -scores for significant clusters revealed by the cluster randomisation comparison between the N200 and baseline for semantic, affordance, and neutral priming conditions.

N200 analyses: Comparison between conditions. Independent *t*-tests were also carried out to examine the difference between the N200s of the different conditions. Again, multiple comparisons were corrected using the cluster randomisation procedure. The resulting significant clusters are shown in Table 2 and Figure 3.

When subtracting the neutral from the semantic priming condition the presence of an early negative cluster, $c(S - N)_1$, shows that the onset of the N200 was significantly earlier for semantically than neutrally primed target words. The later positive cluster, $c(S - N)_2$, also indicates that the offset of the N200 is earlier in the semantic than the neutral priming condition. Similar comparisons also revealed that the N200 was earlier in the affordance priming condition than the neutral priming condition, $c(A - N)$. However, there was no significant difference between the latency of the onset of the N200 between the semantic priming condition and the affordance priming condition, only that the offset of the N200 was earlier in the former condition, $c(S - A)$.

Table 2

Summary of significant clusters in the comparisons between the N200 of the semantic, affordance, and neutral conditions.

Conditions compared	No. of clusters	Name of cluster	Polarity	Duration	<i>P</i> -value
Semantic – Neutral	2	$c(S - N)_1$	Negative	176–300 ms	$p = .002$
		$c(S - N)_2$	Positive	368–500 ms	$p < .001$
Affordance – Neutral	1	$c(A - N)$	Negative	200–292 ms	$p < .001$
Semantic – Affordance	1	$c(S - A)$	Positive	320–500 ms	$p < .001$

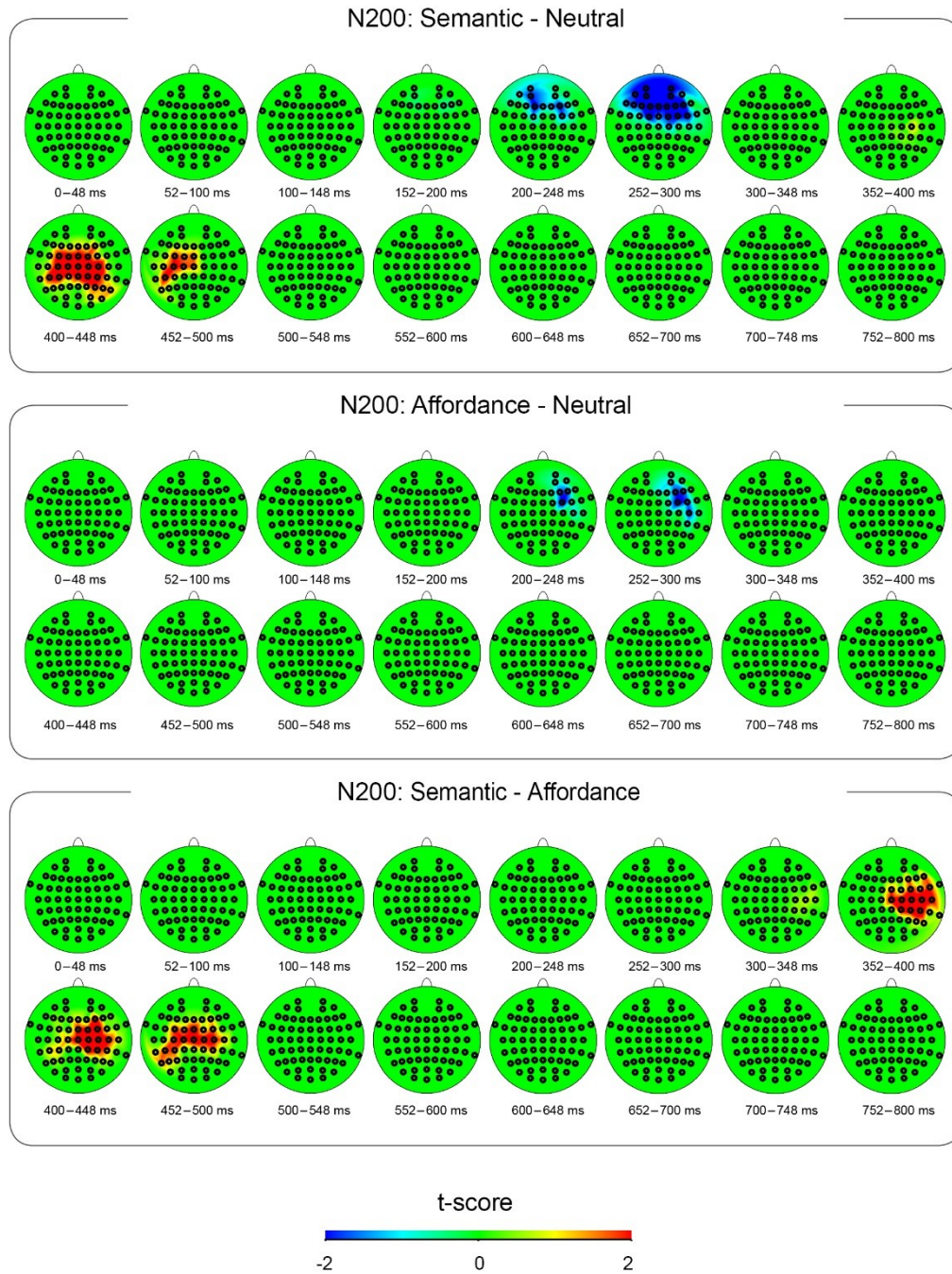


Figure 3. Scalp maps showing t -scores for the significant clusters revealed by the cluster randomisation comparing semantic, affordance, and neutral priming N200s.

Summary of N200 results. Given that the onset of the N200 is thought to reveal the earliest time a participant has access to information required to make their task-related judgement, it is normal to find that onset latencies for this component are highly correlated to behavioural reaction times. This was indeed the case when comparing our semantic and neutral priming conditions, with the reaction times and N200 onset both being earlier in the semantic than the neutral priming condition. However, while reaction times were found to be significantly faster in the semantic priming condition than the affordance priming condition, we found no significant difference in the onset of the N200 between these conditions. A logical explanation for this disparity lies in the fact that reaction times are only garnered during go trials, while the N200 is the result of a subtraction of ERP between go and nogo trials. Thus, it is possible that the relatively early onset of the N200 for affordance priming is a result of greater activity during nogo trials, which would not be reflected in reaction times. Therefore, to test this hypothesis we conducted separate analyses of ERP for go and nogo trials.

Analyses of go trials. Paired sample *t*-tests were used to compare the ERPs of the semantic and neutral priming conditions for go trials only. As before, individual *t*-tests were conducted for each sample recorded over each of the electrodes and multiple comparisons then corrected using the cluster randomisation procedure. The significant clusters are displayed in Table 3 and Figure 4. Both semantic and affordance related priming evoked earlier activity in go trial targets when compared with the neutral priming condition. However, activity for semantic primed targets occurred ~100 ms earlier than those primed with affordance, as indicated by the presence of the negative polarity cluster, $c(S - A)Go$.

Table 3

Summary of significant clusters in the comparisons between the go trial ERPs of the semantic, affordance, and neutral conditions.

Condition	No. of clusters	Name of cluster	Polarity	Duration	<i>P</i> -value
Semantic – Neutral	1	c(S – N)Go	Negative	428–708 ms	$p < .001$
Affordance – Neutral	1	c(A – N)Go	Negative	520–728 ms	$p = .001$
Semantic – Affordance	1	c(S – A)Go	Negative	440–556 ms	$p < .001$

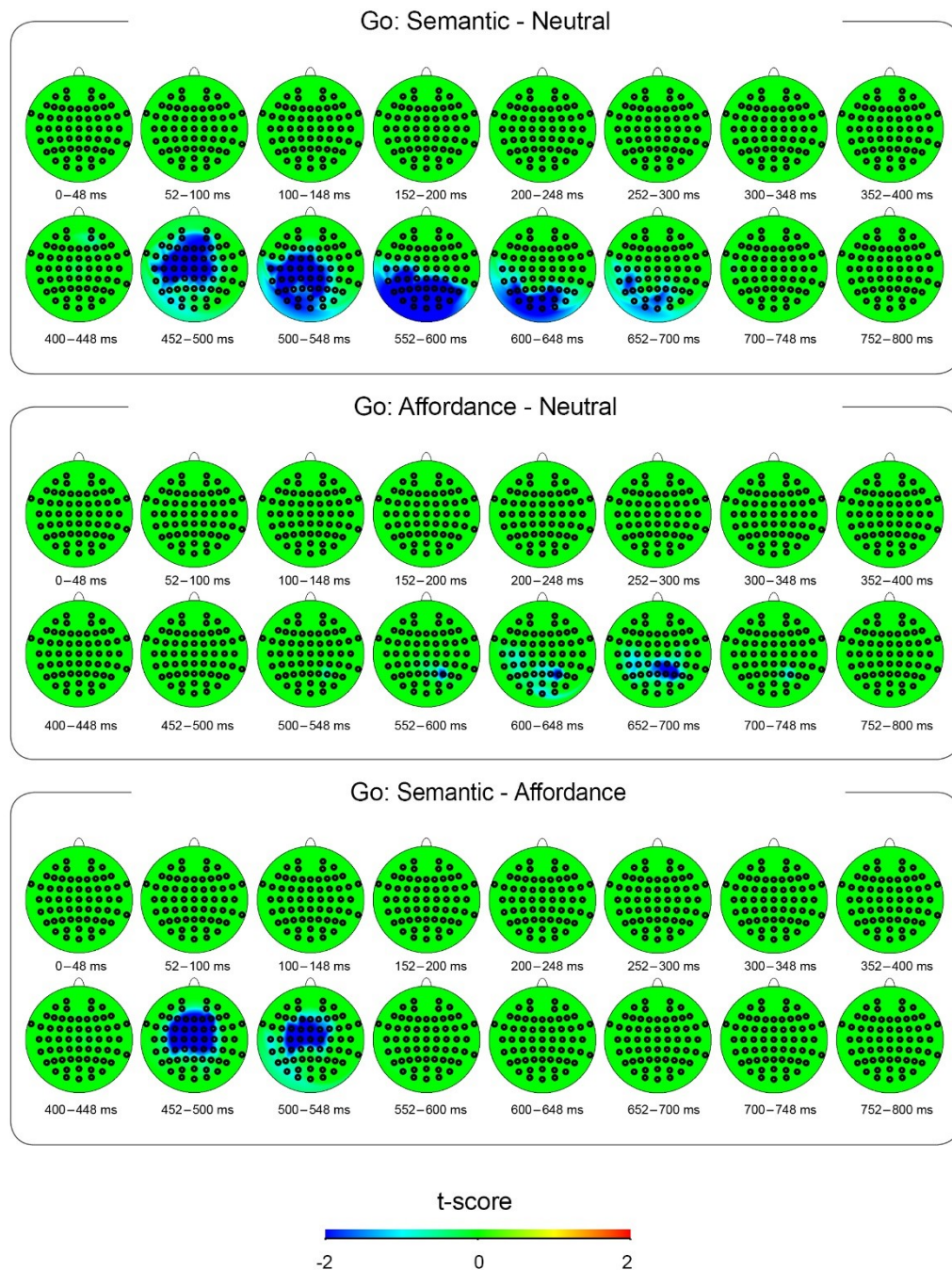


Figure 4. Scalp maps showing t -scores for significant clusters revealed by the cluster randomisation comparison between semantic, affordance, and neutral priming conditions in go trials.

Analyses of nogo trials. The significant clusters resulting from the cluster randomisation procedure for nogo trials are displayed in Table 4 and Figure 5. As in the go trials, both semantic and affordance priming of targets in

nogo trials resulted in significantly earlier activity than in the neutral priming condition. However, in this case, a direct comparison of semantic and affordance priming showed that the onset of activity was significantly earlier in affordance priming, as revealed by the positive polarity cluster, c(S – A)Nogo₁. The later cluster, c(S – A)Nogo₂, did reveal greater negative amplitudes due to semantic priming, but later, from 492–628 ms.

Table 4

Summary of significant clusters in the comparisons between the nogo trial ERPs of the semantic, affordance, and neutral conditions.

Condition	No. of clusters	Name of cluster	Polarity	Duration	<i>P</i> -value
Semantic – Neutral	1	c(S – N)Nogo	Negative	500–632 ms	<i>p</i> = .001
Affordance – Neutral	1	c(A – N)Nogo	Negative	176–352 ms	<i>p</i> = .001
Semantic – Affordance	2	c(S – A)Nogo ₁	Positive	296–472 ms	<i>p</i> = .002
		c(S – A)Nogo ₂	Negative	492–628 ms	<i>p</i> < .001

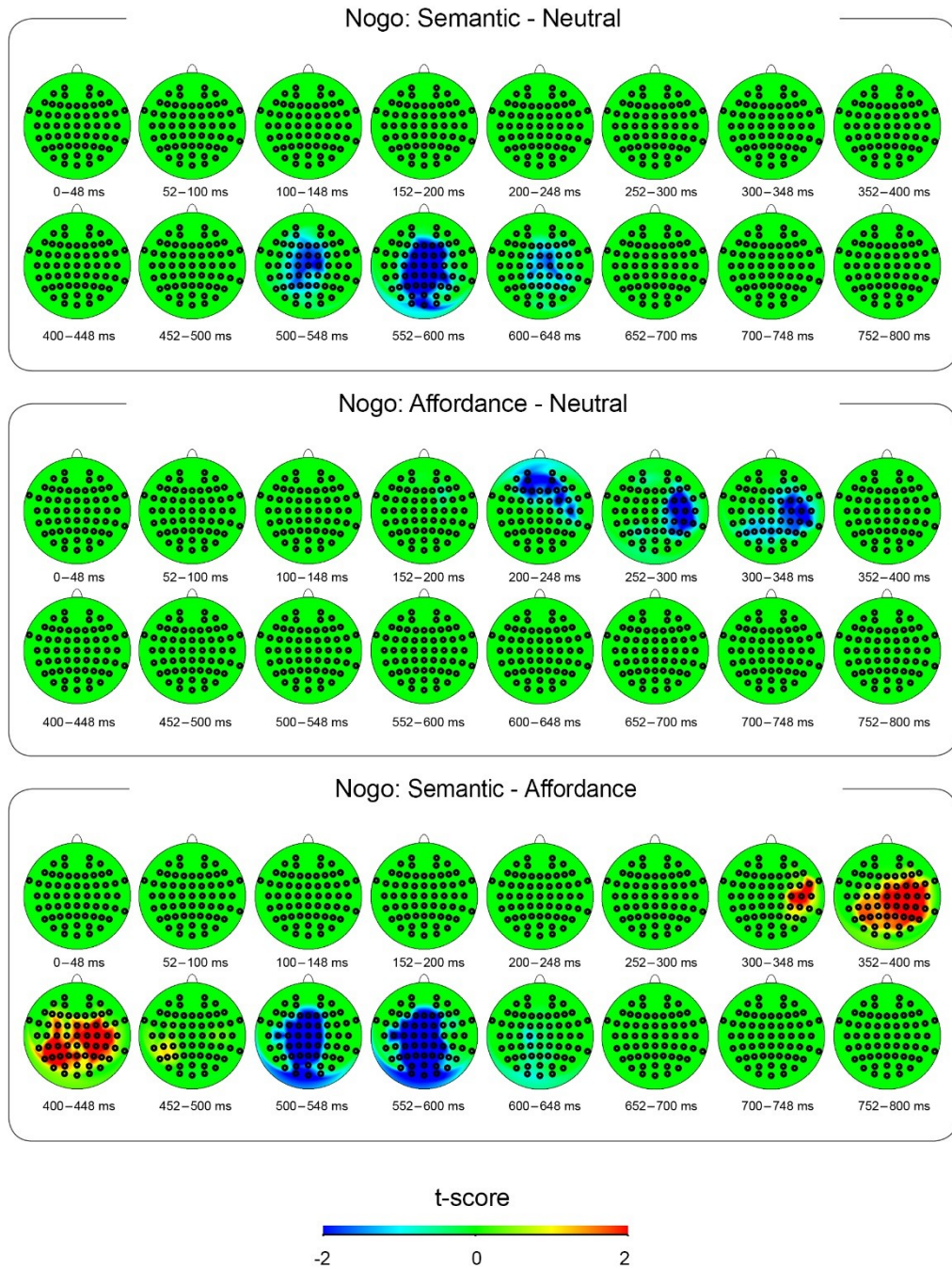


Figure 5. Scalp maps showing t -scores for the significant clusters revealed by the cluster randomisation comparison between semantic, affordance, and neutral priming conditions in nogo trials.

2.5 Discussion

In this study, we examined the relative time course of access to an object's semantic or action-affordance features when reading its name. The availability of these different types of information was ascertained through an examination of the N200 ERP component, which can be used to determine when specific task-related information becomes available to a participant in a go/nogo paradigm. In our study, participants made a semantic decision related to a written object name, categorising the described object as either manmade or natural. These target object names were primed by written words that were related to the target through a shared affordance, semantic taxonomy or were unrelated to the target in a neutral priming condition.

The results showed that the onset of the N200 was earlier when the target words were primed with either semantic or affordance related primes, at around 210–250 ms post target onset, than when they were preceded with an unrelated word, where the onset was at 280 ms. Importantly, there was no significant difference in N200 onset latency between affordance and semantic related primes. This would normally indicate that the two types of related priming conditions offer equivalent facilitation of the semantic decision made on the target words. However, this was found to be at odds with the behavioural reaction time data. Only semantic priming facilitated decision latencies, with latencies during the priming of affordances not differing significantly from the neutral priming condition. The explanation we pursued to explain for this disparity relates to the methodology used to calculate the N200 component, which is a difference wave of stimuli presented in go and nogo trials. This analysis draws upon all of the trials tested in the experiment, while reaction times are only provided for go trials. The disparity between reaction times and

N200 latencies suggests that there is an asymmetric difference in ERPs between go and nogo trials that is modulated by the priming condition. From an embodied perspective this would not be unexpected, as it is possible that the motor preparation afforded by the objects described in the prime words could interact with a later task-related manual response. To investigate this explanation, we conducted separate ERP analyses for go and nogo trials. In go trials we found that the onset of activity in the semantic priming condition was significantly earlier than the other two priming conditions, starting around 430 ms after target onset. While the onset of activity in the affordance priming condition was earlier than that of the neutral condition, this difference was relatively late, at around 520 ms. This could explain why affordance priming had no significant effect on reaction times, as the associated activity was proximal to the behavioural response times of around 560–580 ms, and too late to influence those responses. Thus, it would appear that the temporal aspect of go-response ERPs is in line with the behavioural latency differences. Conversely, in the ERPs from nogo trials, the effect of affordance priming started at 180 ms, significantly earlier than semantic priming at around 500 ms. This comparison of go and nogo trials shows how the parity in the N200 onset in semantic and affordance priming conditions mask quite different underlying activities, with early activation of semantic representations in go trials, and early affordance related activity in nogo trials.

In part, these findings follow established semantic priming results, with activation from the prime word facilitating the activation of the proceeding semantically related targets. This is clearly evident in the semantic priming condition, where we find facilitation of behavioural semantic decision latencies and early activity in the go trial ERPs. We also found activity related to affordance priming in go trials, but in a much later temporal window. Normally,

these particular results would be indicative of a post-lexical mental simulation account of affordance (Mahon & Caramazza, 2008) but they are in conflict with other studies that have found an affordance-related facilitation in lexical decision latency (Myung et al., 2006; Rüeschemeyer, Lindemann, van Rooij, van Dam & Bekkering, 2010).

One potential reason why we did not find a behavioural effect of affordance priming previously seen in lexical decisions is due to the task used in our study. This is not related particularly to the semantic decision task per se, but rather the relationship between the task and the two priming conditions. In the semantic priming condition, the taxonomic relation between prime and target ensured that they would share the semantic feature directly probed by the task i.e., prime and target would either both be natural or both be manmade. In contrast, the primes and targets in the affordance condition were selected such that their only shared feature should be the grip used to manipulate them. As such, natural primes would always be paired with artificial targets and vice versa. Thus, prime-target pairs in the affordance condition are always unrelated with respect to the attended semantic feature directed by the behavioural task (i.e., natural vs. manmade). This means that the semantic priming condition has a direct relationship between prime, target, and task, whereas in the affordance condition the relationship between prime and target was orthogonal to the task. Therefore, it is possible that reaction times in affordance and semantic priming conditions may have been modulated by differences in the relationship between prime and task, rather than the relationship between prime and target. It must be noted, that this distinction cannot be applied to the temporal disparities shown in the study by Amsel et al. (2013), as they compared the temporal onset of distinct and explicit semantic decisions, rather than comparisons of priming in the same decision.

In Amsel et al. (2013) the onset of the N200 ERP component revealed that participants were able to differentiate between living and non-living entities from as early as 160 ms, whereas the graspability of the object was retrieved around 300 ms. It is concluded that this relatively late access to grasp-related affordances indicates that they do not play a crucial role in the conceptual representation of objects. In our own study, N200 latencies when priming affordance and semantic features of target words were equivalent, from around 210 ms. Although similar, there are some important methodological divergences between our two studies that could explain the differences between our N200 latencies. Firstly, the affordances related to Amsel et al.'s stimuli appeared to be based on the object's geometry, rather than a stored representation of use. For example, "mouse" is categorised as graspable, but a "motorbike" is not. In terms of affordances, the experience one has with using or manipulating an object is an important aspect of the sensorimotor activity elicited (Calvo-Merino, Glaser, Grèzes, Passingham & Haggard, 2005; Rüeschemeyer et al., 2010; Siakaluk et al., 2008). Therefore, one could categorise a motorbike as a "graspable" object, as it is manipulated primarily through its handlebars. Conversely, a mouse is unlikely to have a stored affordance, generated through past interactions, but would rely upon an intrinsic volumetric affordance inferred from its size. Physical size provides a salient affordance in visual stimuli, with direct vision-to-action activation obviating the requirement for higher level knowledge (Rumiati & Humphreys, 1998). However, in a linguistic modality, volumetric affordances have to be mediated through stereotyping of object properties. Therefore, in Amsel et al. the temporal onset of affordance seen in the N200 would have included any delay required to infer a volumetric affordance. In contrast, our study used a combination of stored and volumetric affordance for each prime/target pair. This could be particularly important given that Amsel et

al. based their temporal estimates upon a manipulation of the question posed in an explicit decision task, i.e., between making a living/non-living or graspable/non-graspable judgment.

One of our central questions is whether the availability of implied geometric information to an explicit decision task, as tested in Amsel et al., can provide an ecologically valid estimate of the temporal onset of affordance. We suggest that this is challenged by our finding of early activity associated with affordance priming in nogo trials, a consequence of the manual motor preparation generated by the shared affordances between prime and target. In nogo trials, this motor preparation is incompatible with the requirement of the participant to withhold a manual response, and the inhibition of the response becomes evident in the ERP. The spatial distribution of this activity, evident in right pre-frontal electrodes, is similar to the activity found in previous research in the right inferior frontal gyrus during the inhibition of motor responses (Chikazoe, Konishi, Asari, Jimura & Miyashita, 2007; Hampshire, Chamberlain, Monti, Duncan & Owen, 2010). Lesion studies also illustrate the involvement of the frontal lobe in inhibiting affordances that are automatically elicited by visual objects. One study found that some patients with frontal lobe lesions would grasp and use any objects in their field of vision without any real purpose for doing so (Lhermitte, 1983; Riddoch, Edwards, Humphreys, West & Heafield, 1998). Lhermitte (1983) argued that this “utilization behaviour”, as he termed it, resulted from the inability of the frontal lobe to perform the usual inhibitory function on the parietal lobe’s motor programs. Research shows how the parietal lobe is involved in the integration of visual and somatosensory information and converting this into motor commands (see Fogassi & Luppino, 2005, for a review). The temporal period of this affordance related activity, spanning P2 and N2 components, is also consistent with previous accounts of

these components reflecting stimulus evaluation and response selection (Gajewski, Stoerig & Falkenstein, 2008; Potts, 2004). Gajewski et al. (2008) argued that this might be more effortful when an incorrect response is activated by misleading cues. We posit that there is a similar modulation of the P2/N2 complex in our study due to the effort required to inhibit a response once the motor system had been primed to respond. We suggest that this is the source of the early activity observed in our affordance primed nogo trials.

A particularly noteworthy aspect of this account of our affordance effects is that the task-related manual response was not directly related to the affordance of the object. While participants were asked to respond or withhold a manual response, the left index finger button press required was not directly related to the grip afforded by either the prime or target referent object. Similarly, generalised effects have been found in previous research (Postle, Ashton, McFarland & De Zubicaray, 2013; Rueschemeyer et al., 2010; Siakaluk et al., 2008). Rueschemeyer et al. found that lexical decisions were quicker and more accurate for names of manipulable objects when participants simultaneously executed a motor action. In this case the action, requiring participants to run their finger along the edge of a desk, was not specific to the afforded actions of the objects. Postle et al. (2013) also found that it did not matter which body part was being described by their linguistic stimuli, the right hand was affected indifferently. This shows that the motor preparation generated through affordance priming does not necessarily have to be related to a specific motor program, such as a particular grip, but can be broadly tuned to include other manual activity.

2.6 Conclusions

The main aim of this study was to investigate the deeply embodied claim that the sensorimotor information related to the form or function of an object, is fundamental to its conceptual representation and plays a privileged role in the comprehension of their linguistic descriptors (Glenberg & Gallese, 2012; Glenberg & Robertson, 1999). Conversely, it has been suggested that access to action-affordances is not privileged above other semantic features that make up an object's conceptual representation and that their activation is a result of post-lexical mental simulation of referent object use (e.g., Amsel et al., 2013; Mahon & Caramazza, 2008). In support of the former theory, we established that the priming of affordance evokes the rapid activation of motor representation during the reading of object names. This is indicative of somatotopic activity in the motor system associated with the affordance of the named object, similar to that shown across a range of studies during the reading of action words (Hauk, Shtyrov & Pulvermüller, 2008; Pulvermüller, Härle & Hummel, 2001; Pulvermüller, Lutzenberger & Preissl, 1999; Shtyrov, Hauk & Pulvermüller, 2004). However, while listeners do seem able to extract embodied information from linguistic representations, this information does not appear to play a fundamental role in the semantic integration processes related to our task. The early activity related to affordance priming, seen from around 180 ms, was strictly limited to nogo trials. This indicates that this activity is related to the inhibition of the afforded motor preparation, as participants seek to withhold the manual response related to the task. While taxonomically related primes facilitated semantic decisions, affordance related primes did not. In go trials the onset of activity related to affordance priming was relatively late, starting at around 520 ms, compared to an onset of 430 ms for semantic priming. This set

of findings is perhaps most consistent with theories that posit multiple processing routes in comprehension, such as the language and situated simulation (LASS) theory (Barsalou, Santos, Simmons & Wilson, 2008). This would allow for a distinction between the early activation of the motor representation afforded by the described object and the route used to access abstract conceptual information during comprehension. Whereas semantic-priming can occur by recruiting the linguistic system's method of activating associated words in a distributional semantic network, affordance-priming involves the situated simulation route. Our research suggests that the early simulation activity is activated automatically and in a similar time frame to categorical knowledge. Later affordance related activation could either be the result of another simulation cycle or integration of information across the two routes.

3. An ERP Examination of the Activation of Functional and Volumetric Object Affordances When Reading Object Names

3.1 Chapter Abstract

Reading the name of an object is thought to generate brain activity associated with the actions afforded by the referent object (Glenberg & Robertson, 2000). This study used ERPs to investigate the precise timing in which two types of affordance, functional and volumetric, are activated in the brain after reading object names. Functional affordances are actions associated with using an object and volumetric affordances are actions used to pick up an object. In Experiment 1 we found that activity related to functionally manipulable objects was elicited first, ~216 ms, and was widespread across the scalp. Activity associated with objects whose graspability is based on their geometric properties was elicited ~372 ms, located at frontotemporal electrodes in the left hemisphere. The specific hand-grip used to hold functionally manipulable objects was activated later, around 530 ms. For graspable objects that are not manipulated during use, it was around 225 ms. Experiment 2 revealed that the motor program for a specific hand grip was only activated early (370 ms) for functionally manipulable objects when it was relevant, i.e., for executing a response. For volumetric objects, brain activity associated with a specific grasp was generated early on (270 ms), only when the participant was withholding a motor response. These findings suggest that functional and volumetric affordances are processed in separate brain systems. Functional manipulation is activated early on via a lexico-semantic route and volumetric affordances are activated as a result of

pattern-matching between semantic information provided by the object name and proprioceptive information from the participant's body.

3.2 Introduction

It is well established that reading object names produces motor activation related to the manipulation of that object (see review by Willems & Hagoort, 2007). Research suggests that the affordance of an object is particularly significant to the semantic representation of objects that require greater manipulation during use (Binkofski & Buxbaum, 2013; Bub & Masson, 2012; Siakaluk et al., 2008). For example, a hammer requires greater manual manipulation whilst being used, compared to a grape which is held for only a brief period before it enters the mouth. Bub and Masson (2006) made the distinction between volumetric and functional affordances. The former referring to actions used to pick up an object based on its size and shape; the latter referring to actions performed whilst using the object. These action affordances are thought to play an important role in language comprehension (Bub, Masson & Cree, 2008; Glenberg & Robertson, 1999). According to the Indexical Hypothesis, nouns are indexed to mental representations of the objects or events to which they refer (Glenberg & Robertson, 1999; 2000). The meaning of a word is derived from our sensorimotor experiences with the referent in real life. When we read the name of an object the associated affordances of that object become available and this gives meaning to the word form.

The Two Action Systems (2AS) theory, postulates that these two types of affordance are generated in separate brain systems (Binkofski & Buxbaum, 2013; Buxbaum & Kalénine, 2010). One system pertains to actions based on the structure of an object (size, shape and location; structure-based affordances), which we refer to as volumetric affordances, and one to actions during use of the

object (function-based affordances), which we term functional affordances. According to this theory, structure-based affordances are activated online via the updating of spatiomotor information transferred to the retina, limbs, head and hands; whereas function-based affordances access conceptual representations in long-term memory. They propose that structure-based affordances pass through a dorso-dorsal stream consisting of bilateral intraparietal sulcus (IPS) and dorso-lateral fronto-parietal regions. According to their theory, information about structure-based affordances is fleeting (lasting milliseconds) and is only weakly associated with the conceptual representation of objects. Function-based affordances, on the other hand, involve the ventro-dorsal stream consisting of the left superior temporal lobe and inferior parietal areas. These affordances show strong, enduring activation (lasting several minutes; Buxbaum & Kalénine, 2010). This theory predicts that structure-based affordances can be activated outside of conscious awareness, whereas function-based affordances require the person's intention to act or achieve a goal, such as reaching to grasp a mug of coffee. In support for the 2AS theory, research has been carried out on patients with ideomotor apraxia, who have difficulty in using objects or even pantomiming the functional use of an object. In this study, patients with apraxia (due to left inferior parietal lobe damage) were shown pictures of objects and then asked to select the most appropriate hand gesture for contacting the object (Buxbaum, Sirigu, Schwartz & Klatzky, 2003). The healthy control participants and non-apractic patients chose functional hand gestures, whereas the apractic patients chose structural gestures. This suggests that functional actions are more closely associated with an object's conceptual representation compared to structural affordances. When the part of the brain that processes functional actions is damaged, patients are forced to choose structural actions. Further evidence came from healthy participants in a fMRI

study (Buxbaum, Kyle, Tang & Detre, 2006). Participants were shown images of manipulable objects (e.g., tools) and made decisions about which responses would be appropriate for grasping it or for using it. Compared to volumetric gestures, functional responses resulted in greater activation in left inferior frontal gyrus (IFG), posterior superior temporal gyrus (STG), and inferior parietal lobule (IPL). Several other neuroscientific studies have also found differences in brain activity associated with grasping an object to move it (volumetric affordance), compared with activity related to grasping an object to use it (functional affordance; Brandi, Wohlschläger, Sorg & Hermsdörfer, 2014; Ramayya, Glasser & Rilling, 2009; van Schie & Bekkering, 2007).

Volumetric affordances pertain to Gibson's (1979) original definition of an affordance, which is an action that is directly perceived from the observation of an object in the real world. We might not expect this type of affordance to have a stored mental representation or to be elicited during object name reading, as there are no visual cues to provide information about the size and shape of the object (Buxbaum & Kalénine, 2010; Jax & Buxbaum, 2010). Functional affordances on the other hand, are well-established motor programs that inform us how to use an object, which become strongly associated with the semantic representation of an object through Hebbian learning (Pulvermüller, 1999), so we would expect this type of affordance to be activated when processing object names (Buxbaum & Kalénine, 2010). Nevertheless, research has shown that volumetric affordances can also be linguistically-generated (Bub & Masson, 2012; Bub, Masson & Cree, 2008; Glover, Rosenbaum, Graham & Dixon, 2004). This may involve a simulation process whereby a person activates a mental picture which informs them about the geometric properties of the object. Alternatively, it may be that the experience of picking up objects leads to

the grasping action becoming associated with the conceptual representation of that object via Hebbian learning, in much the same way as functional actions.

Our interest in the timing in which these two types of affordance are activated during object name reading, is that it helps answer whether both functional and volumetric affordances contribute to the conceptual representation of an object, or rely on a mental simulation of experience with that object. Activation during early semantic processing (~200 ms; Hauk, Coutout, Holden & Chen, 2012) would suggest that the affordance was deeply rooted in the conceptual representation of the object. Whereas post-N400 activation might suggest that the affordance is the result of later semantic processing, such as spreading activation to associated sensorimotor areas once the word has been fully registered. Several behavioural studies have looked at when these two different types of affordances might be activated during linguistic processing (Bub & Masson, 2012; Bub, Masson & Cree, 2008; Masson, Bub & Newton-Taylor, 2008). In a lexical decision study, participants were presented with a letter string for 300 ms and then an image of a hand gesture which they had to replicate using the correct response device (e.g., pinch, poke, trigger or closed grasp; Bub, Masson & Cree, 2008; Experiment 5). Results showed that functionally compatible responses (responses that would be afforded by the referent object during use) were significantly quicker compared to incompatible responses, whereas for volumetric actions there was no significant difference between compatible and incompatible trials. However, when there was no time limit for responding, as in Bub et al. (2008; Experiment 4), both functional and volumetric affordances showed a congruency effect, meaning that both types of affordance were activated when identifying words. Nevertheless, these compatibility effects were only present when the participants were encouraged to focus on the meaning of the words using a

lexical decision task. When responses involved attending to the colour of the words, the congruency effects were not present for either gestural type. They concluded that although both volumetric and functional affordances play a role in the conceptual representation of objects, functional affordances appear to possess a special role. Given that only functional affordances were activated when object names were presented for a brief time (300 ms), this might suggest that volumetric affordances are generated through a mental simulation whereby information about the object's size can be retrieved.

Another feature of functional affordances is that they are generally associated with greater manipulation of an object and therefore involve greater and longer lasting activation of motor areas (Rüeschemeyer, Lindemann, van Rooij, van Dam & Bekkering, 2010; Siakaluk et al., 2008). In one priming study, participants listened to the names of objects and then were shown a picture of a hand gesture (e.g., a finger poke) at one of four different time points: 150 ms before the word was played, at word onset, halfway through the presentation of the word or after the word had been played (Bub & Masson, 2012). As soon as they saw the hand gesture, they were required to copy the gesture shown using the appropriate response device. There was a priming effect for functional hand gestures performed at word onset when the referent object afforded the same grasp, but a negative priming effect for volumetric hand gestures. The functional gestures continued to show a priming effect when performed at the middle and end of the word presentation, whereas the volumetric grasps only showed a priming effect at the middle of the word and this had disappeared by the end of the word. They concluded that volumetric grasps were generated more slowly, and that activation was brief, whereas functional grasps were generated quickly and sustained activation for longer. They hypothesised that this pattern of results reflected the generation of multiple affordances in the parietal lobe,

followed by the subsequent resolution of this competition and selection of the correct response (with help from the frontal lobe; Bub & Masson, 2012). They argued that the negative priming effect shown for volumetric affordances, at word onset, was due to competition from the functional affordances which showed greater activation early on. Their conclusions suggest that both types of affordance are generated in the same part of the brain, but functional affordances show stronger activation. Other studies have primed functional and volumetric affordances with contextual information, such as a sentence (Bub & Masson, 2010; Lee, Middleton, Mirman, Kalénine & Buxbaum, 2013; Masson, Bub & Warren, 2008), or with the initiation of a related motor response (Bub, Masson & Cree, 2008; Jax & Buxbaum, 2010). Affordance priming effects have even been found in the absence of a sentential context and without the need for a related motor response (Myung, Blumstein & Sedivy, 2006; Rüeschemeyer, et al., 2010). For example, using eye-tracking, Myung et al. (2006) discovered that when participants listened to names of objects, they spent longer looking at pictures of other objects that shared the same manipulation features (e.g., piano and typewriter) compared to objects that did not (e.g., piano and blanket).

The purpose of the current study was to provide a direct examination of the timing of functional and volumetric affordance activation during word recognition, using a technique with high temporal resolution; event-related potentials (ERPs). We compared ERP activity related to three types of words: nouns representing objects that would be picked up as if for transport, and thus generate a volumetric affordance (volumetric affordance condition; e.g., a grape); nouns representing objects that would be manually manipulated during use, and thus generate a functional affordance (functional affordance condition; e.g., a hammer); and nouns representing objects that do not afford any manual manipulation (non-manipulable condition; e.g., puddle). Although ERPs are not

an appropriate method for informing the precise location of brain activity, they can provide some indication of where functional and volumetric affordances are being processed. Previous research has shown that tools, which involve manual manipulation during use, activate greater motor activity in the brain compared to other nouns (Creem-Regehr & Lee, 2005). As the functional use of an object requires greater manual manipulation than simply picking up an object, we would expect to see more brain activity in motor areas for words referring to functionally manipulable objects, compared to other graspable objects (Rüeschemeyer et al., 2010; Siakaluk et al., 2008).

In an additional condition, we examined whether motor activity associated with early affordance activation is not related to the specific hand-grip used to hold the object, but instead is a more general or abstract motor activity (Postle, Ashton, McFarland & De Zubicaray, 2013; Rüeschemeyer, et al., 2010). To explore when the particular hand-grip was being activated, participants held a piece of wood in either a precision or power grip, which was either compatible or incompatible with the grip afforded by the noun referent. The power and precision grips in these conditions have been coined micro-affordances (Ellis & Tucker, 2000), that is a component of the action afforded by an object, which might include the direction of wrist-rotation, the direction of reach, the hand used, or the hand posture adopted for the action. For example, when a precision-grip is used to pick up a grape, it would be classed as the volumetric precision affordance; whereas when a hammer is grasped for use the grip would be considered the functional power affordance. Therefore, the stimuli presented in this experiment are to be further split between those that are manipulated with a grip compatible with that primed by the held object, or incompatible.

In a second experiment, we used a lexical decision task to establish whether affordances are generated during the early stages of lexical access. In this study, the participants had to indicate whether the letter string was a word or not by grasping a response device in either a precision or power grip. Again, the response was sometimes compatible and sometimes incompatible with the grasp used to pick up (volumetric condition) or use (functional condition) the object. Behavioural studies have shown evidence of affordance activation during lexical decision tasks (e.g., Bub, Masson & Cree, 2008; Myung et al., 2006; Rüeschemeyer et al., 2010) but are unable to inform us of underlying brain processes. Using ERPs, we may be able to see affordances being generated even in the absence of any significant behavioural results. If affordances are activated as early as lexical processing, this would be evidence that they are not simply the result of post-semantic spreading activation (Mahon & Caramazza, 2008) but are possibly an integral part of the object's conceptual representation (Barsalou, 1999; Bub & Masson, 2012). Myung et al. (2006) and Rüeschemeyer et al. (2010) both found significantly quicker responses for functionally manipulable objects during their lexical decision studies. Based on this finding and the consensus that functional affordances play a more significant role in an object's conceptual representation (Bub & Masson, 2012; Buxbaum & Kalénine, 2010), we predict that we are more likely to see functional affordances activated during this early stage of processing. Whereas, volumetric affordance activation would be expected later on after a mental simulation has taken place, as they depend on the perceptual features of an object (Jax & Buxbaum, 2010).

3.3 Experiment 1

In this experiment, we used ERPs to investigate the timing of access to knowledge related to functional and volumetric affordances, evoked when

reading the names of objects. The nouns referred to objects that were either graspable based on their geometric properties, manually manipulated during use or could not be grasped at all. The participants responded only to probe words (names of animals) that were semantically unrelated to the target words, to avoid any potential interference from motor preparation/responses; which are known to facilitate the evocation of affordances. The second objective of this experiment was to find out when the specific hand-grips related to these two types of affordance are elicited. While reading the object names, each of the participants held an object in a power-grip or precision-grip, which was sometimes compatible with the grip used to grasp or use the referent object they were reading. ERP analyses were carried out to establish the relative time course of compatibility effects.

3.3.1 Method

Participants. Sixty native monolingual English speakers were paid £12 for participating in the experiment. The data from two of the participants was not included in the final analysis due to excessive EEG and EOG artefacts (more than a third of trials had artefacts). The 58 participants included in the final analysis (35 females) were aged 18–32 ($M = 21.7$; $SD = 2.98$). All participants were right-handed as assessed with the Edinburgh Handedness Inventory (Oldfield, 1971), had no history of neurological impairment and reported having normal, or corrected-to-normal, vision.

Stimuli. Linguistic stimuli used in the experiment consisted of 140 concrete nouns describing common objects or, in the case of probe words, animals. Eighty of the nouns referred to graspable objects, half of which were objects that afforded a precision grip (e.g., pen, leaf), with the other half affording a power grip (e.g., parsnip, torch). Both these categories of stimuli were also equally split between those whose affordances are related

predominantly to size (volumetric affordance; e.g., leaf, parsnip), and half whose affordances would be generated through use (functional affordance; e.g., torch, pen). This resulted in 20 stimuli in each of four categories (Functional-Precision, Functional-Power, Volumetric-Precision, and Volumetric-Power). A further 40 stimuli described objects that are not able to be manipulated manually (Non-manipulable; e.g., cloud), and twenty animal names used as non-critical probe words (e.g., camel). Where possible stimuli were balanced in terms of linguistic characteristics: word length, SUBTLEX word frequency, uniqueness point, orthographic neighbourhood size, OLD20; all $ps > .1$. For 10 of the stimuli, some of these characteristics were not available. The full list of stimuli can be found in Appendix B.

Procedure. The participants were seated in a quiet, dimly lit booth. Stimuli were presented using E-Prime 2.0 (Schneider & Zuccoloto, 2007) on a CRT monitor (30.5cm height by 40.5cm width; 100Hz refresh rate) positioned one metre from the participant. Responses were collected using an E-Prime button box. Throughout the experiment, each participant held a wooden object in their right hand. Half of the participants held a small piece of wooden dowel between their finger and thumb, in a precision grip, and the other half held a wooden rolling pin with their entire hand, in a power grip (see Figure 6). This meant that sometimes the participants were holding an object sharing the same hand grip as that necessary to grasp (volumetric compatible) or to use (functional compatible) the stimulus referent and sometimes they were holding an object with a hand grip that was not afforded by the stimulus (volumetric incompatible, functional incompatible).

Each trial began with a fixation point, “ + ”, which appeared at the centre of the screen for 600–800 ms. After the fixation point, one of the nouns would be presented for 1500 ms or until the participant responded. The participants

were required to respond only to animal names (probe words) by pressing the first button on the button box with their left index finger. At the end of each trial, a blink symbol was displayed for 1500 ms, giving the participant the opportunity to blink if necessary. The participants were asked to avoid blinking or making eye movements until the blink symbol was displayed, in order to reduce contamination of the EEG data. All stimuli were typeset in black Courier New font, 26 point, on a white background. A sequence of 21 practice trials was completed by each participant prior to the main experiment, using a separate set of stimuli. In the main experiment, each of the critical stimuli were presented once in a randomised order using E-Prime. Participants were given a rest period halfway through the trials for as long as they needed.

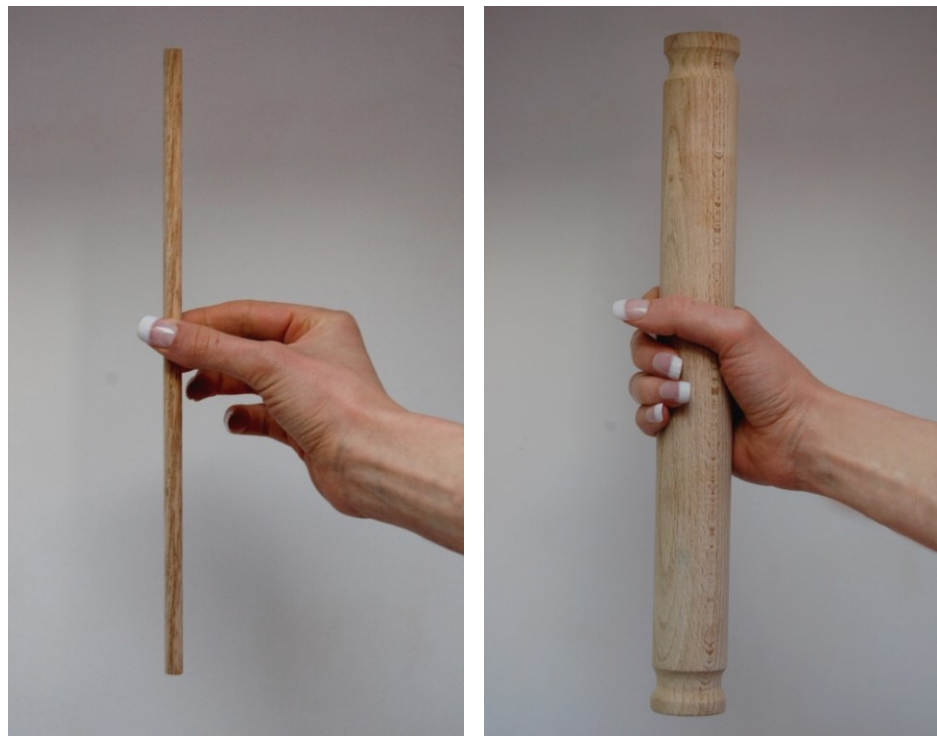


Figure 6. Wooden objects held by participants during the experiment (left, precision grip; right, power-grip).

EEG recording. BrainVision Recorder (Version 1.10, Brain Products GmbH) was used to collect the scalp voltages from 61 Ag/AgCl active electrodes (actiCAP, Brain Products, Gilching, Germany). The sensors were arranged in the International 10–20 configuration and secured in place on the participant’s scalp by an elastic cap. An additional two sensors were positioned below and adjacent to the participant’s right eye to monitor eye movements. All scalp electrode impedance measurements were kept below 20k Ω . The EEG signals were amplified by a BrainAmp MR Plus amplifier (Brain Products, Gilching, Germany).

EEG analyses. Vision Analyser (Version 2.0, Brain Products GmbH) was used to process the data. EEG was sampled at a rate of 250Hz and filtered offline with a band-pass filter of 0.1–30Hz (with a roll-off slope of 48 dB/oct) and subjected to a 50Hz notch filter. The EEG recordings were segmented into 1000 ms epochs, spanning from 200 ms pre-stimulus onset until 800 ms post-stimulus. Separate ERPs were generated for each of the five experimental conditions: functional compatible, functional incompatible, volumetric compatible, volumetric incompatible and non-manipulable. Baseline correction was performed using the average EEG activity between -100 ms and 0 ms. The electrodes were referenced to the left mastoid electrode (TP9) and then re-referenced offline to the average of the left and right (TP10) mastoid data. The central anterior-frontal electrode (AFz) was used as the ground. Segments containing artefacts were rejected from analyses. Participants with less than two-thirds of their segments intact after artefact removal were excluded from the analyses. To make comparisons between the different conditions, we adopted Maris and Oostenveld’s (2007) cluster randomisation technique (see Section 2.3.5 in Chapter 2 for details). Comparisons between conditions were conducted across all electrodes and post zero-point sample points using

pairwise analyses comparing each electrode-time sample pair between two of the tested conditions (e.g., functional compatible with functional incompatible). The analyses were carried out on the segment of data between 150 and 700 ms after stimulus presentation.

3.3.2 Results

Electrophysiological results: Functional vs. volumetric analyses.

Independent *t*-tests were carried out to examine the difference in electrophysiological activity between the functional, volumetric and non-manipulable. Multiple comparisons were corrected using the cluster randomisation procedure. The resulting significant clusters are shown in Table 5 and Figure 7. Comparing the functional and non-manipulable trials revealed one negative cluster of activity from 216–556 ms, $c(F - N)_1$, beginning at midline central electrodes and then spreading across the entire scalp. The comparison between volumetric and non-manipulable trials resulted in two clusters; a negative cluster from 372–484 ms, $c(V - N)_1$, at frontal and central electrodes in the left hemisphere and a positive cluster from 528–672 ms, $c(V - N)_2$, across occipital and parietal areas. When comparing the functional and volumetric conditions, the only significant difference was an early negative cluster from 208–436 ms, $c(F - V)$, revealing that the negative activity in the functional condition was significantly earlier than the negativity in the volumetric condition. This cluster also revealed that the negativity seen in the volumetric condition was lateralised to the left, whereas the negativity in the functional condition was located more broadly and extended across both hemispheres.

Additional analysis: Functional vs. non-manipulable (all clusters).

The positive activity in the volumetric condition was not present in the functional data but the analyses showed there was no significant difference between the two conditions (see Table 5 and Figure 7). For this reason, we

carried out a modified version of the previous analysis to check for any sub-threshold clusters.

Table 5

Significant clusters: Comparing functional and volumetric affordances.

Conditions compared	No. of clusters	Name of cluster	Polarity	Duration	<i>P</i> -value
Functional – Nonmanipulable	1	c(F – N)	Negative	216–556 ms	$p < .0001$
	[2]*	[c(F – N) ₂]	[Positive]	[588–640 ms]	$p = [.001]$
Volumetric – Nonmanipulable	2	c(V – N) ₁	Negative	372–484 ms	$p < .001$
		c(V – N) ₂	Positive	528–672 ms	$p = .004$
Functional – Volumetric	1	c(F – V)	Negative	208–436 ms	$p = .001$

*cluster information in square brackets was found using the modified analysis

This analysis is almost identical to the one described in Section 2.3.5, except rather than comparing all clusters to the *p*-value generated from the Monte Carlo distribution of the largest cluster data points, an independent Monte Carlo distribution was formed for each cluster meaning that each cluster was tested against its own distribution. Due to the multiple comparisons made with this methodology, the Bonferroni Correction was applied to each cluster statistic. The potential benefit of this more extensive analysis was that smaller clusters which might have been concealed by larger clusters were able to be judged on their own merit, rather than through comparison with the largest cluster. The results of this all-cluster analysis when comparing the functional and non-manipulable conditions was a positive cluster from 588–640 ms, c(F – V)₂ at occipital and parietal areas at the midline and in the right hemisphere

(See Figure 8). This reveals that both the functional and volumetric affordance conditions share this late positive activity.

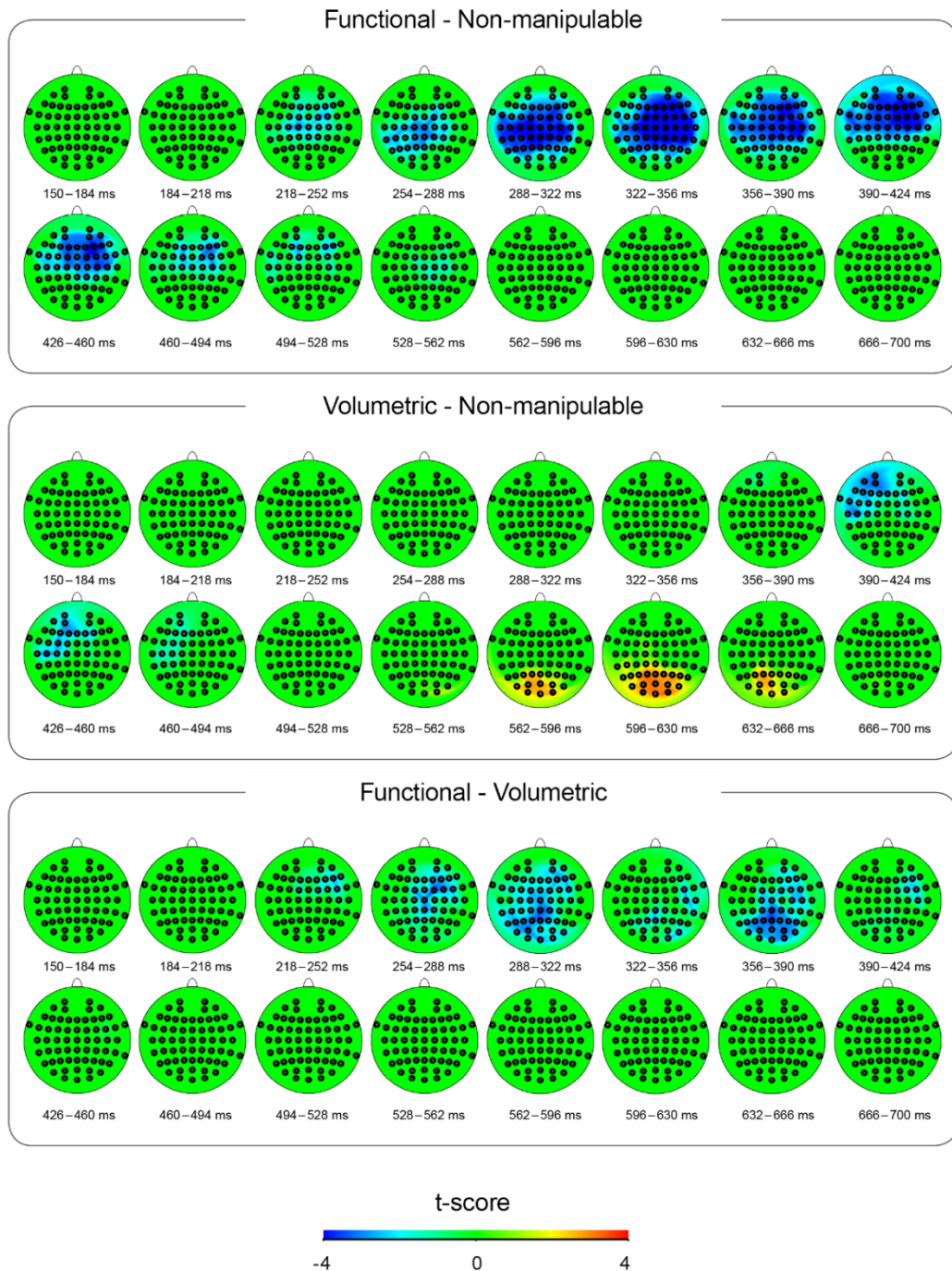


Figure 7. Scalp maps showing t -scores for significant clusters revealed by the cluster randomisation comparison between the functional, volumetric and non-manipulable conditions.

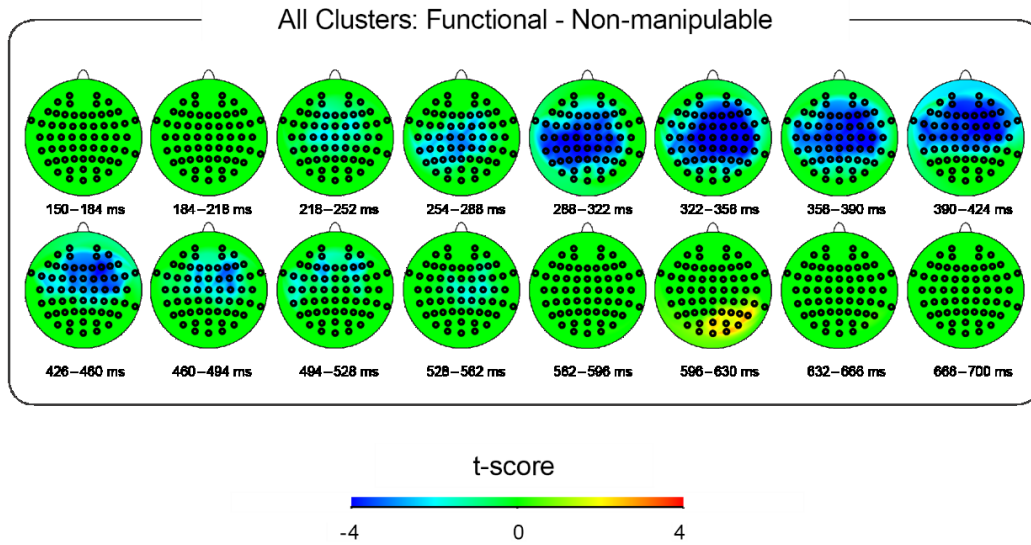


Figure 8. Significant clusters resulting from the all-cluster randomisation test comparing the functional and non-manipulable conditions.

Compatible vs. Incompatible Analyses. Independent *t*-tests were carried out to examine the difference in electrophysiological activity between the compatible and incompatible trials for both functional and volumetric conditions. Multiple comparisons were corrected using the cluster randomisation procedure. The resulting significant clusters are shown in Table 6 and Figure 9. Comparing the compatible and incompatible trials in the functional condition revealed a positive cluster from 528–644 ms, $c(\text{FC} - \text{FI})$, in temporo-parietal and occipital areas in the left hemisphere. A comparison of the compatible and incompatible trials within the volumetric condition resulted in two significant clusters: a negative cluster from 224–284 ms, $c(\text{VC} - \text{VI})_1$, at the temporo-parietal region in the left hemisphere and a positive cluster from 552–592 ms, $c(\text{VC} - \text{VI})_2$, at frontal, temporal, central and centro-parietal electrode sites in the left hemisphere.

In the final analysis, we compared the compatible–incompatible difference for the volumetric trials with the compatible–incompatible difference

for functional trials. There were two significant clusters. The first was a positive cluster from 236–280 ms, in the left hemisphere, at central, centro-parietal, parietal and parieto-occipital electrodes. The second was a positive cluster from 328–368 ms, also in the left hemisphere but spread more widely from fronto-central, central, centro-parietal, parietal, temporo-parietal and parieto-occipital electrodes. This second cluster was the result of strong negativity in the volumetric condition and weak positivity in the functional condition, presumably, this was why they were not seen in the separate analyses. This is likely to be a continuation of the early negativity we saw in the, $c(\text{VC} - \text{VI})_1$, cluster which did not reach the significance threshold in the previous analysis.

Table 6

Significant clusters: Comparing compatible and incompatible trials.

Conditions compared	No. of clusters	Name of cluster	Polarity	Duration	<i>P</i> -value
Functional compatible – Functional incompatible	1	$c(\text{FC} - \text{FI})$	Positive	528–644 ms	$p < .0001$
Volumetric-compatible – Volumetric-incompatible	2	$c(\text{VC} - \text{VI})_1$	Negative	224–284 ms	$p = .019$
		$c(\text{VC} - \text{VI})_2$	Positive	552–592 ms	$p = .008$
(Functional compatible - incompatible) – (Volumetric compatible – incompatible)	2	$c(\text{FC} - \text{FI}) - (\text{VC} - \text{VI})_1$	Positive	236–280 ms	$p < .0001$
		$c(\text{FC} - \text{FI}) - (\text{VC} - \text{VI})_2$	Positive	328–368 ms	$p = .025$

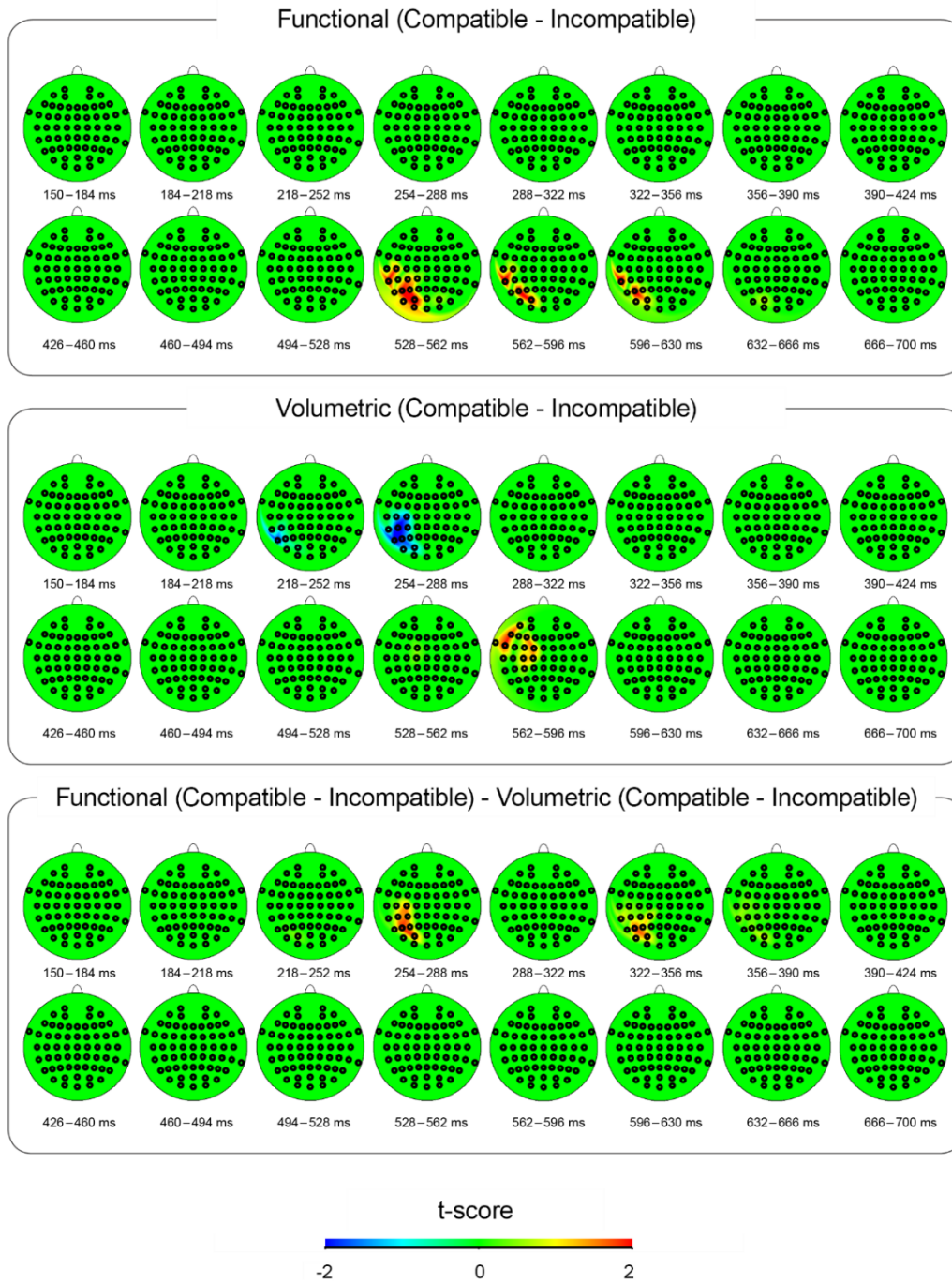


Figure 9. Scalp maps showing t -scores for significant clusters revealed by the cluster randomisation comparison between compatible and incompatible trials for the functional and volumetric conditions.

3.3.3 Discussion of Experiment 1

As predicted, based on previous findings (e.g., Bub & Masson, 2012), the brain activity associated with functionally manipulable objects was significantly earlier (216–556 ms) than the activity associated with objects manipulable solely on the basis of their structure (372–484 ms). Also consistent with Bub and Masson's (2012) findings, was the discovery that brain activity associated with functional affordances was longer lasting compared to volumetric affordances. Additionally, we found that brain activity related to functionally manipulable objects was more widespread across the scalp, compared to volumetric affordance activity which was restricted to the left frontal, fronto-temporal and temporal electrodes. These findings cohere with Siakaluk et al.'s (2008) body-object interaction (BOI) theory which posits that the greater the ease in which a person can physically interact with an object, the richer the sensorimotor representation of that object. They argue that the conceptual representation of an object is a distributed system of sensorimotor information created in the brain incorporating visual, auditory, olfactory, motor and emotional information about that object (Barsalou, 1999). As functionally manipulable objects involve greater manipulation, the sensorimotor concept will be richer and likely involve an integration of information from a wider network of brain areas associated with the person's experiences with that object.

According to Buxbaum and Kalénine (2010), we should not expect to see volumetric affordances activated during object name reading. They argue that this type of affordance is only elicited during direct perception of visual objects, where the geometric properties can be perceived. In consonance with their argument, it is possible that the delay in activation of volumetric affordances was due to the initial need to generate a mental picture or simulation of the object, so that the shape and size of the object and therefore its structural

affordance, could be deduced from this information. However, when we examined the timing of activation for a specific grip, it was the volumetric affordance condition that showed the earliest activity (224–284 ms), not the functional affordance (528–644 ms). Furthermore, this activity was almost as early as the previous analysis for functionally manipulable objects, indicating that holding an object in a particular grasp gesture primes the brain for processing objects that afford being grasped accordingly. This is similar to the finding by Glover et al. (2004), who showed that when participants read the word “grape” and then reached to grasp an object, their grip aperture was significantly smaller than when they had first read the word “apple”.

One possible reason why the specific grip for functionally manipulable objects was activated later, is that the hand-grip afforded by the referent object was not relevant to the task. Buxbaum and Kalénine (2010) argue that functional affordances are only activated when it is relevant to the pursuit of some goal, for example, if a person wanted to use a knife to cut a slice of cake. Furthermore, they suggest that functional actions are only distantly related to the structure of an object, if at all. Given that the participants were simply holding a wooden object in a stationary hand grip, this primes the proprioceptive system for a particular object-structure but not necessarily the action involved in object use. It is also possible that the generation of functional affordances requires semantic retrieval first, in order to access stored knowledge relevant to the use of the object.

3.4 Experiment 2

Given the early affordance-related activity shown in Experiment 1, the main aim of this experiment was to establish whether affordances can be evoked during lexical processing. If so, this would suggest that the conceptual

representation of objects has a deeply embodied component that is more than merely a consequence of spreading activation during semantic processing. To test for this, we used a lexical decision task. Bub, Masson and Cree (2008) did not find any evidence of affordance-activation in their lexical decision study unless the participants were encouraged to attend to the meaning of the word. However, their results were purely reliant on reaction times and ERP activity related to affordance is present even when there is not a significant effect in response times. We were therefore interested to see whether the ERPs in this study might elucidate previously undiscovered evidence of affordance-activation during visual word recognition. It would be particularly striking if volumetric affordances were still activated at this early stage of object name processing. An additional benefit of adopting a lexical decision task is that it ensures the ERP activity related to affordances is kept clear from any additional task-related semantic processing going on. Secondly, in Experiment 1 we failed to see early activation of the specific hand-grip in the functional affordance condition. For this reason, we made the affordance relevant to the task by requiring participants to execute a manual response that was sometimes congruous with the grip that would be used to grasp the referent object.

To create a clearer division between the stimuli used in the two affordance categories, the functionally-manipulable objects were all manmade and the objects in the volumetric condition were all graspable organic items. The semantic representation of manmade objects relies more heavily on their functional use, compared to natural objects whose representation depends more on their perceptual features such as colour, shape and size (Farah & McClelland, 1991; Ferri, Riggio, Gallese & Costantini, 2011).

3.4.1 Method

Participants. Forty right-handed (assessed using the Edinburgh Handedness Inventory; Oldfield, 1971), native English speakers were paid £12 for their participation in the experiment. The data from five of the participants was not included in the final analysis due to excessive EEG and EOG artefacts. The remaining 35 participants (21 females) were aged 18–32 ($M = 21.7$; $SD = 2.7$). The participants had normal, or corrected-to-normal, vision and no history of neurological impairment.

Stimuli. The stimuli consisted of 60 concrete nouns referring to manually manipulable objects and 60 nonsense strings of letters (non-words) generated using the English Lexicon Project (Balota et al., 2007). Half of the nouns described manmade objects and half described natural objects. Within each of these semantic categories, half were objects that afforded being grasped with a precision-grip (e.g., pencil, cherry) and half afforded being grasped with a power-grip (e.g., kettle, banana). This meant that there were 15 object names in each condition (manmade-power; manmade-precision; natural-power; natural-precision). All stimuli were balanced in terms of linguistic characteristics (word length, SUBTLEX word frequency, uniqueness point, orthographic neighbourhood size, OLD20; all $ps > .1$). A full list of the stimuli can be found in Appendix B.

Procedure. The participants were seated in a quiet, dimly lit booth. Stimuli were presented using E-Prime 2.0 (Schneider & Zuccoloto, 2007) on a CRT monitor (30.5cm height by 40.5cm width; 100Hz refresh rate) positioned one metre from the participant. A letter string would be presented on the screen and the participant had to decide whether it was a word or not. Half of the participants were asked to respond to words only (go condition) and half were asked to respond to non-words (nogo condition). Within each response group,

half responded using a device that was grasped using the palm of their hand (power-grip response device) and half responded by pressing a button between their forefinger and thumb (precision-grip response device; see Figure 10 for a photo of the response devices). This meant that participants in the “go” group would sometimes be responding using a grasp response that would be used to pick up the referent object (compatible condition; e.g., a power-grip response to the word “hammer”) and at other times they would be responding to an object with a grip that would not be used to pick up the object (incompatible condition; e.g., precision grip response to the word “cucumber”). Participants who were required to respond to non-words would sometimes be withholding a compatible response (e.g., withholding a precision-grip to the word “dart”) or withholding an incompatible response (e.g., withholding a power-grip to the word “eraser”).

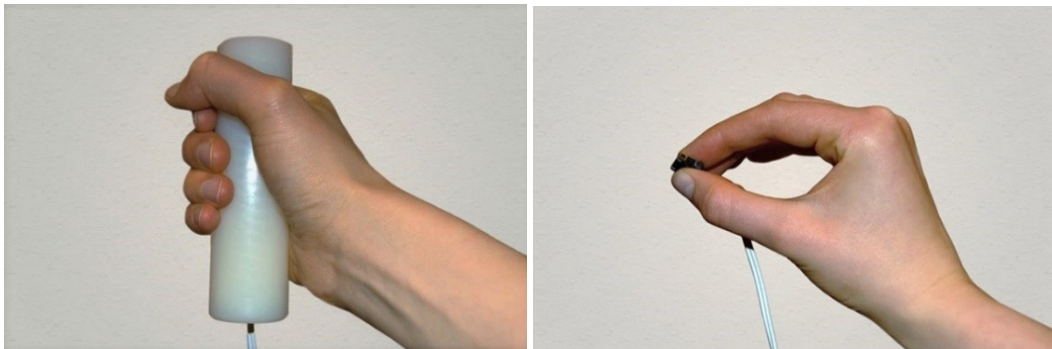


Figure 10. The response devices: power-grip (left) and precision-grip (right).

Each trial began with a fixation point, ‘+’, which appeared at the centre of the screen for 600–800 ms. After the fixation point, a letter string would be presented for 1500 ms or until the person responded. At the end of each trial a blink symbol was displayed for 1500 ms, giving the participant the opportunity to blink if necessary. The participants were asked to avoid blinking or making eye movements until the blink symbol was displayed, in order to reduce

contamination of the EEG data. All stimuli were typeset in Courier New, point size 26, in black on a white background. A sequence of 16 practice trials was completed by each participant prior to the main experiment, using a separate set of stimuli. In the main experiment, the stimuli were presented 3 times in a randomised order using E-Prime, totalling 360 trials. Participants were given a rest period after every 70 trials for as long as they needed.

EEG recording. BrainVision Recorder (Version 1.10, Brain Products GmbH) was used to collect the scalp voltages from 61 Ag/AgCl active electrodes (actiCAP, Brain Products, Gilching, Germany). The sensors were arranged in the International 10–20 configuration and secured in place on the participant's scalp by an elastic cap. An additional two sensors were positioned below and adjacent to the participant's right eye to monitor eye movements. All scalp electrode impedance measurements were kept below 20k Ω . The EEG signals were amplified by a BrainAmp MR Plus amplifier (Brain Products, Gilching, Germany).

EEG analyses. Vision Analyser (Version 2.0, Brain Products GmbH) was used to process the data. EEG was sampled at a rate of 500Hz and filtered offline with a band-pass filter of 0.1–40Hz (with a roll-off slope of 12 dB/oct) and subjected to a 50Hz notch filter. The EEG recordings were segmented into 1000 ms epochs, spanning from 200 ms pre-stimulus onset until 800 ms post-stimulus. Separate ERPs were generated for the different experimental conditions (manmade-compatible-go; manmade-incompatible-go; natural-compatible-go; natural-incompatible-go; manmade-compatible-nogo; manmade-incompatible-nogo; natural-compatible-nogo; natural-incompatible-nogo). Baseline correction was performed using the average EEG activity between -200 ms and 0 ms. The electrodes were referenced to the left mastoid electrode (TP9) and then re-referenced offline to the average of the left and right

(TP10) mastoid data. The central anterior-frontal electrode (AFz) was used as the ground. Segments containing artefacts were rejected from analyses. Participants with less than two-thirds of their segments intact after artefact removal were excluded from the analyses. Comparisons between compatible and incompatible trials and between the manmade and natural conditions were conducted using the Monte Carlo cluster analysis procedure described in Section 2.3.5. Analyses were carried out on the section of the ERP segments between 200–700 ms.

3.4.2 Behavioural Results

Accuracy data. The average proportion of correct responses across all conditions was found to be 95% and above. An ANOVA was conducted comparing accuracy between the 2 conditions (manmade, natural), 2 response types (go, nogo) and 2 compatibilities (compatible, incompatible). There were no significant differences, $ps > .05$.

Reaction times. An ANOVA was conducted comparing the reaction times within each semantic category (manmade, natural) with compatibility (compatible, incompatible). The only significant effect was between the two semantic categories, with natural items being responded to quicker ($M = 592.24$ ms, $SD = 92.22$) compared to manmade items ($M = 606.36$, $SD = 93.84$; $F(1, 18) = 7.49$, $p = .014$).

3.4.3 Electrophysiological Results

Paired sample t -tests were used to compare the ERPs of the compatible manmade trials with the incompatible manmade trials. Individual t -tests were conducted for each sample recorded over each of the electrodes and multiple comparisons were then corrected using the cluster randomisation procedure. The significant clusters are displayed in Table 7 and Figure 11. The results showed a negative cluster, 372–498 ms, at central, central-parietal, parietal and

occipito-parietal electrodes in the left hemisphere and at the midline, c(MC – MI)Go. The comparison between compatible and incompatible trials in the natural condition resulted in a positive cluster, 508–576 ms, at frontal, fronto-temporal and fronto-central electrodes in the left hemisphere, c(NC – NI)Go. When the compatibility analyses from the natural and manmade conditions were compared, there were two significant positive clusters. The first cluster, 370–428 ms, was located at fronto-central and central electrodes at the midline, c(NC – NI) – (MC – MI)Go₁, and the second cluster, 430–478 ms, was located in the right hemisphere at parietal electrodes, c(NC – NI) – (MC – MI)Go₂.

Table 7

Compatible vs. incompatible for natural and manmade object names: Go trials

Conditions compared	No. of clusters	Name of cluster	Polarity	Duration	<i>P</i> -value
Manmade Go (Compatible-Incompatible)	1	c(MC – MI)Go	Negative	372–498 ms	<i>p</i> < .0001
Natural Go (Compatible-Incompatible)	1	c(NC – NI)Go	Positive	508–576 ms	<i>p</i> = .005
Natural Go (Compatible-Incompatible) – Manmade Go (Compatible-Incompatible)	2	c(NC – NI) – (MC – MI)Go ₁	Positive	370–428 ms	<i>p</i> = .01
		c(NC – NI) – (MC – MI)Go ₂	Positive	430–478 ms	<i>p</i> = .005

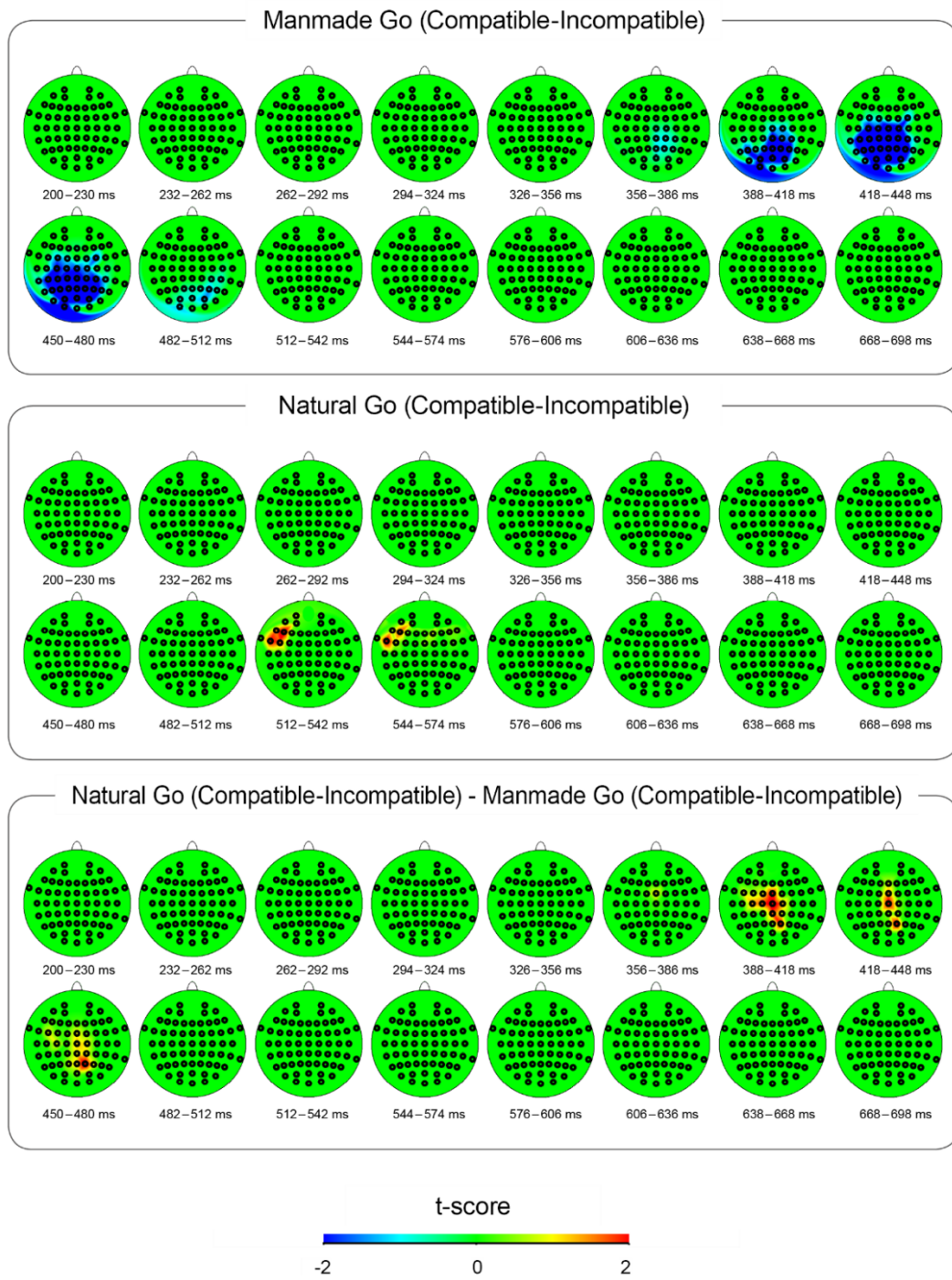


Figure 11. Scalp maps showing significant clusters revealed by the cluster randomisation comparison between compatible and incompatible trials for manmade and natural object names during go trials.

Nogo trials: Compatible vs. incompatible. When comparing the compatible and incompatible trials for the manmade condition there was a positive cluster, 540–586 ms, located at central, centro-parietal and parietal electrodes at the midline and electrodes either side of the midline, $c(\text{MC} - \text{MI})\text{Nogo}$ (see Table 8 and Figure 12 for results). A comparison between compatible and incompatible trials for the natural condition resulted in a negative cluster from 272–312 ms at central, parietal and parieto-occipital electrodes at the midline, $c(\text{NC} - \text{NI})\text{Nogo}$. Comparing the natural and manmade compatibility analyses resulted in a negative cluster, 534–592 ms, at centro-parietal, parietal and parieto-occipital electrodes at the midline, and in the right hemisphere, $c(\text{NC} - \text{NI}) - (\text{MC} - \text{MI})\text{Nogo}$.

Table 8

Compatible vs. incompatible for natural and manmade object names: Nogo trials

Conditions compared	No. of clusters	Name of cluster	Polarity	Duration	<i>P</i> -value
Manmade Nogo (Compatible-Incompatible)	1	$c(\text{NC} - \text{NI})\text{Nogo}$	Positive	540–586 ms	$p = .003$
Natural Nogo (Compatible-Incompatible)	1	$c(\text{MC} - \text{MI})\text{Nogo}$	Negative	272–312 ms	$p = .009$
Natural Nogo (Compatible-Incompatible) – Manmade Nogo (Compatible-Incompatible)	1	$c(\text{NC} - \text{NI}) - (\text{MC} - \text{MI})\text{Nogo}$	Negative	534–592 ms	$p < .0001$

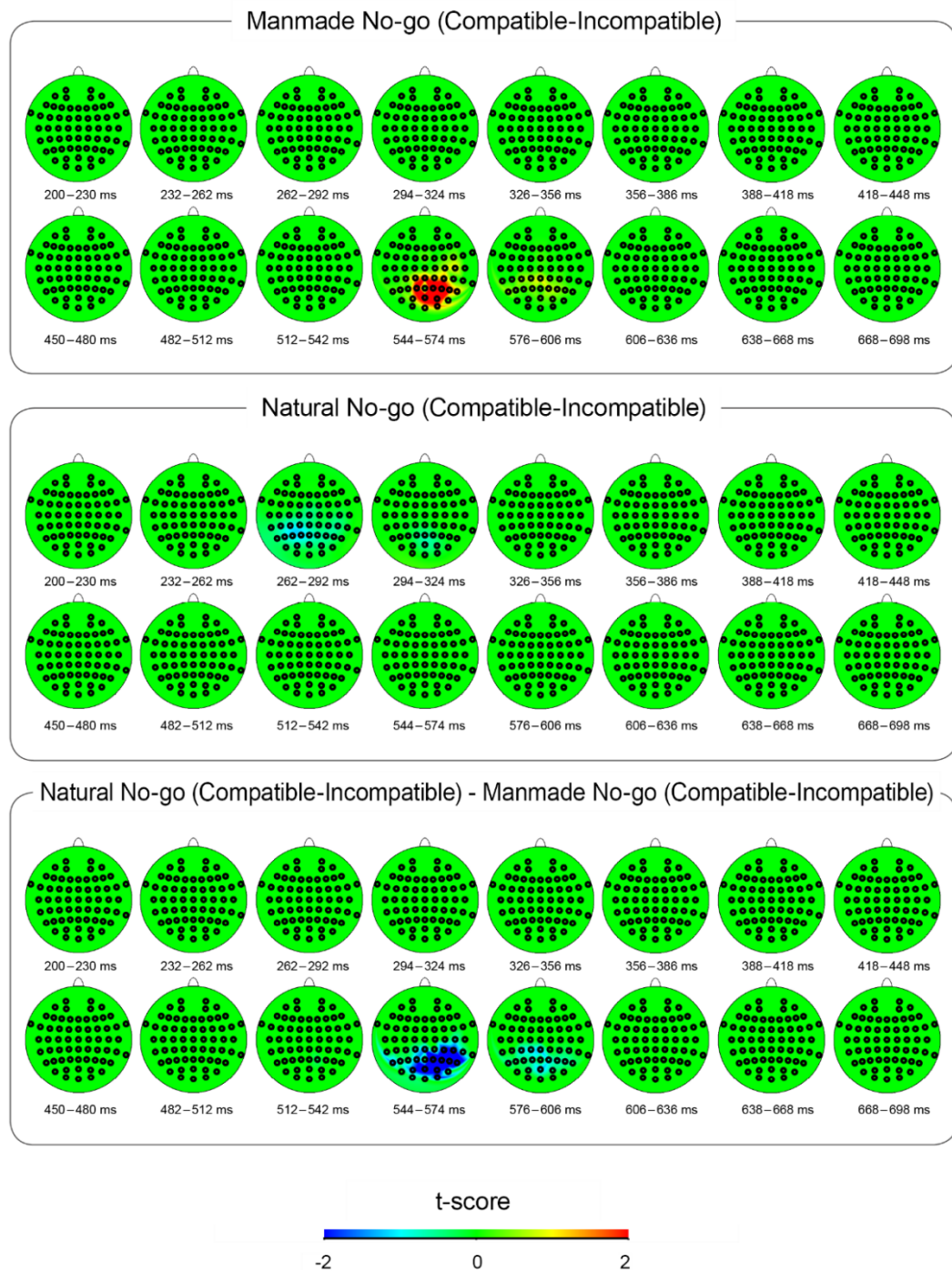


Figure 12. Scalp maps showing significant clusters revealed by comparison between compatible and incompatible trials for manmade and natural object names during nogo trials.

3.4.4 Discussion of Experiment 2

Following our predictions, when participants were required to execute a response, the specific grip adopted during functional use of an object was elicited at around 370–500 ms after reading the name of that object. This is within the usual time frame for N400 semantic activity and is very similar to the brain activity seen in Experiment 1, for the stimuli in the volumetric affordance condition. During trials when a response was required, the grip related to the geometric properties of the object was not evoked until 500 ms post-stimulus onset. However, when participants were withholding a response, the opposite pattern was found: late affordance activation for functionally manipulable objects, 540–586 ms, and early activation for objects with a volumetric affordance, 272–312 ms. These findings also support the argument that functional affordances are only activated when they are applicable to the situation. When the participants were required to respond using an action that would be afforded by the referent object (making the affordance relevant to the task) there was early activation of functional affordances. Whereas, when participants were required to withhold a response so that the motor affordance was irrelevant to the task, activation of functional affordances was much later. Additionally, the results of this experiment follow the same trend as Experiment 1 (Chapter 2) with the specific volumetric grip only being activated when the participant was inhibiting their response.

3.5 Overall Discussion

In these experiments, we examined the differences in the timing of access to linguistically-generated functional and volumetric affordances during object name reading. In Experiment 1 we found that brain activity associated with functionally manipulable objects began early, ~216 ms. This activity was

widespread across the scalp, including fronto-central electrodes (cluster c(F-N) in Figure 7), which are associated with the premotor cortex and supplementary motor area (Puzzo, Cooper, Vetter & Russo, 2010). These areas are involved in planning and controlling body movements. Research suggests that the temporal lobe begins to access semantic information about a word's referent from around 150–160 ms after reading the name of an object (Amsel, 2011; Amsel et al., 2013; Hauk et al., 2012; Moseley, Pulvermüller & Shtyrov, 2013; Wamain, Pluciennicka & Kalénine, 2015). In this study, the brain activity also extended to anterior frontal, frontal and temporo-frontal electrodes. As aforementioned, the magnitude of this activity may reflect the semantic richness of functionally manipulable objects, due to greater sensorimotor experience (Barber, Otten, Kousta & Vigliocco, 2013; Siakaluk et al., 2008). Research has shown that the more interaction a person has with an object, the greater the extent of motor activity related to that person's mental representation of the object (Calvo-Merino et al., 2005; Rüeschemeyer, Lindemann, van Rooij, van Dam & Bekkering, 2010; Siakaluk et al., 2008; Yee, Chrysikou, Hoffman & Thompson-Schill, 2013). The motor activity was greater for functionally manipulable, compared to volumetric, object names.

The brain activity associated with objects whose graspable characteristics are based on geometry, rather than learned use, occurred in a later time-frame, 372–484 ms. This timing is similar to a previous ERP study which found that the graspability of an object was activated around 340 ms after reading the object name (Amsel et al., 2013). The authors defined graspability as the ability to grasp the object with one hand even if the person had not done this before or was unlikely to do so. They used objects such as “mouse” and “egg”. Although they did include some tools in their selection of stimuli (e.g., “knife”), many of the objects appear to afford being grasped to be picked up and moved, but do

not afford being grasped during use of the object. For this reason, their study seems to have focused predominantly on volumetric affordances. Our study supports their findings as we began to see activity associated with volumetric affordances around 370 ms. This brain activity was located in the left hemisphere at frontal, temporal and central electrodes. These electrodes are located over the dorsolateral prefrontal cortex, precentral gyrus and supplementary motor area, which are thought to be active during the mental simulation of body movements (Grèzes & Decety, 2001). This might suggest that the individual needs further information, such as activating a mental image of the object, to access details about its structure and consequently the associated structural affordances. This fits with a mental simulation theory of affordance activation (Bergen & Wheeler, 2010; Borghi et al., 2007).

Our volumetric affordance results also paralleled those found by van Schie and Bekkering (2007), who discovered that actions associated with transporting the object towards the “final goal location” showed activity in left frontal regions. Volumetric affordances are synonymous with grasping to move an object and similarly, in this experiment, we saw activity in the left frontal regions. This is also corroborated by other findings showing that manipulating objects with the left or right hand, results in the recruitment of a left lateralised brain network (Brandi et al., 2014; Garcea, Almeida & Mahon, 2012). Also, the left temporal lobe, where we see the volumetric activity, is associated with linking conceptual information about an object with the associated word form (Acres, Taylor, Moss, Stamatakis & Tyler, 2009; Mesulam et al., 2013). This brain activity was present in both the functional and volumetric conditions, with conceptual information related to functionally manipulable objects being accessed first. When comparing the functional and volumetric conditions, the only significant difference was an early negative cluster from 208–436 ms, $c(F -$

V), revealing that the negative activity in the functional condition was significantly earlier than in the volumetric condition. This cluster also revealed that the negativity seen in the volumetric condition was lateralised to the left, whereas in the functional condition it was located more broadly and extended across both hemispheres. As manipulating an object during use requires greater motor activity, compared to merely picking up an object, it is not surprising that there is greater sensorimotor activity in the ERP data for names of functionally manipulable objects (Anelli, Nicoletti & Borghi, 2010).

To investigate when a particular hand-grip was being mentally prepared, we asked participants to hold a wooden object in a power or precision grip, which either shared the micro-affordance of the referent object (compatible) or not (incompatible). The compatibility analysis for the functional affordance condition revealed a late positive cluster from 528–644 ms, c(FC – FI). This suggests that the specific grip associated with the use of an object is not processed until much later, after N400 semantic processing. The functional affordances were generated just before an expected response was warranted (responses to probe words were around 500 ms). This is possibly because, as Buxbaum and Kalénine (2010) argue, functional affordances are not activated unless there is an intention to act upon an object. In this study, participants were only responding to probe words with a button press, so the functional affordance was not relevant to the task. Given that the participant was merely holding an object in a stationary position with their right hand, in either a power or precision grip, it is plausible that this alone was not enough to generate an affordance specific to that grip.

When comparing the compatible and incompatible trials in the volumetric affordance condition, we discovered an early negative cluster from 224–284 ms at temporo-parietal electrode sites in the left hemisphere. The

location of this activity was over the angular gyrus, which is situated in the parietal lobe near the superior edge of the temporal lobe. The angular gyrus is associated with lexical-semantic integration; a process of coding whether incoming information matches the present context (Price, Bonner, Peelle & Grossman, 2015). In the current experiment, this result reflects the time point at which the participants have processed the meaning of the noun and activated the associated grip affordance. The angular gyrus then judges whether this fits with the present proprioceptive information from the participant's motor system, about the grasp they are using to hold the wooden object. Presumably, the left side activation reflects the corresponding side of the body that is holding the object. The motor activity during this epoch is located at C3 electrode, in the left hemisphere, which corresponds to the hand area of the motor cortex, controlling the right hand (Pfurtscheller, Stancak & Neuper, 1996). Studies show how viewing an object or reading the name of an object, such as an apple, can influence subsequent grip aperture when preparing to grasp an object (e.g., Glover et al., 2004) or influence what items are noticed in an array (e.g., Myung et al., 2006). It is possible that the size of the object is being accessed at this early stage of semantic processing and this is then being matched for compatibility with the participant's current hand gesture.

The volumetric compatibility data also revealed a late positive cluster, from 548–596 ms, which was around the same time as the functional cluster from 528–644 ms, c(FC – FI). It appears to be located in a different region of the left hemisphere, at frontotemporal, frontocentral and centro-parietal electrodes, but the difference between the two clusters was not statistically significant. In both the functional and volumetric conditions, the positive cluster was characterised by incompatible trials displaying greater negativity in the frontal lobe and compatible trials displaying greater positivity in the parietal

and occipital lobes. This activity is around the time that participants usually begin to respond to stimuli (515–919 ms; $M = 679$ ms). For this reason, we can assume that when participants are preparing to respond this activates a motor program for the appropriate response. The prepared grip and activated affordance of the referent object interfere with each other, as they are both competing for the hand area of the motor system. Even though the participants were not responding to the critical stimuli, it is interesting to see this strong frontal negativity, perhaps signifying inhibition of the affordance when the participant's grip was incompatible with the referent object; the posterior positivity seemingly reflecting pattern-matching of affordance and grip.

The findings of the second experiment served to confirm our hypotheses from the first experiment. Firstly, when the participant was required to respond to object names with a grasp relevant to the referent object, we saw earlier activity associated with functionally manipulable (manmade) objects, from around 370–500 ms, $c(MC - MI)Go$. This suggests the specific affordance for manmade objects was elicited during N400 semantic processing. Previous findings suggest that motor activity associated with early affordance activation is not related to the specific hand-grip used to hold the object, but instead is a more general or abstract motor activity (Postle, Ashton, McFarland & De Zubicaray, 2013; Rueschemeyer et al., 2010). This is what we saw in the first experiment, with motor activity beginning around 216 ms. Grip-specificity appears to be actuated once the person has semantically processed the need for its activation. This supports previous research showing that functional affordances are only generated when the participant intends to grasp a tool to use it (Lindemann, Stenneken, van Schie & Bekkering, 2006; Roche & Chainay, 2017). During the nogo trials, when a response was not required by participants, a similar effect was seen in the brain activity as for functional affordances in the

first experiment; a late positive cluster from 540–586 ms, c(MC – MI)Nogo.

This makes sense as participants were not responding to the critical stimuli in Experiment 1 (they were all nogo trials).

When the participant was required to respond to natural object names in Experiment 2, the compatibility effect was not seen until much later on, around 508–576 ms, which was just before participants began to respond. Whereas, when participants had to withhold a response, the early activity seen in the previous experiment for the volumetric compatibility analysis was present: a negative cluster from 272–312 ms in the left hemisphere at central, centro-parietal and parietal electrodes. Interestingly, we only see this early activity for the volumetric/natural condition when a response is being withheld. The participant makes a semantic or lexical decision around 160 ms (Hauk et al., 2012), which then enables them to make the decision to inhibit a response on nogo trials. When the participant is holding an object or response device, that matches the grasp afforded by the referent object, they then must inhibit the affordance which is reflected in this early negative cluster. During the go trials there is no need to inhibit the primed affordance, so we do not see the associated activity until just before a response is needed, around 500 ms.

Whereas motor activity is thought to play an essential role in the semantic representation of manmade objects, particularly tools (as we saw from the c(F – N) cluster), natural objects are associated more with their perceptual features, such as colour and shape (Aravena et al., 2010; Ferri et al., 2011). In this study, we argue that the hand gesture of the participant is being matched with the size of the object which has been deduced from early semantic processing of the object name. Functionally manipulable objects require N400 semantic retrieval before affordances are activated, which involves accessing knowledge relevant to use of the object. Interestingly, responses to natural

objects were quicker than to manmade objects which has been shown by previous research (Anelli et al., 2010; Borghi, et al., 2007; Ferri et al, 2011; Gerlach, 2009). These authors have argued that processing manmade object names takes longer due to the recruitment of sensory and motor brain activity (Ferri et al., 2011).

According to 2AS theory, volumetric and functional affordances are processed via separate systems in the brain (Buxbaum & Kalénine, 2010). Functional affordances recruit the ventro-dorsal system, which is the lexico-semantic route. This fits with our results given that the timing of retrieval for functional affordances in this study was during N400 semantic processing. Volumetric affordances use the dorso-dorsal route which relies on a visual-motor matching process (Buxbaum & Kalénine, 2010). The activation of volumetric affordances during noun processing goes against Buxbaum and Kalénine's (2010) 2AS theory, which suggests that this type of affordance can only be activated online through visual perception of the structure of an object. However, we argue that our results appear to follow a similar pattern-matching process, whereby the angular gyrus matches whether the size of the object (retrieved through early semantic processing) is congruent with the participant's grasp.

It would appear that a particular micro-affordance is not activated via the same route for functionally manipulable objects as it is for objects that afford being grasped purely based on their geometric properties. Our results show that although functionally manipulable objects also have an affordance based on their geometric properties, inhibiting this does not interfere with semantic processing in the same way it does for the objects in the volumetric condition. This is perhaps because functional affordances are more influenced by movement, rather than preparing to grasp a particular size of object. Functional

affordances, on the other hand, are associated with a more complex motor representation related to grasping, manipulating and moving the object during use. This does not just involve the simple preparation of a hand grasp but also involves repeated hand and/or arm movements. For example, a hammer is held in a power-grip during use, but the functional action is an arm-swinging motion. Therefore, the functional affordance is not manual at all. This might explain why the early motor activity related to functionally manipulable objects is unrelated to the grasp the participants were using to hold the wooden object. This would also explain why we do not see any facilitation of functional affordances in our response times, as the participants' responses in Bub, Masson and Cree's (2008) study were actions related to the use of the object, not just the grasp used to hold it.

As aforementioned, volumetric affordances are weaker and generally thought to rely on visual input (Bub & Masson, 2012; Buxbaum & Kalénine, 2010). Our research suggests that they can be activated with the help of a prepared hand grasp. In one experiment, Bub and Masson (2012; Experiment 1) found a negative priming effect for volumetric affordances at object name onset, which was not seen for functional affordances. They noted that this was consistent with previous findings found for action verbs. However, they argued that their finding was due to weaker activation of volumetric affordances and greater competition from functional affordances. Our findings show earlier activation of volumetric affordances, which may be related to the early negative priming effect seen in Bub and Massons' (2012) study. We argue that this negative priming effect at word onset, consistent with the action affordance data, might reflect the early pattern-matching process we have discussed.

Our findings could also have implications for how we teach children names of objects. Developmental research shows how pre-schoolers learn about

novel objects using information about how those objects are used and categorise them accordingly, rather than grouping them based on perceptual similarity (Greif, Nelson, Keil & Gutierrez, 2006; Nelson, Egan & Holt, 2004; Nelson, Frankenfield, Morris & Blair, 2000). Furthermore, a one-year-old's ability to correctly demonstrate the functional use of toys predicts their language score at two years old (Adams, 2016; Ungerer & Sigman, 1984). This suggests that when teaching children object names, the emphasis should be on helping them develop a rich semantic concept through engaging in play; focusing on their experience with the objects, rather than the traditional method of matching words to pictures.

3.6 Conclusion

Our results show how objects with a functional affordance activate early motor activity linked to a stored representation of the referent, which is not specific to the actual grip used to pick up the object. Grip-specific affordance appears to come much later, during N400 semantic processing, possibly suggesting that it is being generated through a simulation of functional object use. Furthermore, the specific grip is only generated when there is an intention to act on the object. The early widespread brain activity from around 200 ms seems to be linked to other aspects of the object's semantic concept, such as motor activity related to body movements during use of the object. This activity has become associated with the object's concept through Hebbian learning and is automatically elicited when reading the name of a manmade/functionally manipulable object. As for natural objects, early brain activity is only seen for a specific grip on nogo trials. This suggests that the act of inhibiting a specific grip causes a clash between early semantic processing of the size and/or shape of the object and motor information from the grip the participant is withholding. This

reveals that some pattern-matching process is occurring early on, possibly in the angular gyrus, for objects whose graspability is based on the perceptual properties of the object.

4. An Electrophysiological Exploration of the Semantic Representation of Objects and Actions

4.1 Chapter Abstract

Hammers are used to hammer, saws saw, and we pin with a pin. Names of common tools are often also used to refer to the action associated with them; but for these words, which is most fundamental to their conceptual representation, the action or the object? We used words such as these to examine the relative timing of access to semantic information related to the noun or verb form in an ERP experiment. We presented participants with the names of tools, with the ERPs recorded during this visual word recognition converted to separate correlational waveforms using the verb or noun frequency of the word as the covariate. The findings revealed that brain activity correlated with verb frequency had an earlier onset, beginning around 190 ms, followed by activity related to noun frequency, at approximately 290 ms. We also correlated ERP activity associated with the referent object's manipulability ratings, which resulted in positive brain activity from around 500 ms. In the final analysis, we correlated the ERP activity generated while the participants read the tool names, with the participants' ratings for how frequently they used the referent objects and how often they had observed the objects being used by someone else. The ERPs for frequency of object use showed an N400 effect from around 270–430 ms, and for observation of use it was around 270–360 ms. Our findings reveal that motoric actions associated with a word are generated during the earliest stages of semantic processing, reflecting their significance to the conceptual representation of the word form. This is followed by brain activity

related to the object concept during N400 semantic processing and then, later on, a mental simulation of the specific manipulations of an object during use, which is reflected in a post-N400 late positive component (LPC). The conceptual representation of an object appears to be related to how frequently the object has been used (and observed being used) and this is indicated by the N400 effect overlapping both the action representation and object concept ERP timings.

4.2 Introduction

As aforementioned, there is substantial evidence that object names elicit motor activity related to the interactions we have with the referent object in real life. However, it is unclear what this motoric activity represents, or when specific motor programs associated with an object are activated during linguistic processing. This study looks at the timing of access to different information associated with an object: the associated actions during use, the conceptual representation of the object, manipulability, and the timing of access to an individual's personal use of the object.

The first part of this study looked at when the representation of actions and objects is activated during word reading. Previous research has looked at the differences in neural processing of object names (nouns) and action words (verbs) in order to explore when and where semantic information related to these words is processed. One lexical decision study found topographical differences between nouns and verbs from around 200 ms (Pulvermüller, Lutzenberger & Preissl, 1999). Nouns referring to visual objects recruited neuronal activity in the occipital lobe, whereas verbs showed greater activation of motor and premotor areas of the brain. Similarly, an EEG study looking at the neural distinction between nouns and verbs in Chinese showed differences

between nouns and verbs in the occipital lobe and motor cortex during 150–250 ms and 380–450 ms epochs (Zhao, Dang & Zhang, 2017). The authors of these studies concluded that these differences were due to a semantic differentiation between the words, because nouns referring to objects are thought to have higher visual associations and verbs referring to actions have a greater association with motoric actions (Pulvermüller, Lutzenberger & Preissl, 1999). Furthermore, action words are somatotopically organised in the motor cortex according to which body part performs the action, e.g., leg actions such as “kick” activate the leg area of the motor cortex and arm-related actions such as “write” activate the area of the motor cortex corresponding to arm movements (Mollo, Pulvermüller & Hauk, 2016). This effector-specific activity occurs from around 150 ms which is thought to be when lexical access and the earliest stage of semantic information retrieval occurs (Amsel et al., 2013; Hauk et al., 2012; Moseley et al., 2013; Schendan & Kutas, 2003). Noun concepts belonging to different semantic categories have also been shown to be processed in separate cortical regions (Dekker, Mareschal, Johnson & Sereno, 2014). For example, areas of the brain active during tool name processing included the left middle temporal gyrus and the inferior frontal gyrus, which are involved in planning and processing actions related to tool use (Beauchamp, Lee, Haxby & Martin, 2002; Fagg & Arbib, 1998); whereas, processing of animal names involved the primary occipital cortex, the lateral occipital complex and the right fusiform gyrus which are involved in processing faces and body parts (Dekker et al., 2014). Furthermore, words referring to the names of manipulable objects are thought to activate areas of the brain involved in interactions with the referent (Barsalou, 2008; Bub and Masson, 2012; Buxbaum & Kalénine, 2010; Chao, Haxby, Martin, 1999; Dekker et al., 2014; Glover, Rosenbaum, Graham, and Dixon, 2004; Myung et al., 2006; Willems & Hagoort, 2007). These findings

suggest that in order to access the meaning of words, it is necessary to activate the same brain areas that would be involved while looking at, or using, that object in real life (Glenberg & Robertson, 1999, 2000).

These sensorimotor brain activations during word processing are thought to develop during our experience with the referent object, or during the execution of the action in real life (Dekker et al., 2014; Kiefer, Sim, Liebich, Hauk & Tanaka, 2007; Scorolli et al., 2011). One explanation that has been offered to elucidate these findings is the Words As Tools (WAT; Borghi & Cimatti, 2009) theory, whereby two separate systems in the brain work in unison to enable us to process language; an abstract processing system and a concrete processing system, similar to LASS theory's linguistic and simulation systems (Barsalou et al., 2008). The system that is most engaged during linguistic processing will depend on the method in which that word was acquired (mode of acquisition; MOA; Wauters, Tellings, Van Bon & Van Haften, 2003). If a word is learnt during interaction with the object then it will be grounded in sensorimotor experience (Kiefer et al., 2007) via Hebbian learning (Pulvermüller et al. 1999; Pulvermüller, Moseley, Egorova, Shebani & Boulenger, 2014). Whereas abstract words like “diplomacy” are learnt through linguistic descriptions (Borghi, Flumini, Cimatti, Marocco & Scorolli, 2011) and social interaction (Scorolli et al., 2001), the acquisition of concrete words can occur naturally after the first time a person encounters it (Pulvermüller, 2012). Words referring to manipulable objects, such as “cup”, are learnt more often through grasping the object, and therefore the object concept becomes grounded in sensorimotor experience. WAT proposes that abstract and concrete words are both represented in the linguistic and sensorimotor systems but to differing extents, with concrete words being distributed more in the embodied system and abstract words more in the linguistic system (Rüschemeyer, Brass &

Friederici, 2007). For example, Rüeschemeyer et al. (2007) found that motor verbs (e.g., “to grasp”) produced greater signals in posterior premotor, primary motor (M1), somatosensory (S1) cortices and secondary somatosensory (S2) cortex compared to abstract verbs (e.g., “to think”). In support for WAT theory, Scorolli et al. (2011) carried out a study looking at German and Italian noun-verb pairs that were either: concrete nouns and verbs (hand actions with graspable objects; e.g., “to squeeze” with “a sponge”), abstract nouns and verbs (non-graspable objects with non-motor verbs; e.g., “to admire” with “the sunset”), or a combination of the two (non-graspable object with hand action or graspable object with non-motor verb). In this study, the noun was followed by the verb for the German version of the experiment, whereas the verb was followed by the noun for the Italian experiment, reflecting the different syntactic structures of the two languages. Compatible noun and verb pairs, whether both concrete (CC) or both abstract (AA) were processed quicker than mixed pairs (CA, AC). Moreover, when the first word was a concrete word, the noun-verb/verb-noun pair was processed quicker regardless of which grammatical class it belonged to (i.e., whether it was noun first or verb first; German or Italian). They argue that this supports an embodied view of language processing (e.g., Barsalou et al., 2003), whereby noun-verb/verb-noun pairs are processed quicker in the same system because there is a cost to processing time when there is a switch between systems. However, noun-verb/verb-noun pairs beginning with a concrete word are processed faster because abstract words require more time to process as a consequence of their MOA. Concrete words facilitate the processing of abstract words by providing a context that is semantically rich due to its embodied nature.

Although several studies have looked at differences between nouns and verbs regarding where they are processed in the brain, only a few have looked at

the timing of access to information related to nouns and verbs. The importance of looking at timing is that it can help us to infer which stage of linguistic processing this brain activity reflects (Hauk, Shtyrov & Pulvermüller, 2008). We can then deduce whether it is early lexico-semantic access or post-lexical processing, such as mental imagery, being revealed by these findings (Hauk, Shtyrov & Pulvermüller, 2008). As aforementioned, previous research has explored when a semantic differentiation between nouns and verbs is processed by the brain (Pulvermüller, Lutzenberger & Preissl, 1999; Zhao, Dang & Zhang, 2017). In this study, we looked at words that refer both to graspable objects and the manual action that is imposed upon that object, e.g. “hammer” (we hammer [verb] a nail in with a hammer [noun]) or “drill” (we drill [verb] a hole in a wall using a drill [noun]). These words are denominal verbs meaning they were derived from nouns (Clark & Clark, 1979).

We recorded ERPs during visual word processing in order to see how word frequency is reflected in brain activity, according to how frequently each word is used as an object name (noun frequency) and as an action word (verb frequency). We were interested in the timing and distribution of neural activity associated with the word’s noun frequency and verb frequency. Word frequency is a measure of the number of times a word occurs in a given corpus of written texts (Grainger, 1990). Research shows that words which are more frequently seen are recognised quicker than less familiar words, known as the word frequency effect (Grainger, 1990). For example, the word “window” is a frequently used word in English language, with a word-frequency rating of 86, whereas “spade” has a much lower frequency rating of 2.13.

In the current study, we selected object names that represented the breadth of noun-to-verb frequency ratio seen across the English vocabulary. Approximately half of these had a higher verb than noun frequency (e.g., whisk),

while the remainder had a higher noun than verb frequency (e.g., pencil). The innovative part of the experimental design is that we used the same stimuli in each of the conditions; the same words represented the nouns and verbs. The only differentiator is the proportion of time they are used in those roles. We adopted a similar technique to that used in a previous study (Hauk, Davis, Ford, Pulvermüller & Marslen-Wilson, 2006) which correlated EEG, measured while participants were presented words in a lexical decision task, with the psycholinguistic properties of those words (such as word length and word frequency), to explore the time course of access to this information. From an embodied point of view, we might expect to see differences in the timing of access to the noun and verb frequency ERPs, related to the extent to which the word form is associated with sensorimotor activity. As Scorolli et al. (2011) argue, concrete words are processed quicker than abstract words due to greater use of the sensorimotor system of processing. Research shows there is facilitation of lexical decisions for words referring to objects in which a person can more easily interact with physically (Body-object interaction; BOI; Siakaluk et al., 2008). This suggests that the greater the motor interaction with the referent object, the quicker decisions are made. Action words are acquired more often through motor interaction compared to nouns (Pulvermüller, 2012; Scorolli et al., 2011), and therefore, according to theories of embodiment, should be processed earlier than the object concept, which has a greater association with perceptual features.

In addition to this, we were interested to see when access to specific information about how to manipulate the referent object occurs during object name reading. If manipulability is an essential aspect of an object's conceptual representation, then we might expect it to be activated during a similar time to the ERP covariate with noun frequency, i.e., associated with the object concept.

Madan, Chen & Singhal (2016) found an increased P300 effect (from 275–325 ms) for objects rated as highly manipulable, compared to objects rated as having low manipulability. However, in their study the objects were presented pictorially, and therefore manipulability features would be perceived directly. In our study, it is necessary for the relevant information about the object to be accessed via semantic processing of the word form, so we might expect activation to be later. Nevertheless, Bub & Masson (2008) found a priming effect for the names of functionally manipulable objects after 300 ms of exposure to the word. In their study, participants were preparing to execute a motor response which may have facilitated access to the objects' affordances, so these effects may also be earlier than we expect to find in the current study. Therefore, we were interested to see when manipulability representation would be activated from reading the name of an object, without any priming of motor action from a prepared motor response.

In the final analysis of this experiment, we investigated when brain activity related to an individual's personal experience with an object is activated when reading its name. Reading the names of tools is thought to activate the actions associated with those objects, i.e., their affordances (Bub & Masson, 2012; Glenberg & Robertson, 1999, 2000) and this is thought to result from the person's sensorimotor experience becoming integrated into their conceptual representation of that object (Kiefer, Sim, Liebich, Hauk & Tanaka, 2007; Pulvermüller, 1999). It has been argued that this sensorimotor activity plays a vital role in language comprehension (Bub & Masson, 2012; Glenberg & Robertson, 1999). If this is the case, then we should expect to see brain activity related to personal experience being generated during semantic processing of the word, rather than during a post-semantic spreading of activation.

Beilock, et al. (2008) found that the more experience participants had of performing particular actions, the greater their comprehension of language describing those actions. In their experiment, participants listened to sentences describing everyday actions or actions that would be performed during a game of ice hockey, whilst using functional magnetic resonance imaging (fMRI) to study the participants' brain activity. The participants were either experienced ice hockey players, had watched a lot of ice hockey (ice hockey fans) or had no experience of ice hockey at all (novices). The participants also completed a language comprehension task where they listened to sentences describing ice hockey or everyday actions and were shown an illustration of a person performing an action. They then had to decide, as quickly as possible, whether the image showed the action described in the sentence. Ice hockey players and fans were significantly quicker and more accurate in matching the ice hockey-related pictures to the corresponding sentences, compared to everyday actions. Whereas, the novice participants did not show a performance advantage for either of the sentence contexts. The fMRI results showed that activation of the left dorsal premotor cortex was positively correlated with hockey experience; experienced hockey players showed the greatest activation of this area, followed by the fans. This was also correlated with the response times for the ice hockey-related sentences, with experienced ice hockey players performing quickest. Less ice hockey experience was associated with increased activity in bilateral primary sensory motor regions whilst listening to the hockey-related sentences and this was related to decreased comprehension. Activation of bilateral sensory motor regions is often seen when processing simple movements. The authors concluded that for effective comprehension, it is necessary to recruit neural activity associated with specific action plans related to the described actions, which requires first-hand experience of those actions becoming integrated into

the linguistic concepts. In other words, experience in performing an action or even simply observing those actions, is important for language comprehension.

Similarly, actions performed on objects are thought to be embodied in the conceptual representation of those objects (Barsalou et al., 2008; Dutriaux & Gyselinck, 2016). In one experiment, participants heard words presented auditorily and had to decide whether they referred to concrete or abstract entities, whilst performing a manual “patty-cake” action or a mental rotation (Yee et al., 2013). In a subsequent experiment, the participants named greyscale pictures of objects whilst either performing the patty cake action or no action. Afterward, the participants were asked to rate how much manual experience they had with each of the objects on a scale of 1–7 (low to high frequency of manipulation). The participants had greater difficulty making the concrete/abstract judgement or naming the objects when concurrently performing the manual action; difficulty increased with the amount of manual experience they previously had with the objects. This suggests that mentally processing the concept of an object involves a motor simulation of the way those objects are manipulated in everyday life. Processing the object concept recruits the same neural circuits that are involved in executing the actions associated with using the object. To ascertain the significance of sensorimotor processing during linguistic comprehension, it is important to establish when this associated activity is being generated (Hauk, Shtyrov & Pulvermüller, 2008). For this reason, we were interested to see when these representations of previous object use are activated.

To determine when the sensorimotor activity was being generated, we asked the participants to rate how frequently they had used specific objects and how often they had seen those objects used by someone else. We correlated the participants’ reported ratings with the ERP activity collected while they read the

names of those objects, to see when activity related to an individual's experiences with those objects was being activated. If experience is an integral part of conceptual processing (Yee et al., 2013) and plays an important role in comprehension (Beilock et al., 2008), we would expect that greater frequency of use would be associated with sensorimotor activity during object concept processing. If the observation of object use is also essential to linguistic understanding, then the ERPs related to participants' observation of object use should likewise be processed during this time. Previous research findings suggest that action-experience produces greater sensorimotor activity than mere observation (Beilock et al., 2008; Calvo-Merino et al., 2005; Cannon et al., 2014), so we expect there to be a greater relationship between the object concept and actual interaction with an object, than observation of use. However, if brain activity related to previous experience is evoked as a result of spreading activation or an epiphenomenal mental simulation (Mahon & Caramazza, 2008; Mahon, 2015), then we would expect it to occur after the object concept has been processed, i.e. later than the noun frequency ERP covariate.

4.3 Method

4.3.1 Participants

Sixty native English speaking psychology students from the University of Plymouth participated for course credit. All participants were right-handed as assessed using the Edinburgh Handedness Inventory (Oldfield, 1971), had normal or corrected-to-normal vision and no history of neurological impairment. Four of the participants' data was not included in the final analyses due to excessive EEG and EOG artefacts or a significant proportion of incorrect responses during the experiment. The remaining 56 participants (35 females) were aged 18–31 ($M = 20.05$; $SD = 2.47$).

4.3.2 Stimuli

The stimuli were 36 concrete nouns, referring to manmade objects that are manipulated manually during use. All of these words are also used as verbs in the English language (e.g., hammer, hose; see Appendix C for a full list of the stimuli). Logarithmic noun and verb frequencies for each word were obtained from the online CELEX database (Baayen, Piepenbrock & Gulikers, 1995). The noun-to-verb frequency ratios for each word are mapped on the graph in Figure 13; the line of best fit revealed that the data followed a linear trend.

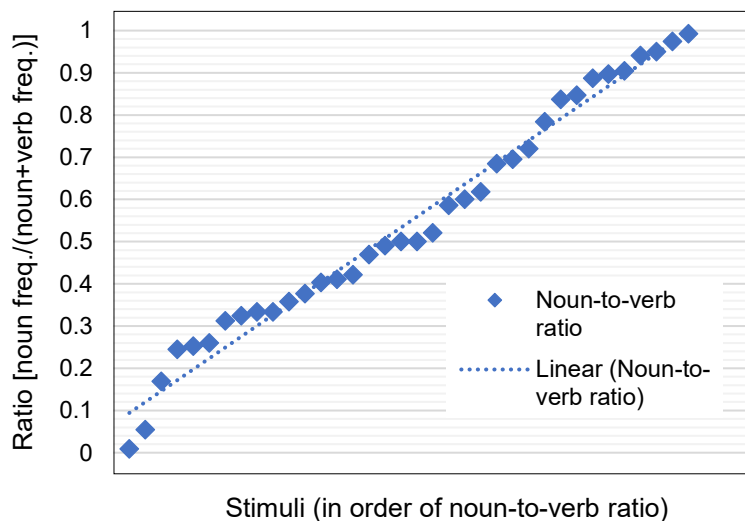


Figure 13. The data points illustrating the noun-to-verb ratio and the line of best fit.

4.3.3 Procedure

Firstly, the participants were asked to categorise the stimuli to check if they understood what object each word referred to (the “knowledge question”; categories included gardening, sport, cooking/eating and stationery). Secondly, they were asked to rate how much each object is manipulated manually during use, on a Likert scale of 1–7. They were also asked to estimate how often they

used each item (frequency of use) and how often they had seen someone else using the object (observation of use). They gave their ratings on a 7-point Likert scale (ranging from 1: *several times a day*, to 7: *never*). We carried out correlations between the frequency of use and observation of use ratings for each of the object names. As might be expected, the two ratings were significantly positively correlated for all except one of the items (“tie”; $r = .06$). That is, participants had greater experience of the actual use of objects that they also had experience of observing others use. These positive correlations between the two ratings varied between $r = .28$ and $r = .96$ according to the particular stimuli being rated (see Appendix C for details).

For the main part of the experiment, the participants were seated in a quiet, dimly lit booth. The stimuli were presented, one at a time, on a CRT monitor (30.5cm height by 40.5cm width; 100Hz refresh rate) positioned one metre from the participant, using E-Prime 2.0 (Schneider & Zuccoloto, 2007). The stimuli were displayed in Courier New, point size 30, in black on a white background. Each trial began with a fixation point, which appeared at the centre of the screen for 600–800 ms. After the fixation point, a target word would be presented for 1500 ms. At the end of each trial, a blink symbol was displayed for 1500 ms, giving the participant the opportunity to blink if necessary. The participants were asked to avoid blinking or making eye movements until the blink symbol was displayed, in order to reduce contamination of the EEG data. After every 3–5 trials the participants would be given a word quiz to check they had been paying attention to the words presented on the screen. The quiz asked them, “What was the last word you saw on the screen?”. The participants used the number pad on the computer keyboard to select the number that corresponded to the correct word (1, 2 or 3). Participants with a high rate of incorrect answers to the quiz ($> 10\%$) were excluded from the EEG analyses. A

sequence of 15 practice trials was completed by each participant before the main experiment, using a separate set of stimuli. In the main experiment, the stimuli were presented five times in a randomised order using E-Prime, totalling 180 trials. The words used as distractor stimuli in the quiz (i.e., the incorrect answers) were randomly selected by E-Prime. Participants were given a rest period every 60 trials, for as long as they needed.

4.3.4 EEG Recording

BrainVision Recorder (Version 1.10, Brain Products GmbH) was used to collect the scalp voltages from 61 Ag/AgCl active electrodes (actiCAP, Brain Products, Gilching, Germany). The sensors were arranged in the International 10–20 configuration and secured in place on the participant's scalp by an elastic cap. An additional two sensors were positioned below and adjacent to the participant's right eye to monitor eye movements. All scalp electrode impedance measurements were kept below 20k Ω . The EEG signals were amplified by a BrainAmp MR Plus amplifier (Brain Products, Gilching, Germany).

4.3.5 EEG Analyses

Vision Analyser (Version 2.0, Brain Products GmbH) was used to process the data. EEG was sampled at a rate of 500Hz and filtered offline with a band-pass filter of 0.1–40Hz (with a roll-off slope of 48 dB/oct) and subjected to a 50Hz notch filter. The EEG recordings were segmented into 1000 ms epochs, spanning from 200 ms pre-stimulus onset until 800 ms post-stimulus. Baseline correction was performed using the average EEG activity between -200 ms and 0 ms. The electrodes were referenced to the left mastoid electrode (TP9) and then re-referenced offline to the average of the left and right (TP10) mastoid data. The central anterior-frontal electrode (AFz) was used as the ground. Segments containing artefacts were rejected from analyses. Participants with less than two-thirds of their segments intact after artefact removal were

excluded from the analyses. Also, EEG data related to object names seen by participants who had given incorrect answers to the knowledge question were excluded from the analysis as it was assumed that the participant did not know what the object was (see Appendix C for number of exclusions).

Separate correlations were performed to calculate the Pearson's correlation coefficient for the relationship between the EEG voltage for each stimulus and the word frequencies (noun frequency, verb frequency) and the participant's ratings (manipulability, frequency of use, observation of use), for all experimental trials across all sample time points between 100 and 700 ms. Monte Carlo cluster analyses were carried out on the participants' data to find clusters of brain activity related to the five different conditions: noun frequency, verb frequency, manipulability, frequency of use and observation of use.

4.4 Results

4.4.1 Noun and verb frequency

Noun frequency. Electrophysiological data was found to be significantly correlated with the noun frequency of the words across two clusters of activity (see Table 9 and Figure 14 for results). The first cluster was negative, cN₁, from 292–372 ms and began at fronto-central and central electrodes at the midline. This activity spread to frontal, central and parietal electrodes across the scalp but the greatest activity was at and around the midline central electrodes and in the right parieto-occipital electrodes. The second cluster, cN₂, was positive, from 382–670 ms and located at frontal, fronto-central and central electrodes in the left hemisphere; fronto-temporal, central and centro-parietal electrodes in the right hemisphere; and frontal and central electrodes in the midline.

Verb frequency. The ERP activity for object names associated with verb frequency also revealed two significant clusters. The first one, 192–294 ms, was

positive, beginning in parietal and occipital regions, especially in the right hemisphere and then moving forward to central and frontal electrodes and terminating at midline central electrodes (Table 9 and Figure 14). The second cluster, 348–566 ms, was positive and located in the right hemisphere at central, centro-parietal, parietal and parieto-occipital electrodes, cV_2 .

Noun vs. verb frequency. Analysing the differences between ERPs correlated to noun and verb frequency revealed two significant clusters of differential activity. These were the product of activity correlated to verb frequency being subtracted away from activity related to noun frequency. The first of these was a negative cluster from 192–288 ms, located at the midline at centro-parietal, parietal, parieto-occipital and occipital electrodes and moving to parietal electrodes in the right hemisphere (Table 9 and Figure 14). The $c(N - V)_1$ cluster confirms that the early verb frequency cluster, cV_1 , is significantly earlier than the noun frequency cluster, cN_1 . The second cluster, $c(N - V)_2$, from 296–392 ms was also negative, beginning at midline fronto-central and central electrodes and moving to the posterior half of the scalp including centro-parietal, parietal, parieto-occipital and occipital electrodes in both hemispheres and along the midline. This cluster revealed that the noun frequency activity was significantly more negative during this period, spanning the noun frequency negative cluster and the beginning of the verb frequency positive cluster. This shows that the verb frequency positivity has an earlier onset compared to the noun frequency. In particular, there was greater negativity in posterior electrodes. There was no significant difference between the late positivity seen in the noun and verb frequency conditions.

Table 9

Significant clusters of brain activity associated with noun frequency, verb frequency and manipulability.

Condition	No. of clusters	Name of cluster	Polarity	Duration	<i>P</i> -value
Noun frequency	2	cN ₁	Negative	292–372 ms	<i>p</i> = .001
		cN ₂	Positive	382–670 ms	<i>p</i> < .0001
Verb frequency	2	cV ₁	Positive	194–294 ms	<i>p</i> = .004
		cV ₂	Positive	348–566 ms	<i>p</i> < .0001
(Noun – verb) frequency	2	c(N – V) ₁	Negative	192–288 ms	<i>p</i> = .02
		c(N – V) ₂	Negative	296–392 ms	<i>p</i> < .0001

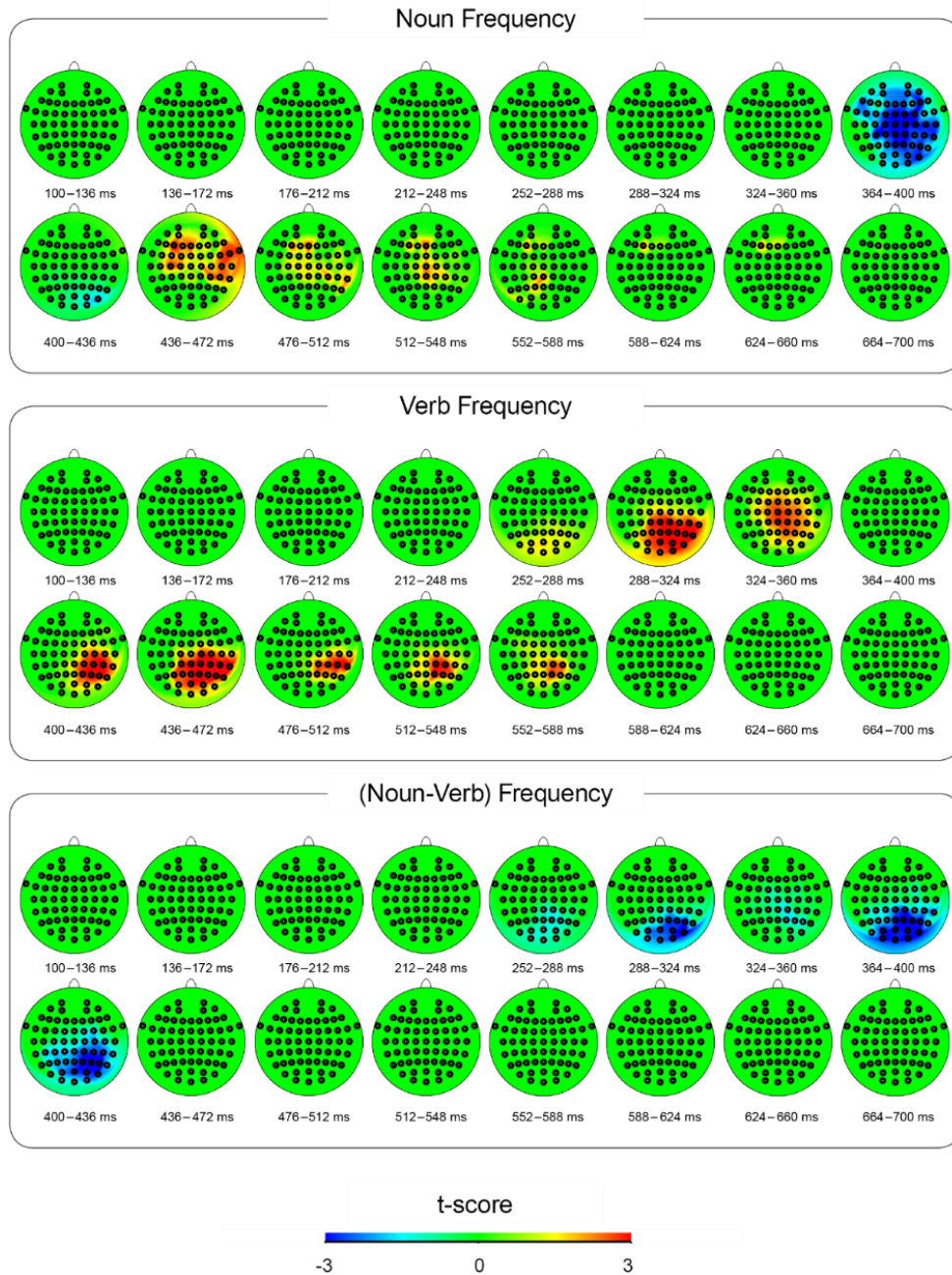


Figure 14. Scalp maps illustrating significant clusters of ERP activity associated with noun frequency, verb frequency and the difference between the two.

4.4.2 Manipulability

We found that ERPs were significantly correlated with the manipulability ratings of the objects across a single positive cluster, spanning from 504–642

ms (cM; Table 10). This activity began in parieto-occipital electrodes and then moved forward through the left hemisphere covering parietal, central and frontal sites and terminating in the fronto-temporal region in the left hemisphere (Figure 15). Figure 16 shows the average values of correlation coefficients pooled across all active electrodes for the noun frequency, verb frequency and manipulability ratings, highlighting the temporal differences in the significant correlations related to each condition.

Table 10

Significant clusters of brain activity associated with noun frequency, verb frequency and manipulability.

Condition	No. of clusters	Name of cluster	Polarity	Duration	<i>P</i> -value
Manipulability	1	cM	Positive	504–642 ms	$p < .0001$

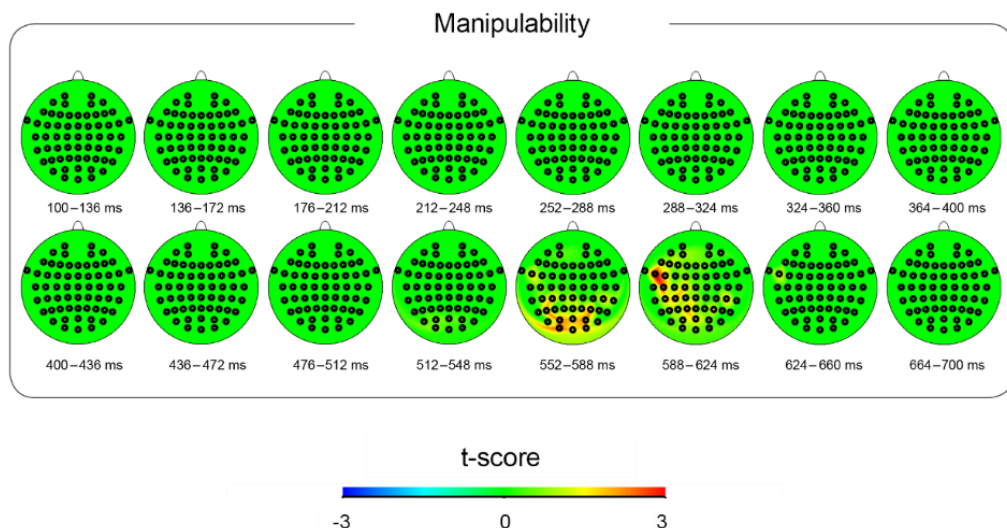


Figure 15. Significant clusters associated with the manipulability of the referent objects.

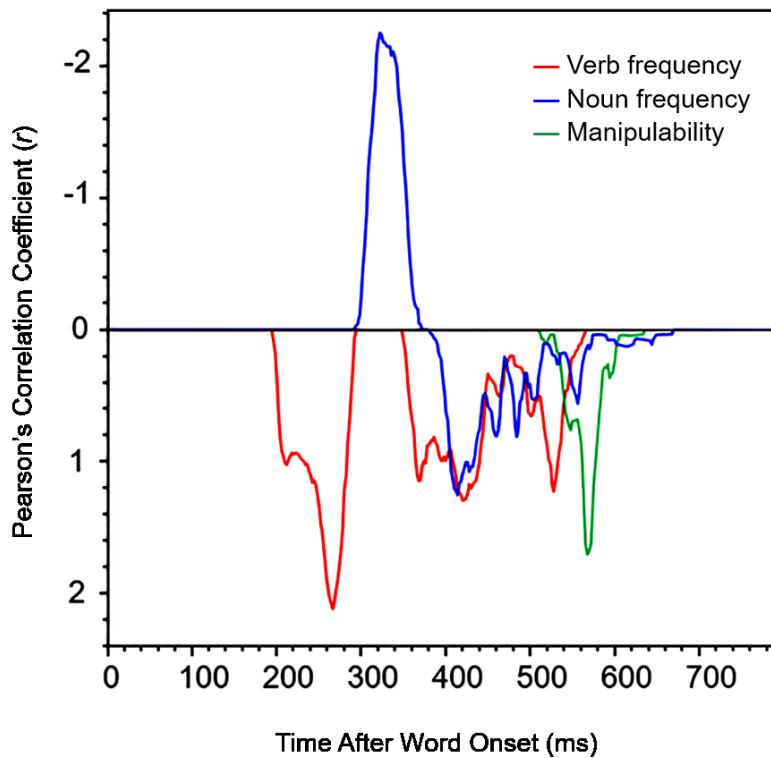


Figure 16. Illustration of the timing and amplitude of the ERP correlation clusters for each condition.

4.4.3 Summary

If our experience of using an object is key to its conceptual representation, then we would expect it to influence semantic access during the time window seen for object processing (i.e., noun frequency results; ~290 ms; N400). If it is generated after semantic integration, during conscious memory retrieval or a later mental simulation of object use, then we would expect later activation (e.g., P600, akin to the manipulability results).

4.4.4 Frequency and observation of object use

Correlating ERP activity with participants' ratings of how frequently they had used the objects, resulted in a cluster of negative activity, 274–432 ms, from frontal to centro-parietal electrodes, particularly at the midline and in the left hemisphere (cF; Table 11 and Figure 17). ERP activity related to the frequency in

which a participant had observed the referent object's use, resulted in a negative cluster, 274–356 ms, located at frontal to centro-parietal electrodes along the midline and to the left and right of the midline (cO; Table 11 and Figure 17).

Figure 18 illustrates the timings of activity from the five different conditions (noun frequency, verb frequency, manipulability, frequency of use, observation of use), after pooling the data from all electrodes to give the average activity for each condition.

Table 11

Details of the significant clusters showing ERP activity related to the three conditions.

Condition	No. of clusters	Name of cluster	Polarity	Duration	<i>P</i> -value
Frequency of use	1	cF	Negative	274–432 ms	$p < .0001$
Observation of use	1	cO	Negative	274–356 ms	$p < .0001$

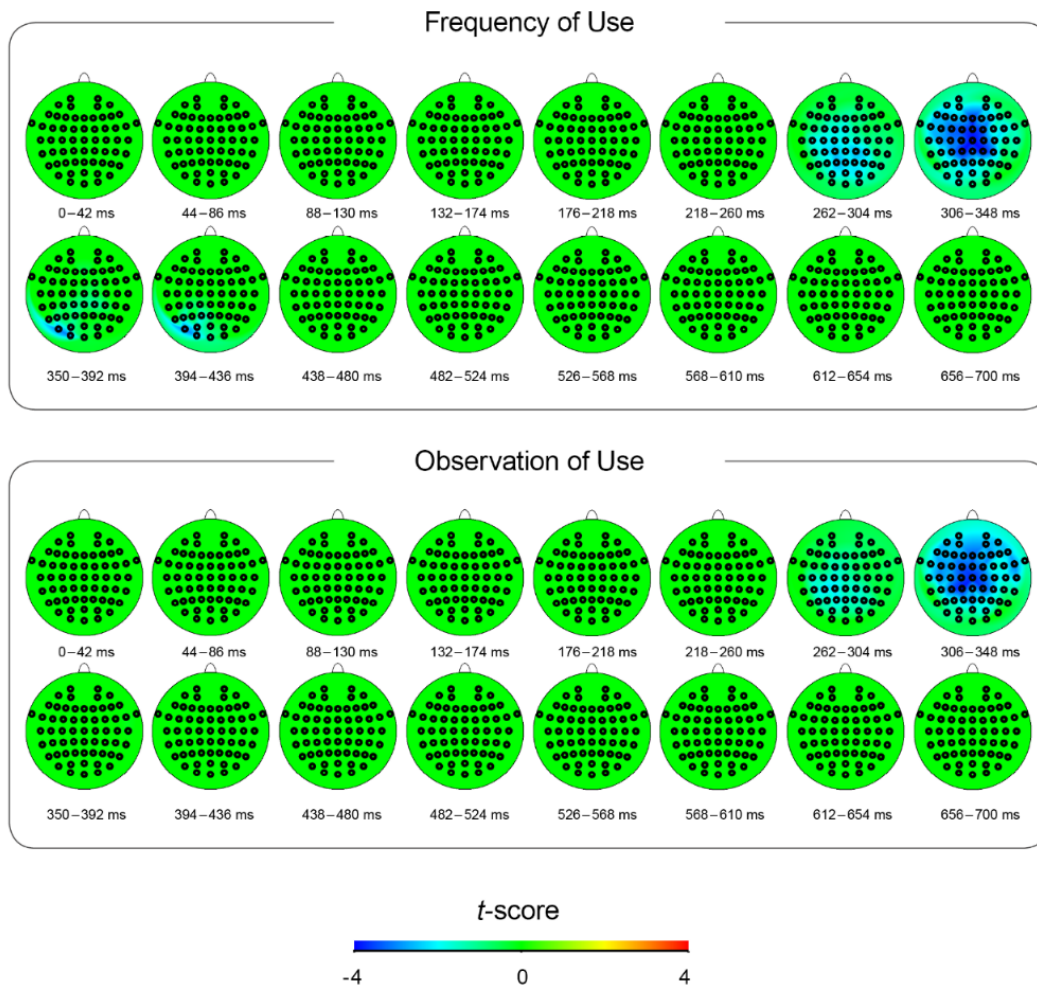


Figure 17. Scalp maps illustrating the significant clusters of ERP activity related to the three different conditions.

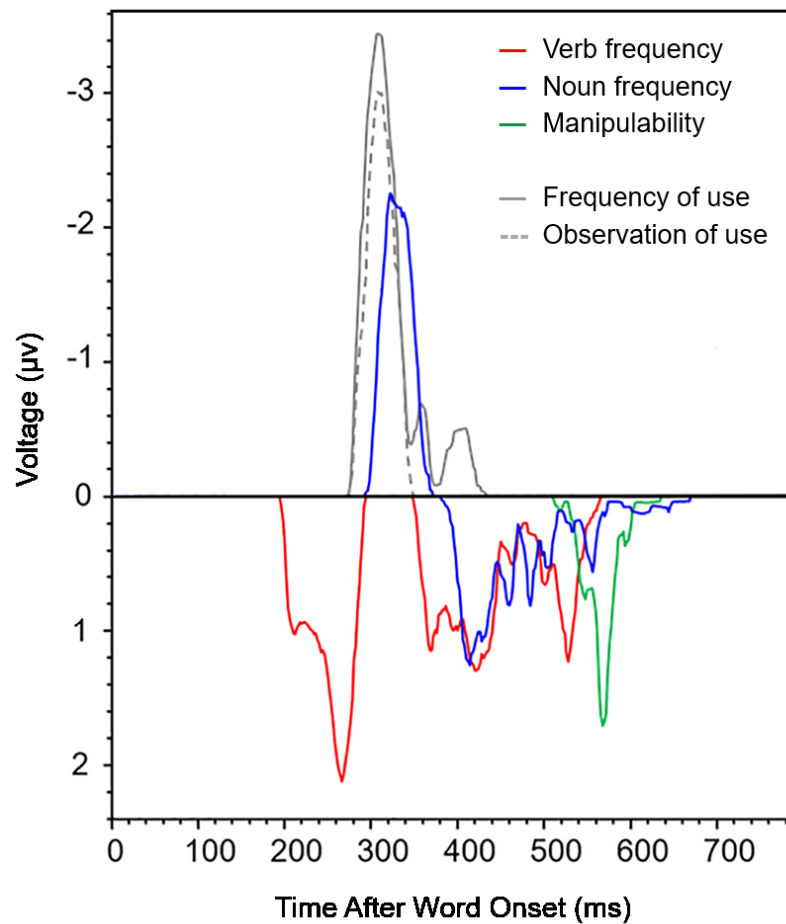


Figure 18. Graph illustrating the timing and amplitude of activity for each condition.

4.4.5 Frequency of use vs. observation of use

Subtracting the observation of use correlational data from the frequency of use data resulted in two significant clusters (displayed in Table 12 and Figure 19). The first cluster was negative, from 364–406 ms, at midline central, centro-parietal, parietal and occipital electrode sites, and also in the left hemisphere at parietal and occipital electrodes, $c(F-O)_1$. This revealed that there was greater negativity in the frequency of use condition during this period. The second cluster was also negative, from 566–622 ms, and was located just right of the midline at central, centro-parietal and parietal electrodes and also at the occipital electrodes in both hemispheres, $c(F-O)_2$. This reflected the

subthreshold negativity in the frequency of use condition and the subthreshold positivity in the observation of use condition, which explains why it did not appear in the separate analyses for these two conditions.

Table 12

Details of the significant ERP clusters comparing the three conditions.

Condition	No. of clusters	Name of cluster	Polarity	Duration	<i>P</i> -value
Frequency – Observation	2	c(F-O) ₁	Negative	364–406 ms	<i>p</i> = .01
		c(F-O) ₂	Negative	566–622 ms	<i>p</i> = .005

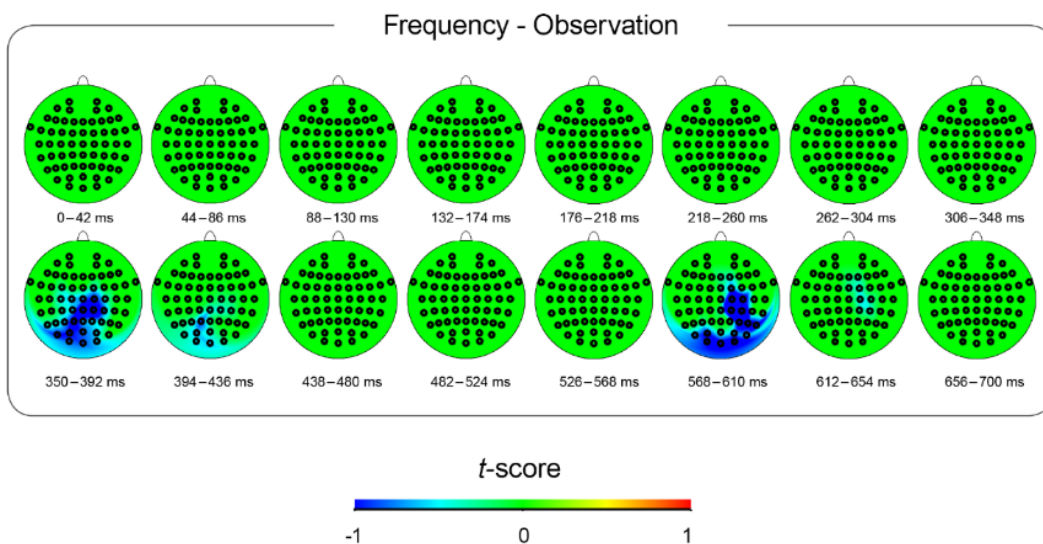


Figure 19. Scalp maps displaying significant ERP clusters resulting from the comparisons made between the three conditions.

4.5 Discussion

This study explored the timing of access to different information associated with an object when reading the names of those objects. This object-related information included the associated actions, the conceptual representation of the object, manipulability and an individual's personal use of the object. The first part of the experiment investigated at which stage of written word processing we access knowledge about actions and objects. In this experiment, participants read words that refer to both names of objects and action words whilst recording their EEG. We then correlated the ERP data with how frequently each word is used as an “action” (verb frequency) and how frequently it refers to an “object” (noun frequency), to find out at which stage of linguistic processing these two types of information are being accessed. The ERP data was also correlated with the participants' rating of each object's manipulability, in order to see when information associated with the manipulability of objects is processed in the brain. We predicted that brain activity associated with the action would be processed first due to the way the word was learnt (in conjunction with the performance of the action; Scorolli et al., 2011). It was expected that the associated action would become part of the conceptual representation of the word form and therefore would be accessed early on during lexico-semantic processing. We predicted that the object concept would be accessed next, as this has a weaker sensorimotor representation. Lastly, we predicted that manipulability would be processed once the relevant information about the object had been accessed.

Our findings followed our predictions. We saw earlier brain activity linked to words that are more associated with their use as verbs compared to nouns, from around 190 ms, displaying a positive cluster of activity at parietal,

occipital, frontal and central electrodes. This activity occurred during the P200 time frame (150–275 ms; Rozyński & Chen, 2015), which is associated with early semantic processing (Hauk et al., 2012). Previous research has shown somatotopically activated motor activity from as early as 150 ms (Mollo, Pulvermüller & Hauk, 2016), which is thought to be the earliest point at which we process semantic information about words (Amsel et al., 2013; Hauk et al., 2012; Moseley et al., 2013; Schendan & Kutas, 2003). Similarly, in another ERP study, Amsel (2011) found that the function and visual-motion features of an object are activated from as early as 100 ms from reading concrete nouns. These features had the greatest influence on neural activity during noun processing from 100–500 ms. Amsel argued that this action-related knowledge is important for accessing word meaning and responsible for early semantic processing.

Brain activity related to words more associated with their use as nouns, compared to verbs, showed a significant effect from 290–370 ms. This coincides with N400 timing, which may reflect activation of the conceptual representation of the object through retrieval of semantic features connected to the word form (Hagoort, Baggio & Willems, 2009). This N400 finding is consistent with other studies that have found conceptual information related to objects accessed around this time (Barber, Kousta, Otten & Vigliocco, 2010; Tsigka, Papadelis, Braun & Miceli, 2014). In Amsel's (2011) study, visual features became activated from 300 ms. Given that Pulvermüller et al. (1999) found that objects have greater visual associations, compared to verbs which have greater motor associations, the timings from Amsel's (2011) study, and ours, further supports the idea that the semantic representation of the object concept is visual in nature. Both the noun and verb frequency analyses showed elicitation of a late positive component (LPC), from 350–670 ms. The LPC has been associated with

the retrieval of information from episodic memory and conscious thought (Johnson, Barnhardt & Zhu, 2003). Pulvermüller, Lutzenberger and Preissl (1999) found EEG frequency differences between verbs and nouns in high-frequency EEG (30Hz) activity at ~500 ms, which they argue reflected the semantic processing of the words; visual processing for object names and motor processing for action words.

The manipulability of the object was not processed until later, beginning at around 500 ms and continuing until 640 ms, displaying a positive waveform. Madan et al. (2016) found that images of functionally manipulable objects evoke greater positive slow-wave amplitude around 400–800 ms, at Pz and C3 electrodes (corresponding to the area of the brain controlling the right hand), compared to those with low functional manipulability which they argue reflects motor simulation processes. The manipulability activity is during a similar time window to the earliest behavioural responses seen in our previous experiments (Chapter 2; Feven-Parsons & Goslin, 2018). Perhaps information about how to manipulate an object influences the motor system around this time, preparing the body to execute an action if this is necessary. These results suggest that this late positive activity is related to a mental simulation of object movement or object use, which occurs post N400 processing and just before participants' usual response times. Proverbio, Adorni and D'aniello (2011) found a larger P300, between 550 and 600 ms, at left hemisphere centro-parietal sites in response to tools, compared to other objects which are not functionally manipulable. Previous research has shown that object-associated manipulations show left lateralised processing in the parietal lobe (Brandi et al., 2014; Garcea et al., 2012; Kellenbach, Brett & Patterson, 2003; Proverbio et al., 2011). Although EEG has a poor spatial resolution, we saw activity from occipital, parietal and centro-parietal electrodes in the left hemisphere. Previous findings

suggest that manipulation features are activated from object names around 200–300 ms (Myung et al. 2006). These studies used motor priming, but they do suggest that other affordance-related information is activated earlier than we saw in this study. Similarly, our experiment found affordance-priming effects from around 200 ms (Chapter 2; Feven-Parsons & Goslin, 2018), which suggests that other manipulation information, such as micro-affordances (Ellis & Tucker, 2000), may be accessed earlier. However, our finding from the current study suggests that a complex motor program representing the way the object is manipulated during use is not fully activated until after 500 ms.

Another aim of the study was to test the theory that the conceptual representation of an object is grounded in a person's experience of using that object. The results for the frequency of use data showed a negative cluster, 274–432 ms, at midline central and surrounding electrodes. Again, this was during N400 processing, suggesting that the meaning of object names is embodied through previous use of the referent, as has been argued previously (Dekker et al., 2014; Pulvermüller, 1999). Our results show that the N400 amplitude increases with how frequently the objects have been used; overlapping the timing of object concept activation (290–370 ms; noun frequency) and also the action associated with the word form (192–294 ms; verb frequency). The more frequently an object is used, the greater the embodiment of the object concept. Comparing the two conditions, the frequency of use condition showed greater negativity during two time windows: 364–406 ms and 566–622 ms. The early spike of ERP activity seen in the frequency of use and observation of use analyses were highly similar, showing that the difference was quantitative, not qualitative. Both conditions shared the same ERP representation, but there was greater activation for the frequency of use condition compared to observation of use. The location of activity was around centro-parietal electrode sites at the

midline, where N400 activity is often seen, perhaps reflecting the greater richness of the semantic representation (Barber, Otten, Kousta & Vigliocco, 2013; Kounios et al., 2009; Rabovsky, Sommer & Abdel Rahman, 2012). This was predicted from Beilock et al.'s (2008) study, where there was greater motor activity associated with linguistic descriptions of ice hockey for participants who had direct experience of playing it, compared to merely watching it. The late cluster reflects more prolonged activation of the N400 for objects that the participants had greater personal experience of using. This later difference activity between the two conditions occurs at around the same time as the manipulability ERP. This might suggest that processing the manipulability of the object when reading its name, may also have developed through the previous use of that object.

4.6 Conclusion

We cannot distinguish between actions and objects completely when object names can refer to both. Our experiment presents words on a continuum where the extent to which the word form is related to an action varies. The greater the association with an action, the earlier we see brain activity related to the concept. The action related to the word form was processed as early as 190 ms. Words that were more associated with the object showed brain activity that was later, within N400 timing. Our findings suggest that we process the action associated with a word first, then the object concept, which consequently allows for a mental simulation of the manipulations associated with that object. Furthermore, the semantic representation of the object concept is related to previous use of that object.

5. General Discussion

The purpose of this thesis was to investigate the timing of access to embodied representations during object name processing. In this chapter, I discuss the extent to which the questions posed in the introduction (Chapter 1) are answered by our findings.

5.1 When are affordances activated during object name reading and are they necessary for comprehension?

The first question we asked was whether an object's micro-affordance is activated automatically from reading the name of that object and what the specific timing of this brain activity was. We argued that if affordances are an integral feature of the meaning of object names, then we should see them generated during early lexico-semantic processing. We found that micro-affordances can be activated from as early as 176 ms in our priming study, but we only saw this when the participant was required to withhold a response (nogo trials). This suggests that affordances are activated automatically during an early stage of linguistic processing, as this was a priming study where participants would not have been aware of the primes, or what was being primed. However, when a response was required, the ERP activity associated with affordance priming was not activated until 520 ms at centro-parietal and parietal electrodes. As we only saw early ERP activity during affordance-priming trials when a response was being inhibited, this suggests that it is a motoric action that was being primed, rather than the size or shape of the object. When the participant was withholding a response, we saw negative activity in the frontal lobe (inhibition) which shifted to the corresponding motor region (area

of motor cortex controlling left-hand actions) and parietal lobe (where affordances are thought to be stored; Buxbaum, 2017; Fogassi & Luppino, 2005) reflecting the inhibition of the primed motor action. This was further supported by the finding that the ERP activity was located in an area involved in the inhibition of motor responses (Chikazoe et al., 2007; Hampshire et al., 2010) and the area associated with actions automatically afforded by objects (Lhermitte, 1983).

The affordance priming did not influence the participants' response times. According to LASS theory, even though embodied representations can be an important aspect of linguistic processing and facilitate many comprehension tasks, they are not the only route to understanding. LASS theory suggests that many simple language tasks can be achieved through shallow linguistic processing and do not require access to sensorimotor information. Research shows that between-category decisions, such as deciding whether an object is natural or manmade (as in this study), can be made through amodal linguistic distributed networks (Barsalou, Santos, Simmons & Wilson, 2008; Louwerse, 2011; Mahon & Caramazza, 2008). Furthermore, decision-making was facilitated in this study by the semantically related prime-target pairs always being either both manmade or both natural. On the other hand, the affordance-related prime-target pairs were always in a mismatched semantic pair, i.e., manmade-natural or natural-manmade, which would have the inverse effect on response times in this task. This shows how, although affordances are activated very early during lexico-semantic processing, this is not always necessary for comprehension.

Given that the affordance primed in this study was unrelated to the motor response required during the task (which was a left index finger button press), the affordance priming appears to activate a non-specific motor program, which

was not dependent on the hand that participants would usually use to interact with the object (as they were all right-handed). This is in line with previous findings that actions carried out by the participant can interfere with, or facilitate linguistic processing, regardless of whether the action afforded by the referent object, or described in the sentence, is related (Postle et al., 2013; Rüeschemeyer et al., 2010; Siakaluk et al., 2008).

We found earlier ERP activity associated with object affordances compared to Amsel et al. (2013). Our results differed for many reasons. We adopted an implicit task to access affordances outside of the participant's conscious awareness, whereas Amsel et al.'s task involved an explicit decision about the manipulability of objects. Also, their study focused on objects with a volumetric affordance (affordance based on shape, size and other geometric features), which according to Gibson (1979) and others (Buxbaum & Kalénine, 2010) require direct perception through a visual route. This would necessitate the activation of a mental picture to activate them during linguistic processing, which may be another reason why Amsel et al. (2013) did not see ERP activity related to object affordances until after 300 ms. For many of the objects in their study, the participants would not have had first-hand experience (e.g., mouse) and therefore would not have a stored embodied representation. Direct experience is thought to be necessary for linking sensorimotor information to an object's conceptual representation (Pulvermüller; 1999), which we discuss later in this chapter when we look at the findings from Chapter 4. It is functional affordances, not volumetric affordances, which are thought to have stored sensorimotor representations through experience with the object (Bub & Masson, 2012; Buxbaum, 2017). This leads on to our second question.

5.2 Are micro-affordances activated earlier when reading the names of functionally manipulable objects compared to other graspable objects?

5.2.1 Experiment 1 (Chapter 3)

The first experiment in Chapter 3 examined the argument that affordances are more important to the conceptual representation of words referring to functionally manipulable objects, compared to objects graspable based on their geometric features. Therefore, we expected to see earlier activation of affordances for functionally manipulable objects, as previous researchers have found (Bub, Masson & Cree, 2008). A problem with the experiment in Chapter 2 (Feven-Parsons & Goslin, 2018) is that we used both natural and manmade objects so that the manmade-natural distinction could be used for the category decision task. To make sure we were priming object affordances in the affordance condition, the prime-and-target pair were never semantically related: one was always manmade and the other natural (e.g., “cucumber-hammer” or “tweezers-pea”). Unfortunately, this meant that we could not look at manmade and natural items separately to see whether they produced different affordance effects. We hypothesised that the inclusion of the names of natural objects might have been partly responsible for us not finding affordance effects in the go EEG data or facilitation of response times. In this experiment, we looked at micro-affordances (power-grip and precision-grip, as in Chapter 2) evoked from functionally manipulable items (tools) and objects without a learnt affordance, whose affordance is based purely on geometric features. Participants responded only to animal names, which were semantically unrelated to the target stimuli categories and meant that the participants’ responses did not interfere with the EEG data used in the analyses. The participants responded with a left index finger button press which was unrelated

to the affordances associated with the referent objects. Throughout the experiment, they held a wooden object in either a power or precision grip, which half of the time was compatible with the affordance of the object and half the time was incompatible.

Early negative activity associated with functionally manipulable objects was activated from 216–556 ms, which was widespread across the scalp. For other graspable objects, the cluster of brain activity was from 370–480 ms. One explanation for these results is that the longer lasting and higher amplitude of negativity for names of functionally manipulable objects, in comparison to volumetric object names, could be reflecting their richer semantic representation linked to greater sensorimotor associations. Functionally manipulable objects involve greater BOI during use (Siakaluk et al., 2008). Barber, Otten, Kousta & Vigliocco (2013) found that greater N400 responses were related to the greater semantic richness of concrete words, compared to abstract words. Abstract word processing was more likely to involve a superficial process of recruiting associated linguistic knowledge, whereas concrete words involved deep processing of multimodal information. However, in our study, objects in the volumetric condition still showed greater N400 amplitude compared to non-manipulable entities, for which a person has had less sensorimotor experience. Concepts such as “church” or “cloud” are more abstract, in that we are less likely to have a stored perceptual representation that is easily accessed, like “apple” or “leaf”. This appears to show a gradient of ERP negativity: functionally manipulable objects showing the highest amplitude, followed by graspable objects, and then non-manipulable objects. This constitutes a quantitative difference between the sensorimotor representations of these three types of concept (see Figure 20).

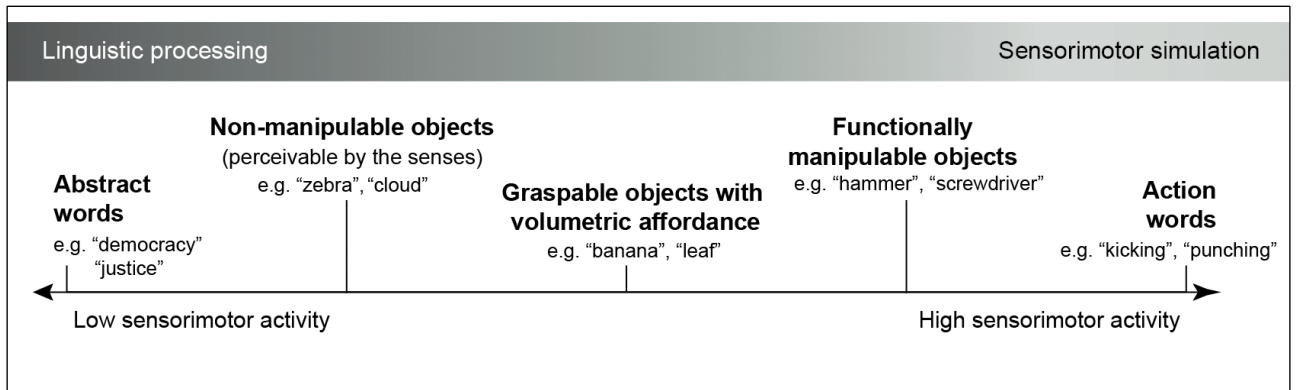


Figure 20. Linguistic and sensorimotor processing continuum.

However, a large body of research has shown that there is a qualitative difference between volumetric and functional affordances (Buxbaum, 2017; Buxbaum & Kalénine, 2010; Kourtis & Vingerhoets, 2015; Lee, Middleton, Mirman, Kalénine & Buxbaum, 2013; Lee, Huang, Federmeier & Buxbaum, 2018). Two AS theory (Buxbaum & Kalénine, 2010), suggests that volumetric and functional affordances are processed in separate brain systems: functional affordances are processed via a lexico-semantic route in the ventro-dorsal system and volumetric affordances are processed via direct perception of objects in the dorso-dorsal system. The second part of the study looked at when and where specific micro-affordance representations were being activated for both functional and volumetric stimuli. We compared trials where participants read the name of an object that afforded a grasp compatible with the one they were using to hold the wooden object, with trials where their hand grasp was incompatible with the referent object's affordance. For functionally manipulable objects, ERP activity related to the compatibility of the grip showed positivity from 528–644 ms, which was also seen for the volumetric condition. Similar brain activity during this time has been found for mental imagery of objects during object name reading (West & Holcomb, 2000), for the mental rotation of visually perceived objects (Schendan & Kutas, 2003) and for processing the

manipulability of an object (Madan et al., 2016; Proverbio et al., 2011). These previous findings might suggest that this ERP activity is related to a mental simulation of object manipulation, post-N400 semantic processing. The location of this positive activity was at temporal and parietal electrodes in the left hemisphere, which is where previous findings have shown object manipulability is processed (see Brandi et al., 2014; Garcea et al., 2012; Kellenbach, Brett & Patterson, 2003; Proverbio et al., 2011).

The late positive cluster associated with grasp compatibility for functional and volumetric objects was much later than the affordance-related activity in Chapter 2, where we saw priming of affordances around 200 ms. The late positive clusters were characterised by greater anterior negativity for incompatible trials and greater posterior positivity for compatible trials. The frontal lobe negativity might reflect the inhibition of the linguistically evoked affordance, which is incompatible with the object they are holding; whereas, when the referent object's affordance matches the grip they are holding the object with, there is no need to inhibit the activation of the parietal lobe's affordance generation (Lhermitte, 1983). This brain activity occurred around the usual time that the participants would be responding (~500 ms; Feven-Parsons & Goslin, 2018); perhaps reflecting a mental simulation process in preparation for a response. Although in the current study they were not responding during these trials, it is interesting that this activity is evoked differentially depending on whether the stimulus affordance was compatible or not. This may be because the object affordance would be a right-hand grasp, as this is the participants' dominant hand, which was the hand they were holding the wooden object with. The positivity seems to signify incompatibility of the hand gesture that is currently engaged with the affordance of the object.

An unexpected, but interesting finding, was the early negative cluster of brain activity related to grasp-compatibility for volumetric objects, activated from as early as 224–284 ms, at the temporo-parietal region (where the angular gyrus is located). We concluded that this reflected pattern-matching between information about the referent object, such as the size or shape of the object, with proprioceptive information from the motor program engaged during the task (hand grasp used to hold the wooden object). Similarly, Glover et al. (2004) found that when participants read the name of an object, the size of the referent object influenced their grip aperture toward a neutral wooden object (i.e., larger grip aperture after reading “apple” and smaller grip aperture after reading “grape”). The inhibition of micro-affordances does not appear to affect the processing of functionally manipulable objects, as it does for the objects in the volumetric condition. We posit that functionally manipulable objects are associated more with the movement related to object use, as opposed to the preparation of a hand grasp associated with a particular size of object. Functional affordances may be more associated with a complex motor representation related to the grasping, manipulating and moving of the object to use it. This would explain why we failed to find an effect in reaction times, unlike Bub et al. (2008). In their experiment, participants carried out actions that were related to the use of the object. Functional affordances are thought to be activated only when necessary for the pursuit of a particular goal (Buxbaum & Kalénine, 2010), whereas in our study, the participant was only holding an object stationary in one hand whilst reading object names. This does not disregard the importance of motor activity during functional object name reading, just that it appears to be representing something different from the micro-affordance related to its geometric properties. The second experiment in Chapter 3 was carried out to elucidate these findings further.

5.2.2 Experiment 2 (Chapter 3)

It was surprising to see that the micro-affordance of functionally manipulable objects did not show early activation, only the late activity also seen for volumetric objects. We questioned whether this might be because they were not relevant to the task (Buxbaum & Kalénine, 2010), which was a button press in response to animal names. Therefore, we carried out a second experiment to explore this further. In Experiment 2 (Chapter 3), we found earlier activation of micro-affordances for functionally manipulable objects, when a compatible grasp response was required (go trials). The ERP activity associated with grasp compatibility for manmade objects during go trials was a negative cluster from 370–500 ms, the usual N400 timing, and was located in central and parietal regions. The N400 reflects stored semantic knowledge (Kutas & Federmeier, 2011), which makes sense given that functional affordances are the learnt actions associated with our understanding of how to use an object (Buxbaum, 2017). When we compared this activity with the ERP for volumetric go trials, the strongest activity for functionally manipulable objects was present at C3, Cz and P2 electrodes. The C3 electrode is located at the hand area of the left motor cortex and corresponds to right hand movements, which is the hand participants' used to respond with. This shows manual motor activation related to the affordance of the object during semantic processing of the object name, but only when relevant to the task (go trials), just as Buxbaum and Kalénine (2010) hypothesised. The micro-affordance for functionally manipulable objects is context-dependent (Buxbaum, 2017). When participants had to inhibit a relevant response to the manmade stimuli, there was late positivity from 540–586 ms, similar to the late positivity seen in Experiment 1 (Chapter 3) in both functional and volumetric conditions, and was also located in the left hemisphere. This positivity was also observed for natural

items during go trials, from 500–580 ms. There was no significant difference during this time frame between the manmade and natural conditions during go trials, suggesting that it was also present for manmade items. This activity was located in the temporo-parietal region (FT7, FC5, F7, F5 electrodes), which may be related to the angular gyrus pattern-matching process discussed earlier.

The ERP related to grasp-compatibility for natural objects during nogo trials was a negative cluster from 272–312 ms. This is during the timing for early lexico-semantic processing and is similar to the ERP activity for grasp-compatibility during the volumetric nogo trials in Experiment 1 (Chapter 3). The early ERP activity related to affordances for graspable objects in the volumetric condition fits with 2AS theory, in that these affordances are evoked quickly but briefly, compared to functional affordances which show delayed, but longer lasting, activation. However, these findings oppose the assumption of the 2AS theory that volumetric affordances are thought to require the direct perception of objects and only functional affordances can be activated from linguistic stimuli. In the two experiments in Chapter 3, we saw negative activity during trials where the referent object's affordance is compatible with the hand grasp that the participant is using to hold the wooden object (Experiment 1; Chapter 3) or response device (Experiment 2; Chapter 3). This is only true when they are holding the object or response device stationary, i.e., inhibiting a response, just as we saw in the priming study in Chapter 2. Therefore, it seems that words referring to natural objects (or objects with only a volumetric affordance) do activate a micro-affordance, but this activity may be a more simple representation such as coding for the hand gesture and size of the object.

Functionally manipulable objects displayed greater negativity from 208 ms when compared to non-manipulable objects (Chapter 2, cluster cS). We questioned why the micro-affordance was not activated during this early period.

What was this ERP representing if not motor activity related to affordances? If affordances are thought to be an integral aspect of meaning-making for object names, then we would expect their representation to be activated during the earliest stages of semantic processing (~160 ms; Hauk et al., 2012) not as late as N400 activity. There is still the possibility that this negative cluster was related to motor activity associated with object use. We hypothesised that micro-affordances are not as significant to the conceptual representation of tools. The action associated with most tools is not the grasp used to pick them up, but the movement involved during use, e.g., an arm-swinging motion from the elbow for using a hammer, or wrist and arm movements for sewing with a needle. During the use of a hammer, the power-grip is already engaged throughout and when sewing, the needle is held continually in a precision-grip. The repeated action during use of an object becomes associated through Hebbian learning (Pulvermüller et al. 1999). Previous research shows that the more motor activity is involved during object use, the more it is elicited when processing the name of that object (Dutriaux & Gyselinck, 2016). Given the location of the ERP activity related to functionally manipulable objects (especially Cz electrode), this early cluster appears to be related to motor activity. In the next section, we discuss when these actions associated with functionally manipulable objects are accessed.

5.3 When are object-associated actions activated during object name reading and when is knowledge about the object accessed?

The purpose of this study was to find out when information about the actions associated with functionally manipulable objects is accessed during object name reading, compared to other information about the object. The

experiments in chapters 2 and 3 were examining micro-affordances, that is, the hand gestures used to grasp an object (Ellis & Tucker, 2000). However, this does not represent the whole story. The actions associated with use are more likely to be significant to the conceptual representation of a functionally manipulable object, compared to micro-affordances. We questioned whether early sensorimotor activations in Chapter 2 represent the actions associated with these objects.

In our study, we measured EEG while participants read denominal verbs (e.g., hammer, drill, wipe). We correlated these ERPs with how frequently those words are used to describe actions (verb frequency), and how often they are used to describe objects (noun frequency). We expected to see access to action-related information during an early stage of linguistic processing, as previous EEG studies demonstrate (Amsel, 2011; Mollo, Pulvermüller & Hauk, 2016). Our findings were in line with these predictions; ERP activity measured during object name reading, associated with the action showed an early cluster of positive activity from 194–294 ms. This activity occurred during the P200 time window, the earliest stage of lexico-semantic processing (Amsel et al., 2013; Hauk et al., 2012; Moseley et al., 2013; Schendan & Kutas, 2003), where previous research has shown somatotopic activation of motor areas in the brain, in relation to action verbs (Mollo et al., 2016). This timing is similar to when Amsel (2011) found function and visual motion features associated with an object were activated during object name processing, from around 100 ms. In our study, the early action-related activity associated with functionally manipulable objects, from 190 ms, could indicate that the early ERP cluster we saw in Chapter 3, for functionally manipulable objects (negativity from 200 ms) was, as hypothesised, related to the action performed during use of the object. Interestingly, denominal verbs originate from the noun. Perhaps the action has

become so deeply embedded in the noun concept, that the action-related motor activity instigates the usage of these nouns to describe the actions themselves.

Based on research demonstrating that the names of objects are more associated with perceptual processing, such as activation in visual brain areas (Pulvermüller, Lutzenberger & Preissl, 1999), and that perceptual features are activated from 200–300 ms (Amsel., 2011), we expected to see information related to the object accessed during this period. Our results followed this hypothesis. ERP activity associated with the object was activated during the N400 component, displaying a negative cluster of activity from 292–372 ms, hinting that conceptual processing of objects involves the retrieval of perceptual features during semantic integration. This object-associated activity was similar to the ERP related to volumetric objects (Chapter 3; Experiment 1). This makes sense as concrete nouns are more associated with their visual features (Pulvermüller, Lutzenberger & Preissl, 1999), as are natural objects (Farah & McClelland, 1991; Ferri et al., 2011) and objects with a volumetric affordance (seen in Chapter 3; Experiments 1 and 2).

Both the object and the action processing shared positive ERP activity, from around 350–670 ms, during the late positive component (LPC; 350–670 ms), which is related to post-N400 episodic memory and conscious thought processing. This might allude to the retrieval of episodic memories related to previous experience of object use, which combine both information about the action, and the object. This is explored further in the following section (5.4). Similarly, Pulvermüller et al. (1999) found activation of visual processing for object names and motor processing for action words around 500 ms, which they suggest reflected semantic processing of the word referents. Their results may echo a similar process to the late LPC in our study.

5.4 When are the specific manipulations associated with an object activated from object names?

In Chapter 4, we also examined when information about the complex motor programs involved in manipulation of the referent object, are activated during object name reading. We correlated the ERPs measured while the participants read the object names, with their ratings of how manipulable the referent objects are. This resulted in a positive cluster, from 504–642 ms, located at parieto-occipital electrodes, moving through the left hemisphere covering parietal, central and frontal sites and terminating in the fronto-temporal region in the left hemisphere.

Previous research has shown that object-associated manipulations reveal left lateralised processing in the parietal lobe (Brandi, Wohlschläger, Sorg & Hermsdörfer, 2014; Garcea, Almeida & Mahon, 2012; Kellenbach, Brett & Patterson, 2003; Proverbio et al., 2011). Brandi et al. (2014) found a left-lateralised occipito-temporo-parieto-frontal network involved in the use of everyday tools, which mirrors the location of the cluster in our study. Furthermore, this activity was during a similar timing to previous object manipulability findings (Madan, Chen & Singhal, 2016; Proverbio et al., 2011). Proverbio et al. found a larger P300 at centro-parietal sites in the left hemisphere, from 500–600 ms, in response to pictures of manipulable tools compared to images of familiar non-tool objects. Madan et al. found that functionally manipulable objects evoked higher a amplitude of slow wave activity, from 400–800 ms, compared to low manipulability objects. The late positive activity we found in our studies (in chapters 3 and 4) was often located in the left hemisphere just as these other studies found. As our participants were all right-handed and would usually grasp and use these objects with their right

hand, the left hemisphere activity situated at central electrodes might signify that activation of manipulations recruits the motor area corresponding to the right hand. This assumption is convincing given that in Chapter 2, affordance related activity was located in the right-hemisphere when the participants were responding with their left hand.

The late positivity in our study may also reflect LPC activity, beginning at a later stage than the LPC we saw for objects and their associated actions in Chapter 4. Schendan and Kutas (2007) found that the LPC was associated with the mental rotation of objects. They found increased amplitude of the P600 (500–700 ms) in response to images of objects that had been seen before but were presented in an uncanonical view; thus suggesting that the LPC represented the mental rotation of those objects. The LPC in our study may signify a mental simulation of rotating the object when manipulating it during use. The manipulability activity overlaps the later activity associated with the object and action ERPs in Chapter 4. The ERP associated with the object concept spans the entire period of the manipulability ERP, perhaps indicating that these manipulations are related to the object concept. Similar late positivity was also found in chapters 2 and 3 for grasp-compatibility of: functionally manipulable objects, volumetric objects, manmade objects during nogo trials, and natural objects during go trials. Thereby suggesting that gesture-specificity for the grasp used to pick up the object is encoded within these manipulation simulations. Moreover, the ERP activity terminated in the fronto-temporal region of the left hemisphere, which we also found for volumetric and natural objects in Chapter 3, asserting that it might be related to angular gyrus pattern-matching. The brain activity associated with object manipulability seems to reflect the amalgamation of perceptual information about the object, the appropriate hand gesture used to grasp the object and the object's associated

actions; enabling preparation for a complex motor program related to the manipulation of the object during use.

LASS theory (Barsalou et al., 2008) posits that embodied representations become activated at various time intervals during linguistic processing, dependent on context requirements. In Chapter 3, we saw that micro-affordances related to functionally manipulable objects were not activated unless necessary for the task. In this study (Chapter 4), the participants read object names and occasionally were prompted to select the one they had just seen, from a choice of three words. The participants were not responding to the target words; therefore the affordances were unnecessary for the task. This manipulation information seems to reflect a late simulation of post-semantic processing, perhaps generated via spreading activation. However, it is interesting to note that these simulations occur during the time that participants would usually respond to stimuli when a response is required (chapters 2 and 3). Almost as if the participant activates the necessary complex manipulations involved in using or grasping the object, merely from reading the name of the object. The late activation of this ERP suggests that the early affordance findings from behavioural studies and our study in Chapter 2 (Feven-Parsons & Goslin, 2018), reflect a simpler action representation, such as the object's micro-affordances (Ellis & Tucker, 2000).

5.5 Is the conceptual representation of functionally manipulable objects built on a person's experience of using those objects and observing others use them?

Our final objective was to find out when brain activity associated with the personal use of an object is activated during object name processing. It is thought that the conceptual representation of an object is grounded in a

person's sensorimotor experience of that object, via Hebbian learning (Pulvermüller et al., 1999). We wondered whether these experiences are activated during semantic processing of the object name, or during a later time window, post-N400, resulting from spreading activation (Mahon & Caramazza, 2008).

We found negativity from 274–432 ms, related to how frequently the participants had used the objects, and negativity from 274–356 ms for how often they had seen those objects used by someone else. Both object use and observation of use were activated during N400 timing, which was very similar to the brain activity related to the object representation, negativity from 290–370 ms (first analysis in Chapter 4). This suggests that the conceptual representation of an object is associated with object use and observation of object use. Furthermore, this activity also overlapped with the ERP for actions related to these manipulable objects. It follows that actions associated with an object are related to an individual's previous use of that object, supporting Pulvermüller's (1999) assertion concerning Hebbian learning.

Comparing the frequency of use activity, with the observation of use activity, resulted in two negative clusters, 364–406 ms and 566–622 ms. This illustrated a quantitative, rather than qualitative, difference between these two ERPs; reflecting greater and longer-lasting activation for object use, compared to observation of use. For both conditions, the ERP activity was located around centro-parietal electrode sites at the midline; perhaps revealing mirror neuron activity. This would mean that the same neurons were being activated when processing the representation of using the object and of observing another using the object. When participants read sentences about ice hockey descriptions during a fMRI study, Beilock et al. (2008) found greater motor activation for individuals who had direct experience of playing ice hockey, compared to fans

who only had experience of watching ice hockey. According to mirror neuron theories, motor activations related to the observation of actions, originate during a person's direct experience of the action (Calvo-Merino et al., 2005; Cannon et al., 2014). The timing and location of this activity appeared to reflect N400 semantic processing. The higher amplitude of negativity during this period, for words referring to objects a person has had more experience of using, perhaps reflects the greater richness of their semantic representation compared to objects a person has more often seen used by someone else. Previous research has found a greater N400 and N700 related to objects with a richer semantic representation (Barber, Otten, Kousta & Vigliocco, 2013). A richer semantic concept would develop through information received via different sensory modalities during use: tactile, visual, somatosensory and action execution. Observation of use would only represent information through the perceptual systems and would, therefore, have a weaker semantic representation. Furthermore, the later difference between use and observation is around manipulability timing, indicating that processing the manipulability of an object is also developed through an individual's previous use.

One limitation of this research is that we cannot be sure whether the brain activity related to object use and observation of use, activated during object name reading, is motor activity. Future research might examine beta frequency and mu waves, which are known to be indicative of motor cortex activation, to see whether these representations of object use and observation of use are linked to motor cortex activity. Also, alternative methods could be used to investigate whether these representations reflect mirror neuron activity during linguistic processing. This was a limitation of the experiments in Chapter 3. We could not be sure if it was motor activity we saw in the functional and

volumetric data. It would be interesting to see whether the greater negativity for functionally manipulable objects, compared to volumetric objects is related to greater motor activity, as we have argued. See Appendix D for an illustration of the ERP timings for all of our results.

5.6 Conclusions

Our findings provide evidence that object affordances are activated automatically from reading object names. Information related to object affordance is available from as early as 176 ms, which is during the earliest stage of semantic processing (Amsel et al., 2013; Hauk et al., 2012; Moseley et al., 2013; Schendan & Kutas, 2003). More complex motor-related information about the actions associated with the use of functionally manipulable objects is accessed from around 190 ms. Semantic processing of functionally manipulable objects incorporates these related actions, along with information related to the perceptual features of the object and the specific motor operations during manual manipulation. This provides these objects with a richer semantic representation, compared to objects that are merely graspable based on their geometric properties. The conceptual representation of functionally manipulable objects appears to be related to the amount of previous experience a person has had of using those objects.

Appendix A: Chapter 2 Stimuli

Semantic		Affordance		Neutral	
Prime	Target	Prime	Target	Prime	Target
Marker	Axe	Potato	Axe	Strawberry	Axe
Eraser	Axe	Cucumber	Axe	Fig	Axe
Tweezers	Axe	Orange	Axe	Bean	Axe
Scalpel	Axe	Pear	Axe	Mushroom	Axe
Marker	Hammer	Potato	Hammer	Strawberry	Hammer
Eraser	Hammer	Cucumber	Hammer	Fig	Hammer
Tweezers	Hammer	Orange	Hammer	Bean	Hammer
Scalpel	Hammer	Pear	Hammer	Mushroom	Hammer
Marker	Drill	Potato	Drill	Strawberry	Drill
Eraser	Drill	Cucumber	Drill	Fig	Drill
Tweezers	Drill	Orange	Drill	Bean	Drill
Scalpel	Drill	Pear	Drill	Mushroom	Drill
Marker	Saw	Potato	Saw	Strawberry	Saw
Eraser	Saw	Cucumber	Saw	Fig	Saw
Tweezers	Saw	Orange	Saw	Bean	Saw
Scalpel	Saw	Pear	Saw	Mushroom	Saw
Spanner	Pin	Strawberry	Pin	Potato	Pin
Spade	Pin	Fig	Pin	Cucumber	Pin
Stapler	Pin	Bean	Pin	Orange	Pin
Trowel	Pin	Mushroom	Pin	Pear	Pin
Spanner	Needle	Strawberry	Needle	Potato	Needle
Spade	Needle	Fig	Needle	Cucumber	Needle
Stapler	Needle	Bean	Needle	Orange	Needle
Trowel	Needle	Mushroom	Needle	Pear	Needle
Spanner	Biro	Strawberry	Biro	Potato	Biro
Spade	Biro	Fig	Biro	Cucumber	Biro
Stapler	Biro	Bean	Biro	Orange	Biro
Trowel	Biro	Mushroom	Biro	Pear	Biro
Spanner	Pencil	Strawberry	Pencil	Potato	Pencil
Spade	Pencil	Fig	Pencil	Cucumber	Pencil
Stapler	Pencil	Bean	Pencil	Orange	Pencil

Appendix A: Chapter 2 Stimuli (continued)

Trowel	Pencil	Mushroom	Pencil	Pear	Pencil
Strawberry	Apple	Spanner	Apple	Marker	Apple
Fig	Apple	Spade	Apple	Eraser	Apple
Bean	Apple	Stapler	Apple	Tweezers	Apple
Mushroom	Apple	Trowel	Apple	Scalpel	Apple
Strawberry	Banana	Spanner	Banana	Marker	Banana
Fig	Banana	Spade	Banana	Eraser	Banana
Bean	Banana	Stapler	Banana	Tweezers	Banana
Mushroom	Banana	Trowel	Banana	Scalpel	Banana
Strawberry	Carrot	Spanner	Carrot	Marker	Carrot
Fig	Carrot	Spade	Carrot	Eraser	Carrot
Bean	Carrot	Stapler	Carrot	Tweezers	Carrot
Mushroom	Carrot	Trowel	Carrot	Scalpel	Carrot
Strawberry	Onion	Spanner	Onion	Marker	Onion
Fig	Onion	Spade	Onion	Eraser	Onion
Bean	Onion	Stapler	Onion	Tweezers	Onion
Mushroom	Onion	Trowel	Onion	Scalpel	Onion
Potato	Lentil	Marker	Lentil	Spanner	Lentil
Cucumber	Lentil	Eraser	Lentil	Spade	Lentil
Orange	Lentil	Tweezers	Lentil	Stapler	Lentil
Pear	Lentil	Scalpel	Lentil	Trowel	Lentil
Potato	Pea	Marker	Pea	Spanner	Pea
Cucumber	Pea	Eraser	Pea	Spade	Pea
Orange	Pea	Tweezers	Pea	Stapler	Pea
Pear	Pea	Scalpel	Pea	Trowel	Pea
Potato	Grape	Marker	Grape	Spanner	Grape
Cucumber	Grape	Eraser	Grape	Spade	Grape
Orange	Grape	Tweezers	Grape	Stapler	Grape
Pear	Grape	Scalpel	Grape	Trowel	Grape
Potato	Cherry	Marker	Cherry	Spanner	Cherry
Cucumber	Cherry	Eraser	Cherry	Spade	Cherry
Orange	Cherry	Tweezers	Cherry	Stapler	Cherry
Pear	Cherry	Scalpel	Cherry	Trowel	Cherry

Appendix B: Chapter 3 Stimuli

Experiment 1

Functional		Volumetric		Non-manipulable		Probe
Precision-grip	Power-grip	Precision-grip	Power-grip			
ballpoint	baton	acorn	avocado	bridge	lighthouse	butterfly
chalk	broom	almond	bottle	castle	maze	camel
chopsticks	brush	apricot	brick	cathedral	meadow	crab
cottonbud	chisel	biscuit	celery	cave	meteor	dolphin
crayon	doorknob	button	clementine	ceiling	mist	elephant
dart	dumbbell	chip	coconut	cellar	moon	fox
fork	handbrake	coin	courgette	cinema	museum	giraffe
highlighter	hoover	crisp	flask	cliff	palace	gorilla
key	hose	crumb	jar	cloud	pavement	kangaroo
match	kettle	daisy	leek	corridor	pharmacy	lion
nailfile	knife	hazelnut	lightbulb	field	prison	monkey
paperclip	lever	jellybean	mango	fog	pub	octopus
peg	microphone	leaf	mug	galaxy	puddle	parrot
pen	mop	marble	nectarine	garage	rain	penguin
scissors	racket	olive	parsnip	garden	restaurant	shark
shoelace	rattle	penny	peach	harbour	river	squirrel
teaspoon	sword	pill	railing	lake	road	tiger
toothpick	torch	popcorn	rhubarb	lawn	shadow	turtle
whistle	umbrella	raisin	swede	theatre	stable	worm
zip	whisk	seed	vase	volcano	stadium	zebra

Appendix B: Chapter 3 Stimuli

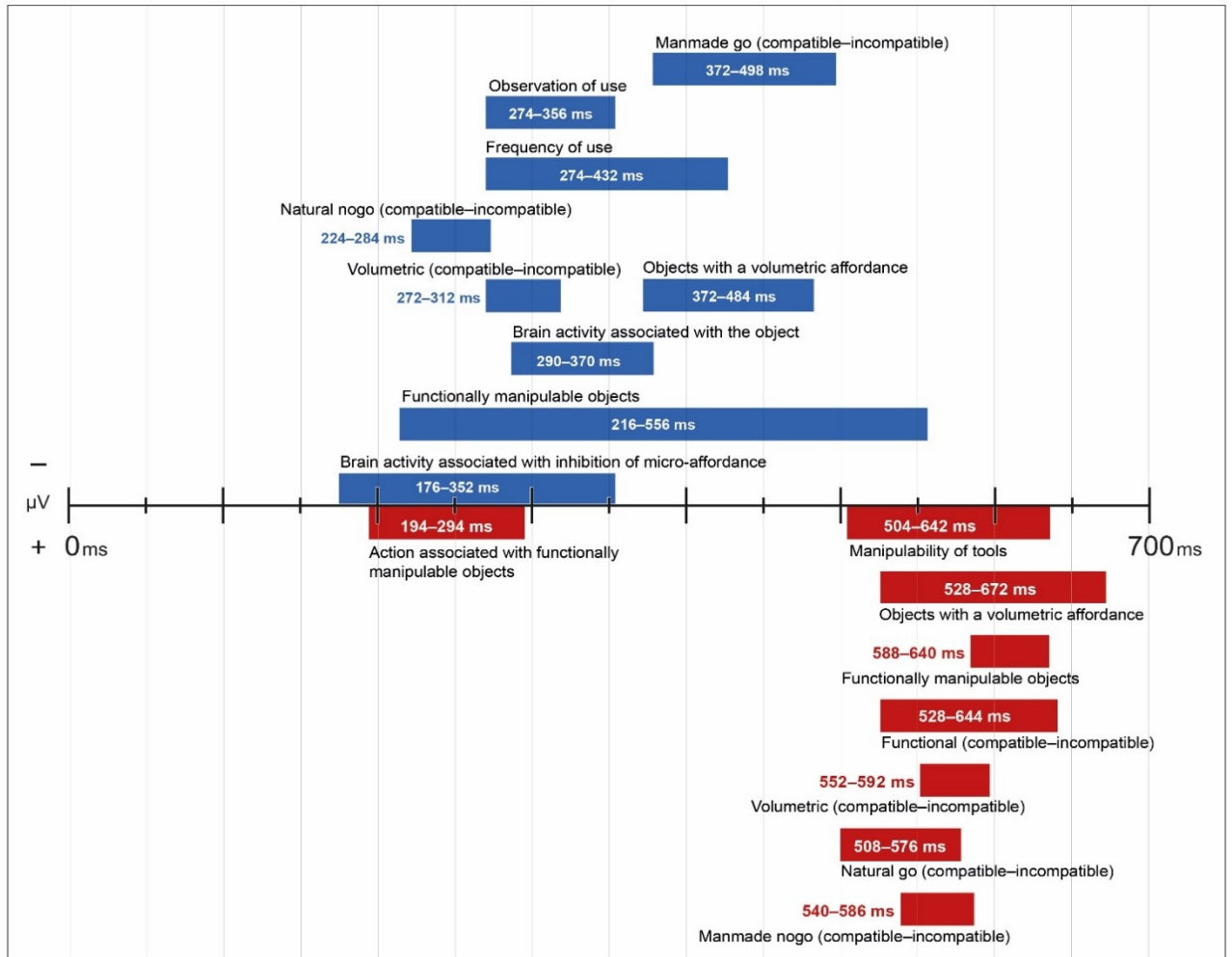
Experiment 2

Manmade object names		Natural object names	
Precision-grip	Power-grip	Precision-grip	Power-grip
crayon	broom	acorn	apple
dart	drill	almond	aubergine
eraser	hammer	cherry	avocado
key	hoover	conker	banana
needle	hose	daisy	carrot
peg	iron	dandelion	celery
pen	kettle	feather	courgette
pencil	knife	grape	cucumber
razor	masher	grass	leek
scalpel	mower	leaf	mango
scissors	peeler	mushroom	parsnip
spoon	racket	olive	pear
tweezers	saw	pea	potato
wand	spade	radish	swede
zip	spatula	sprout	turnip

Appendix C: Chapter 4 Stimuli

Word	Noun frequency	Verb frequency	Ratio	Frequency * Observation Correlation (<i>r</i>) <i>n</i> = 60 <i>p</i> = .05	No. of incorrect answers to knowledge question (out of 60 participants)
wipe	6	668	0.008902	.28	3
whisk	7	122	0.054264	.53	12
rattle	54	266	0.16875	.43	0
rake	33	102	0.244444	.42	1
paddle	24	71	0.252632	.57	1
flush	86	245	0.259819	.49	1
buckle	34	75	0.311927	.74	0
mop	49	102	0.324503	.46	0
scoop	62	124	0.333333	.71	10
bludgeon	7	14	0.333333	.92	1
tie	612	1100	0.357477	.06	0
comb	96	159	0.376471	.41	0
drill	141	209	0.402857	.46	1
brush	296	425	0.410541	.52	0
zip	32	44	0.421053	.44	9
hammer	197	223	0.469048	.31	0
ladle	26	27	0.490566	.72	0
catapult	6	6	0.5	.69	6
sandpaper	6	6	0.5	.45	1
whip	254	234	0.520492	.86	0
plug	170	120	0.586207	.67	11
skewer	18	12	0.6	.53	4
shovel	76	47	0.617886	.54	2
chisel	39	18	0.684211	.51	2
sieve	41	18	0.694915	.77	1
peg	131	51	0.71978	.48	0
sponge	138	38	0.784091	.74	1
telephone	1876	365	0.837126	.78	0
hose	72	13	0.847059	.61	0
spear	220	28	0.887097	.83	0
hoover	52	6	0.896552	.67	1
pencil	332	35	0.904632	.74	2
crayon	32	2	0.941176	.61	7
knife	791	42	0.94958	.96	6
axe	153	4	0.974522	.84	1
towel	392	3	0.992405	.56	0

Appendix D: Timeline Illustrating ERP Findings



6. References

- Acres, K., Taylor, K. I., Moss, H. E., Stamatakis, E. A., & Tyler, L. K. (2009). Complementary hemispheric asymmetries in object naming and recognition: a voxel-based correlational study. *Neuropsychologia*, *47*(8-9), 1836-1843.
- Adams, A. M. (2016). How language is embodied in bilinguals and children with specific language impairment. *Frontiers in Psychology*, *7*, 1209.
- Amsel, B. D. (2011). Tracking real-time neural activation of conceptual knowledge using single-trial event-related potentials. *Neuropsychologia*, *49*(5), 970-983.
- Amsel, B. D., Urbach, T. P., & Kutas, M. (2013). Alive and grasping: Stable and rapid semantic access to an object category but not object graspability. *NeuroImage*, *77*, 1-13.
- Andrews, M., Vigliocco, G., & Vinson, D. (2009). Integrating experiential and distributional data to learn semantic representations. *Psychological Review*, *116*(3), 463.
- Anelli, F., Nicoletti, R., & Borghi, A. M. (2010). Categorization and action: What about object consistence? *Acta Psychologica*, *133*(2), 203-211.
- Aravena, P., Hurtado, E., Riveros, R., Cardona, J. F., Manes, F., & Ibáñez, A. (2010). Applauding with closed hands: neural signature of action-sentence compatibility effects. *PloS one*, *5*(7), e11751.
- Augustin, M. D., Defranceschi, B., Fuchs, H. K., Carbon, C. C., & Hutzler, F. (2011). The neural time course of art perception: An ERP study on the processing of style versus content in art. *Neuropsychologia*, *49*(7), 2071-2081.
- Baayen, R. H., Piepenbrock, R., & Gulikers, L. (1995). The CELEX lexical database. Linguistic data consortium. University of Pennsylvania, Philadelphia.

- Balota, D.A., Yap, M.J., Cortese, M.J., Hutchison, K.A., Kessler, B., Loftis, B., Neely, J.H., Nelson, D.L., Simpson, G.B., & Treiman, R. (2007). The English Lexicon Project. *Behavior Research Methods*, *39*, 445-459.
- Barber, H. A., Kousta, S. T., Otten, L. J., & Vigliocco, G. (2010). Event-related potentials to event-related words: Grammatical class and semantic attributes in the representation of knowledge. *Brain Research*, *1332*, 65-74.
- Barber, H. A., Otten, L. J., Kousta, S. T., & Vigliocco, G. (2013). Concreteness in word processing: ERP and behavioral effects in a lexical decision task. *Brain and Language*, *125*(1), 47-53.
- Barbieri, F., Buonocore, A., Bernardis, P., Dalla Volta, R., & Gentilucci, M. (2007). On the relations between affordance and representation of the agent's effector. *Experimental Brain Research*, *180*(3), 421-433.
- Barsalou, L. W. (1999). Perceptions of perceptual symbols. *Behavioral and Brain Sciences*, *22*(4), 637-660.
- Barsalou, L. W. (2008). Grounded cognition. *Annual Review of Psychology*, *59*, 617-645.
- Barsalou, L.W., Santos, A., Simmons, W.K., & Wilson, C.D. (2008). *Language and Simulation in Conceptual Processing*. In M. De Vega, A.M. Glenberg, & A.C. Graesser, A. (Eds.). Symbols, embodiment, and meaning (pp. 245-283). Oxford: Oxford University Press.
- Battig, W. F., & Montague, W. E. (1969). Category norms for verbal items in 56 categories: A replication and extension of the Connecticut norms. *Journal of Experimental Psychology*, *80*, 1-46.
- Beauchamp, M. S., Lee, K. E., Haxby, J. V., & Martin, A. (2002). Parallel visual motion processing streams for manipulable objects and human movements. *Neuron*, *34*(1), 149-159.

- Beilock, S. L., Lyons, I. M., Mattarella-Micke, A., Nusbaum, H. C., & Small, S. L. (2008). Sports experience changes the neural processing of action language. *Proceedings of the National Academy of Sciences, 105*(36), 13269-13273.
- Bergen, B., & Wheeler, K. (2010). Grammatical aspect and mental simulation. *Brain and Language, 112*(3), 150-158.
- Binder, J. R., & Desai, R. H. (2011). The neurobiology of semantic memory. *Trends in Cognitive Sciences, 15*(11), 527-536.
- Binkofski, F., & Buxbaum, L. J. (2013). Two action systems in the human brain. *Brain & Language, 127*(2), 222-229.
- Borghi, A. M., & Binkofski, F. (2014). *Words as Social Tools: An Embodied View on Abstract Concepts*. Berlin; New York, NY: Springer.
- Borghi, A. M., & Cimatti, F. (2009, January). Words as tools and the problem of abstract word meanings. In *Proceedings of the Annual Meeting of the Cognitive Science Society (Vol. 31, No. 31)*.
- Borghi, A. M., & Scorolli, C. (2009). Language comprehension and dominant hand motion simulation. *Human Movement Science, 28*(1), 12-27.
- Borghi, A. M., Bonfiglioli, C., Lugli, L., Ricciardelli, P., Rubichi, S., & Nicoletti, R. (2007). Are visual stimuli sufficient to evoke motor information? Studies with hand primes. *Neuroscience Letters, 411*(1), 17-21.
- Borghi, A. M., Flumini, A., Cimatti, F., Marocco, D., & Scorolli, C. (2011). Manipulating objects and telling words: a study on concrete and abstract words acquisition. *Frontiers in Psychology, 2*, 15.
- Borovsky, A., Elman, J. L., & Kutas, M. (2012). Once is enough: N400 indexes semantic integration of novel word meanings from a single exposure in context. *Language Learning and Development, 8*(3), 278-302.

- Borreggine, K. L., & Kaschak, M. P. (2006). The action–sentence compatibility effect: It's all in the timing. *Cognitive Science*, *30*(6), 1097-1112.
- Brandi, M. L., Wohlschläger, A., Sorg, C., & Hermsdörfer, J. (2014). The neural correlates of planning and executing actual tool use. *Journal of Neuroscience*, *34*(39), 13183-13194.
- Bub, D. N., & Masson, M. E. (2006). Gestural knowledge evoked by objects as part of conceptual representations. *Aphasiology*, *20*(9), 1112-1124.
- Bub, D. N., & Masson, M. E. (2010). On the nature of hand-action representations evoked during written sentence comprehension. *Cognition*, *116*(3), 394-408.
- Bub, D. N., & Masson, M. E. (2012). On the dynamics of action representations evoked by names of manipulable objects. *Journal of Experimental Psychology*, *141*(3), 502-517.
- Bub, D. N., Masson, M. E., & Cree, G. S. (2008). Evocation of functional and volumetric gestural knowledge by objects and words. *Cognition*, *106*(1), 27-58.
- Buccino, G., Colagè, I., Gobbi, N., & Bonaccorso, G. (2016). Grounding meaning in experience: A broad perspective on embodied language. *Neuroscience & Biobehavioral Reviews*, *69*, 69-78.
- Buxbaum, L. J. & Kalénine, S. (2010). Action knowledge, visuomotor activation, and embodiment in the two action systems. *Annals of the New York Academy of Sciences*, *119*(1), 201-218.
- Buxbaum, L. J. (2017). Learning, remembering, and predicting how to use tools: Distributed neurocognitive mechanisms: Comment on Osiurak and Badets (2016).
- Buxbaum, L. J., Kyle, K. M., Tang, K., & Detre, J. A. (2006). Neural substrates of knowledge of hand postures for object grasping and functional object use: Evidence from fMRI. *Brain Research*, *1117*(1), 175-185.

- Buxbaum, L. J., Sirigu, A., Schwartz, M. F., & Klatzky, R. (2003). Cognitive representations of hand posture in ideomotor apraxia. *Neuropsychologia*, *41*(8), 1091-1113.
- Caligiore, D., & Fischer, M. H. (2013). Vision, action and language unified through embodiment. *Psychological Research*, *77*(1), 1-6.
- Calvo-Merino, B., Glaser, D. E., Grèzes, J., Passingham, R. E., & Haggard, P. (2005). Action observation and acquired motor skills: An fMRI study with expert dancers. *Cerebral Cortex*, *15*(8), 1243-1249.
- Cannon, E. N., Yoo, K. H., Vanderwert, R. E., Ferrari, P. F., Woodward, A. L., & Fox, N. A. (2014). Action experience, more than observation, influences mu rhythm desynchronization. *PLoS One*, *9*(3), e92002.
- Carota, F., Moseley, R., & Pulvermüller, F. (2012). Body-part-specific representations of semantic noun categories. *Journal of Cognitive Neuroscience*, *24*(6), 1492-1509.
- Chao, L. L., Haxby, J. V., & Martin, A. (1999). Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nature Neuroscience*, *2*(10), 913.
- Chatterjee, A. (2010). Disembodying cognition. *Language and Cognition*, *2*(1), 79-116.
- Chikazoe, J., Konishi, S., Asari, T., Jimura, K., & Miyashita, Y. (2007). Activation of right inferior frontal gyrus during response inhibition across response modalities. *Journal of Cognitive Neuroscience*, *19*(1), 69-80.
- Chow, H. M., Mar, R. A., Xu, Y., Liu, S., Wagage, S., & Braun, A. R. (2014). Embodied comprehension of stories: interactions between language regions and modality-specific neural systems. *Journal of Cognitive Neuroscience*, *26*(2), 279-295.
- Clark, E. V., & Clark, H. H. (1979). When nouns surface as verbs. *Language*, 767-811.

- Collette, C., Bonnotte, I., Jacquemont, C., Kalénine, S., & Bartolo, A. (2016). The development of object function and manipulation knowledge: evidence from a semantic priming study. *Frontiers in Psychology, 7*, 1239.
- Coutanche, M. N., & Thompson-Schill, S. L. (2014). Creating concepts from converging features in human cortex. *Cerebral Cortex, 25*(9), 2584-2593.
- Creem-Regehr, S. H., & Lee, J. N. (2005). Neural representations of graspable objects: are tools special? *Cognitive Brain Research, 22*(3), 457-469.
- Dalla Volta, R., Fabbri-Destro, M., Gentilucci, M., & Avanzini, P. (2014). Spatiotemporal dynamics during processing of abstract and concrete verbs: An ERP study. *Neuropsychologia, 61*, 163-174.
- Damasio, A. R. (1989). The brain binds entities and events by multiregional activation from convergence zones. *Neural Computation, 1*(1), 123-132.
- Deacon, D., Hewitt, S., Yang, C. M., & Nagata, M. (2000). Event-related potential indices of semantic priming using masked and unmasked words: Evidence that the N400 does not reflect a post-lexical process. *Cognitive Brain Research, 9*(2), 137-146.
- Dekker, T. M., Mareschal, D., Johnson, M. H., & Sereno, M. I. (2014). Picturing words? Sensorimotor cortex activation for printed words in child and adult readers. *Brain and Language, 139*, 58-67.
- Dove, G. (2009). Beyond perceptual symbols: A call for representational pluralism. *Cognition, 110*(3), 412-431.
- Dove, G. (2011). On the need for embodied and dis-embodied cognition. *Embodied and Grounded Cognition, 129*.
- Dove, G. (2016). Three symbol ungrounding problems: Abstract concepts and the future of embodied cognition. *Psychonomic Bulletin & Review, 23*(4), 1109-1121.

- Dreyer, F. R., Frey, D., Arana, S., Saldern, S. V., Picht, T., Vajkoczy, P., & Pulvermüller, F. (2015). Is the motor system necessary for processing action and abstract emotion words? Evidence from focal brain lesions. *Frontiers in Psychology, 6*, 1661.
- Dutriaux, L., & Gyselinck, V. (2016). Learning is better with the hands free: The role of posture in the memory of manipulable objects. *PloS one, 11*(7), e0159108.
- Ellis, R., & Tucker, M. (2000). Micro-affordance: The potentiation of components of action by seen objects. *British Journal of Psychology, 91*, 451-471.
- Fagg, A. H., & Arbib, M. A. (1998). Modeling parietal–premotor interactions in primate control of grasping. *Neural Networks, 11*(7-8), 1277-1303.
- Farah, M. J., & McClelland, J. L. (1991). A computational model of semantic memory impairment: modality specificity and emergent category specificity. *Journal of Experimental Psychology: General, 120*(4), 339.
- Ferri, F., Riggio, L., Gallese, V., & Costantini, M. (2011). Objects and their nouns in peripersonal space. *Neuropsychologia, 49*(13), 3519-3524.
- Feven-Parsons, I. M., & Goslin, J. (2018). Electrophysiological study of action-affordance priming between object names. *Brain and Language, 184*, 20-31.
- Fogassi, L., & Luppino, G. (2005). Motor functions of the parietal lobe. *Current Opinion in Neurobiology, 15*(6), 626-631.
- Forster, K.I., & Davis, C. (1984). Repetition priming and frequency attenuation in lexical access. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 10*(4), 680-698.
- Gainotti, G., Spinelli, P., Scaricamazza, E., & Marra, C. (2013). The evaluation of sources of knowledge underlying different conceptual categories. *Frontiers in Human Neuroscience, 7*, 40.

- Gajewski, P. D., Stoerig, P., & Falkenstein, M. (2008). ERP-correlates of response selection in a response conflict paradigm. *Brain Research, 1189*, 127-134.
- Galetzka, C. (2017). The story so far: how embodied cognition advances our understanding of meaning-making. *Frontiers in Psychology, 8*, 1315.
- Gallese, V. (2008). Mirror neurons and the social nature of language: The neural exploitation hypothesis. *Social Neuroscience, 3*(3-4), 317-333.
- Gallese, V., & Cuccio, V. (2018). The neural exploitation hypothesis and its implications for an embodied approach to language and cognition: Insights from the study of action verbs processing and motor disorders in Parkinson's Disease. *Cortex*.
- Garcea, F. E., Almeida, J., & Mahon, B. Z. (2012). A right visual field advantage for visual processing of manipulable objects. *Cognitive, Affective, & Behavioral Neuroscience, 12*(4), 813-825.
- Gentilucci, M., & Gangitano, M. (1998). Influence of automatic word reading on motor control. *European Journal of Neuroscience, 10*(2), 752-756.
- Gerlach, C. (2009). Category-specificity in visual object recognition. *Cognition, 111*, 281-301.
- Gibson, J. J. (1979) The theory of affordances. In *The Ecological Approach to Visual Perception* (pp. 127-137). Boston, Massachusetts: Houghton Mifflin.
- Glenberg, A. M., & Gallese, V. (2012). Action-based language: A theory of language acquisition, comprehension, and production. *Cortex, 48*(7), 905-922.
- Glenberg, A. M., & Kaschak, M. P. (2002). Grounding language in action. *Psychonomic Bulletin & Review, 9*(3), 558-565.
- Glenberg, A. M., & Robertson, D. A. (1999). Indexical understanding of instructions. *Discourse Processes, 28*(1), 1-26.

- Glenberg, A. M., & Robertson, D. A. (2000). Symbol grounding and meaning: A comparison of high-dimensional and embodied theories of meaning. *Journal of Memory and Language, 43*(3), 379-401.
- Glover, S., & Dixon, P. (2002). Semantics affect the planning but not control of grasping. *Experimental Brain Research, 146*(3), 383-387.
- Glover, S., Rosenbaum, D. A., Graham, J., & Dixon, P. (2004). Grasping the meaning of words. *Experimental Brain Research, 154*(1), 103-108.
- Gough, P. M., Riggio, L., Chersi, F., Sato, M., Fogassi, L., & Buccino, G. (2012). Nouns referring to tools and natural objects differentially modulate the motor system. *Neuropsychologia, 50*(1), 19-25.
- Grabowski, T. J., Damasio, H., & Damasio, A. R. (1998). Premotor and prefrontal correlates of category-related lexical retrieval. *NeuroImage, 7*(3), 232-243.
- Grainger, J. (1990). Word frequency and neighborhood frequency effects in lexical decision and naming. *Journal of Memory and Language, 29*(2), 228.
- Greif, M. L., Nelson, D. G., Keil, F. C., & Gutierrez, F. (2006). What do children want to know about animals and artifacts? Domain-specific requests for information. *Psychological Science, 17*(6), 455-459.
- Grèzes, J., & Decety, J. (2001). Functional anatomy of execution, mental simulation, observation, and verb generation of actions: a meta-analysis. *Human Brain Mapping, 12*(1), 1-19.
- Grèzes, J., Armony, J. L., Rowe, J., & Passingham, R. E. (2003). Activations related to “mirror” and “canonical” neurones in the human brain: an fMRI study. *NeuroImage, 18*(4), 928-937.
- Hagoort, P., Baggio, G., & Willems, R. M. (2009). Semantic unification. In M. S. Gazzaniga (Ed.), *The cognitive neurosciences*, 4th ed. (pp. 819-836). Cambridge, MA: MIT press.

- Hampshire, A., Chamberlain, S. R., Monti, M. M., Duncan, J., & Owen, A. M. (2010). The role of the right inferior frontal gyrus: inhibition and attentional control. *NeuroImage*, *50*(3), 1313-1319.
- Harnad, S. (1990). The symbol grounding problem. *Physica D: Nonlinear Phenomena*, *42*(1-3), 335-346.
- Hauk, O., & Pulvermüller, F. (2004). Neurophysiological distinction of action words in the fronto-central cortex. *Human Brain Mapping*, *21*(3), 191-201.
- Hauk, O., Coutout, C., Holden, A., & Chen, Y. (2012). The time-course of single-word reading: Evidence from fast behavioral and brain responses. *NeuroImage*, *60*(2), 1462-1477.
- Hauk, O., Davis, M. H., Ford, M., Pulvermüller, F., & Marslen-Wilson, W. D. (2006). The time course of visual word recognition as revealed by linear regression analysis of ERP data. *NeuroImage*, *30*(4), 1383-1400.
- Hauk, O., Shtyrov, Y., & Pulvermüller, F. (2008). The time course of action and action-word comprehension in the human brain as revealed by neurophysiology. *Journal of Physiology-Paris*, *102*(1), 50-58.
- Hoenig, K., Müller, C., Herrnberger, B., Sim, E. J., Spitzer, M., Ehret, G., & Kiefer, M. (2011). Neuroplasticity of semantic representations for musical instruments in professional musicians. *NeuroImage*, *56*(3), 1714.
- Innocenti, A., De Stefani, E., Sestito, M., & Gentilucci, M. (2014). Understanding of action-related and abstract verbs in comparison: a behavioral and TMS study. *Cognitive Processing*, *15*(1), 85-92.
- Jax, S. A., & Buxbaum, L. (2010). Response interference between functional and structural actions linked to the same familiar object. *Cognition*, *115*(2), 350-355.
- Jefferies, E., & Lambon Ralph, M. A. (2006). Semantic impairment in stroke aphasia versus semantic dementia: a case-series comparison. *Brain*, *129*(8), 2132-2147.

- Johnson Jr, R., Barnhardt, J., & Zhu, J. (2003). The deceptive response: effects of response conflict and strategic monitoring on the late positive component and episodic memory-related brain activity. *Biological Psychology*, *64*(3), 217-253.
- Kellenbach, M. L., Brett, M., & Patterson, K. (2003). Actions speak louder than functions: the importance of manipulability and action in tool representation. *Journal of Cognitive Neuroscience*, *15*(1), 30-46.
- Kiefer, M., Sim, E. J., Liebich, S., Hauk, O., & Tanaka, J. (2007). Experience-dependent plasticity of conceptual representations in human sensory-motor areas. *Journal of Cognitive Neuroscience*, *19*(3), 525-542.
- Kounios, J., Green, D. L., Payne, L., Fleck, J. I., Grondin, R., & McRae, K. (2009). Semantic richness and the activation of concepts in semantic memory: Evidence from event-related potentials. *Brain Research*, *1282*, 95-102.
- Kourtis, D., & Vingerhoets, G. (2015). Perceiving objects by their function: An EEG study on feature saliency and prehensile affordances. *Biological Psychology*, *110*, 138-147.
- Kousta, S. T., Vigliocco, G., Vinson, D. P., Andrews, M., & Del Campo, E. (2011). The representation of abstract words: why emotion matters. *Journal of Experimental Psychology: General*, *140*(1), 14.
- Kousta, S. T., Vinson, D. P., & Vigliocco, G. (2009). Emotion words, regardless of polarity, have a processing advantage over neutral words. *Cognition*, *112*(3), 473-481.
- Kutas, M., & Federmeier, K. D. (2011). Thirty years and counting: finding meaning in the N400 component of the event-related brain potential (ERP). *Annual Review of Psychology*, *62*, 621-647.
- Lambon Ralph, M. A., & Patterson, K. (2008). Generalization and differentiation in semantic memory: insights from semantic dementia. *Annals of the New York Academy of Sciences*, *1124*(1), 61-76.

- Lee, C. L., Huang, H. W., Federmeier, K. D., & Buxbaum, L. J. (2018). Sensory and semantic activations evoked by action attributes of manipulable objects: Evidence from ERPs. *NeuroImage*, *167*, 331-341.
- Lee, C. L., Middleton, E., Mirman, D., Kalénine, S., & Buxbaum, L. J. (2013). Incidental and context-responsive activation of structure-and function-based action features during object identification. *Journal of Experimental Psychology: Human Perception and Performance*, *39*(1), 257-270.
- Lhermitte, F. (1983). 'Utilization behaviour' and its relation to lesions of the frontal lobes. *Brain*, *106*(2), 237-255.
- Lindemann, O., Stenneken, P., van Schie, H. T., & Bekkering, H. (2006). Semantic activation in action planning. *Journal of Experimental Psychology: Human Perception and Performance*, *32*(3), 633.
- Louwerse, M. M. (2007). Symbolic or embodied representations: A case for symbol interdependency. *Handbook of Latent Semantic Analysis*, 107-120.
- Louwerse, M. M. (2011). Symbol interdependency in symbolic and embodied cognition. *Topics in Cognitive Science*, *3*(2), 273-302.
- Louwerse, M. M. (2018). Knowing the Meaning of a Word by the Linguistic and Perceptual Company It Keeps. *Topics in Cognitive Science*, *10*(3), 573-589.
- Louwerse, M. M., & Jeuniaux, P. (2008). Language comprehension is both embodied and symbolic. *Symbols and Embodiment: Debates on Meaning and Cognition*, 309-326.
- Louwerse, M. M., & Jeuniaux, P. (2010). The linguistic and embodied nature of conceptual processing. *Cognition*, *114*(1), 96-104.
- Lucas, M. (2000). Semantic priming without association: A meta-analytic review. *Psychonomic Bulletin & Review*, *7*(4), 618-630.

- Madan, C. R., Chen, Y. Y., & Singhal, A. (2016). ERPs differentially reflect automatic and deliberate processing of the functional manipulability of objects. *Frontiers in Human Neuroscience, 10*, 360.
- Mahon, B. Z. (2015). What is embodied about cognition? *Language, Cognition and Neuroscience, 30*(4), 420-429.
- Mahon, B. Z., & Caramazza, A. (2005). The orchestration of the sensory-motor systems: Clues from neuropsychology. *Cognitive Neuropsychology, 22*(3-4), 480-494.
- Mahon, B. Z., & Caramazza, A. (2008). A critical look at the embodied cognition hypothesis and a new proposal for grounding conceptual content. *Journal of Physiology-Paris, 102*(1-3), 59-70.
- Marino, B. F., Gough, P. M., Gallese, V., Riggio, L., & Buccino, G. (2013). How the motor system handles nouns: a behavioral study. *Psychological Research, 77*(1), 64-73.
- Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG and MEG data. *Journal of Neuroscience Methods, 164*(1), 177-190.
- Masson, M. E., Bub, D. N., & Newton-Taylor, M. (2008). Language-based access to gestural components of conceptual knowledge. *Quarterly Journal of Experimental Psychology, 61*(6), 869-882.
- Masson, M. E., Bub, D. N., & Warren, C. M. (2008). Kicking calculators: Contribution of embodied representations to sentence comprehension. *Journal of Memory and Language, 59*(3), 256-265.
- Mesulam, M. M., Wieneke, C., Hurley, R., Rademaker, A., Thompson, C. K., Weintraub, S., & Rogalski, E. J. (2013). Words and objects at the tip of the left temporal lobe in primary progressive aphasia. *Brain, 136*(2), 601-618.

- Meyer, D. E., & Schvaneveldt, R. W. (1971). Facilitation in recognizing pairs of words: Evidence of a dependence between retrieval operations. *Journal of Experimental Psychology, 90*(2), 227.
- Mollo, G., Pulvermüller, F., & Hauk, O. (2016). Movement priming of EEG/MEG brain responses for action-words characterizes the link between language and action. *Cortex, 74*, 262-276.
- Moseley, R. L., Pulvermüller, F., & Shtyrov, Y. (2013). Sensorimotor semantics on the spot: Brain activity dissociates between conceptual categories within 150 ms. *Scientific Reports, 3*, 1928.
- Myung, J.-Y., Blumstein, S. E., & Sedivy, J. C. (2006). Playing on the typewriter, typing on the piano: Manipulation knowledge of objects. *Cognition, 98*(3), 223-243.
- Neininger, B., & Pulvermüller, F. (2003). Word-category specific deficits after lesions in the right hemisphere. *Neuropsychologia, 41*(1), 53-70.
- Nelson, D. G., Egan, L. C., & Holt, M. B. (2004). When children ask, "What is it?" what do they want to know about artifacts? *Psychological Science, 15*(6), 384-389.
- Nelson, D. G., Frankenfield, A., Morris, C., & Blair, E. (2000). Young children's use of functional information to categorize artifacts: Three factors that matter. *Cognition, 77*(2), 133-168.
- Newcombe, P. I., Campbell, C., Siakaluk, P. D., & Pexman, P. M. (2012). Effects of emotional and sensorimotor knowledge in semantic processing of concrete and abstract nouns. *Frontiers in Human Neuroscience, 6*, 275.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9*(1), 97-113.
- Papeo, L., Lingnau, A., Agosta, S., Pascual-Leone, A., Battelli, L., & Caramazza, A. (2014). The origin of word-related motor activity. *Cerebral Cortex, 25*(6), 1668-1675.

- Pecher, D., & Zwaan, R. A. (Eds.). (2005). *Grounding cognition: The role of perception and action in memory, language, and thinking*. Cambridge: Cambridge University Press.
- Pfurtscheller, G., Stancak Jr, A., & Neuper, C. (1996). Post-movement beta synchronization. A correlate of an idling motor area? *Electroencephalography and Clinical Neurophysiology*, *98*(4), 281-293.
- Postle, N., Ashton, R., McFarland, K., & De Zubicaray, G. I. (2013). No specific role for the manual motor system in processing the meanings of words related to the hand. *Frontiers in Human Neuroscience*, *7*.
- Potts, G. F. (2004). An ERP index of task relevance evaluation of visual stimuli. *Brain and Cognition*, *56*(1), 5-13.
- Price, A. R., Bonner, M. F., Peelle, J. E., & Grossman, M. (2015). Converging evidence for the neuroanatomic basis of combinatorial semantics in the angular gyrus. *Journal of Neuroscience*, *35*, 3276-3284.
- Proverbio, A. M., Adorni, R., & D'aniello, G. E. (2011). 250 ms to code for action affordance during observation of manipulable objects. *Neuropsychologia*, *49*(9), 2711-2717.
- Pulvermüller, F. (1999). Words in the brain's language. *Behavioral and Brain Sciences*, *22*(2), 253-279.
- Pulvermüller, F. (2012). Meaning and the brain: The neurosemantics of referential, interactive, and combinatorial knowledge. *Journal of Neurolinguistics*, *25*(5), 423-459.
- Pulvermüller, F., Härle, M., & Hummel, F. (2001). Walking or talking?: Behavioral and neurophysiological correlates of action verb processing. *Brain and Language*, *78*(2), 143-168.

- Pulvermüller, F., Hauk, O., Nikulin, V. V., & Ilmoniemi, R. J. (2005). Functional links between motor and language systems. *European Journal of Neuroscience*, *21*(3), 793-797.
- Pulvermüller, F., Lutzenberger, W., & Preissl, H. (1999). Nouns and verbs in the intact brain: Evidence from event-related potentials and high-frequency cortical responses. *Cerebral Cortex*, *9*(5), 497-506.
- Pulvermüller, F., Moseley, R.L., Egorova, N., Shebani, Z., & Boulenger, V. (2014). Motor cognition-motor semantics: Action perception theory of cognition and communication. *Neuropsychologia*, *55*, 71-84.
- Pulvermüller, F., Shtyrov, Y., & Ilmoniemi, R. (2005). Brain signatures of meaning access in action word recognition. *Journal of Cognitive Neuroscience*, *17*(6), 884-892.
- Puzzo, I., Cooper, N. R., Vetter, P., & Russo, R. (2010). EEG activation differences in the pre-motor cortex and supplementary motor area between normal individuals with high and low traits of autism. *Brain Research*, *1342*, 104-110.
- Rabovsky, M., Sommer, W., & Abdel Rahman, R. (2012). The time course of semantic richness effects in visual word recognition. *Frontiers in Human Neuroscience*, *6*, 11.
- Ralph, M. A. L., Sage, K., Jones, R. W., & Mayberry, E. J. (2010). Coherent concepts are computed in the anterior temporal lobes. *Proceedings of the National Academy of Sciences*, *107*(6), 2717-2722.
- Ramayya, A. G., Glasser, M. F., & Rilling, J. K. (2009). A DTI investigation of neural substrates supporting tool use. *Cerebral Cortex*, *20*(3), 507-516.
- Repetto, C., Colombo, B., Cipresso, P., & Riva, G. (2013). The effects of rTMS over the primary motor cortex: the link between action and language. *Neuropsychologia*, *51*(1), 8-13.

- Riddoch, M. J., Edwards, M. G., Humphreys, G. W., West, R., & Heafield, T. (1998). Visual affordances direct action: Neuropsychological evidence from manual interference. *Cognitive Neuropsychology*, *15*(6-8), 645-683.
- Rizzolatti, G. (2005). The mirror neuron system and its function in humans. *Anatomy and Embryology*, *210*(5-6), 419-421.
- Rizzolatti, G., & Arbib, M. A. (1998). Language within our grasp. *Trends in Neurosciences*, *21*(5), 188-194.
- Rizzolatti, G., & Arbib, M. A. (2012). Neural expectations: A possible evolutionary path from manual skills to language. In *The Nature of Concepts* (pp. 140-166). Routledge.
- Rizzolatti, G., & Umiltà, M. A. (2013). Canonical Neurons. In *Encyclopedia of Sciences and Religions* (pp. 305-305). Dordrecht, Netherlands: Springer.
- Roche, K., & Chainay, H. (2017). Is there a Competition between Functional and Situational Affordances during Action Initiation with Everyday Tools?. *Frontiers in Psychology*, *8*, 1073.
- Rozynski, M. M., & Chen, C. M. (2015). Electrophysiological Changes in P200 Latency and Amplitude of Jittered Orientation Visual Integration Task in Healthy Participants: a Multi-Block Design EEG Study.
- Rumiati, R. I., & Humphreys, G. W. (1998). Recognition by action: dissociating visual and semantic routes to action in normal observers. *Journal of Experimental Psychology: Human Perception and Performance*, *24*(2), 631.
- Rüschemeyer, S. A., Lindemann, O., van Rooij, D., van Dam, W., & Bekkering, H. (2010). Effects of intentional motor actions on embodied language processing. *Experimental Psychology (formerly Zeitschrift für Experimentelle Psychologie)*, *57*(4), 260-266.

- Rüschemeyer, S. A., Brass, M., & Friederici, A. D. (2007). Comprehending prehending: neural correlates of processing verbs with motor stems. *Journal of Cognitive Neuroscience, 19*(5), 855-865.
- Schendan, H. E., & Kutas, M. (2003). Time course of processes and representations supporting visual object identification and memory. *Journal of Cognitive Neuroscience, 15*(1), 111-135.
- Schmitt, B. M., Münte, T. F., & Kutas, M. (2000). Electrophysiological estimates of the time course of semantic and phonological encoding during implicit picture naming. *Psychophysiology, 37*(4), 473-484.
- Schneider, E., & Zuccoloto, A. (2007). E-prime 2.0 [Computer software]: Pittsburg. PA: Psychological Software Tools.
- Scorolli, C., & Borghi, A. M. (2007). Sentence comprehension and action: Effector specific modulation of the motor system. *Brain Research, 1130*, 119-124.
- Scorolli, C., Binkofski, F., Buccino, G., Nicoletti, R., Riggio, L., & Borghi, A. M. (2011). Abstract and concrete sentences, embodiment, and languages. *Frontiers in Psychology, 2*, 227.
- Searle, J. R. (1980). Minds, brains, and programs. *Behavioral and Brain Sciences, 3*(3), 417-424.
- Shtyrov, Y., Hauk, O., & Pulvermüller, F. (2004). Distributed neuronal networks for encoding category-specific semantic information: The mismatch negativity to action words. *European Journal of Neuroscience, 19*(4), 1083-1092.
- Siakaluk, P. D., Pexman, P. M., Sears, C. R., Wilson, K., Locheed, K., & Owen, W. J. (2008). The benefits of sensorimotor knowledge: Body-object interaction facilitates semantic processing. *Cognitive Science, 32*(3), 591-605.

- Sliwinska, M. W., Vitello, S., & Devlin, J. T. (2014). Transcranial magnetic stimulation for investigating causal brain-behavioral relationships and their time course. *Journal of Visualized Experiments: JoVE*, (89).
- Tranel, D., Damasio, H., & Damasio, A. R. (1997). A neural basis for the retrieval of conceptual knowledge. *Neuropsychologia*, *35*(10), 1319-1327.
- Tsigka, S., Papadelis, C., Braun, C., & Miceli, G. (2014). Distinguishable neural correlates of verbs and nouns: A MEG study on homonyms. *Neuropsychologia*, *54*, 87-97.
- Tucker, M., & Ellis, R. (2004). Action priming by briefly presented objects. *Acta Psychologica*, *116*(2), 185-203.
- Ungerer, J. A., & Sigman, M. (1984). The relation of play and sensorimotor behavior to language in the second year. *Child Development*, 1448-1455.
- van Schie, H. T., & Bekkering, H. (2007). Neural mechanisms underlying immediate and final action goals in object use reflected by slow wave brain potentials. *Brain Research*, *1148*, 183-197.
- Vukovic, N., Feurra, M., Shpektor, A., Myachykov, A., & Shtyrov, Y. (2017). Primary motor cortex functionally contributes to language comprehension: An online rTMS study. *Neuropsychologia*, *96*, 222-229.
- Wamain, Y., Pluciennicka, E., & Kalénine, S. (2015). A saw is first identified as an object used on wood: ERP evidence for temporal differences between thematic and functional similarity relations. *Neuropsychologia*, *71*, 28-37.
- Wang, J., Conder, J. A., Blitzer, D. N., & Shinkareva, S. V. (2010). Neural representation of abstract and concrete concepts: A meta-analysis of neuroimaging studies. *Human Brain Mapping*, *31*(10), 1459-1468.

- Wattenmaker, W. D., & Shoben, E. J. (1987). Context and the recallability of concrete and abstract sentences. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *13*(1), 140.
- Wauters, L. N., Tellings, A. E., Van Bon, W. H., & Van Haaften, A. W. (2003). Mode of acquisition of word meanings: The viability of a theoretical construct. *Applied Psycholinguistics*, *24*(3), 385-406.
- Wellsby, M., Siakaluk, P. D., Owen, W. J., & Pexman, P. M. (2011). Embodied semantic processing: the body-object interaction effect in a non-manual task. *Language and Cognition*, *3*(1), 1-14.
- West, W. C., & Holcomb, P. J. (2000). Imaginal, semantic, and surface-level processing of concrete and abstract words: an electrophysiological investigation. *Journal of Cognitive Neuroscience*, *12*(6), 1024-1037.
- Willems, R. M. & Hagoort, P. (2007). Neural evidence for the interplay between language, gesture and action: A review. *Brain and Language*, *101*(3), 278-289.
- Withagen, R., de Poel, H. J., Araújo, D., & Pepping, G.-J. (2012). Affordances can invite behavior: Reconsidering the relationship between affordances and agency. *New Ideas in Psychology*, *30*(2), 250-258.
- Yee, E., Chrysikou, E. G., Hoffman, E., & Thompson-Schill, S. L. (2013). Manual experience shapes object representations. *Psychological Science*, *24*(6), 909-919.
- Zhao, B., Dang, J., & Zhang, G. (2017). EEG source reconstruction evidence for the noun-verb neural dissociation along semantic dimensions. *Neuroscience*, *359*, 183-195.
- Zwaan, R. A., & Taylor, L. J. (2006). Seeing, acting, understanding: Motor resonance in language comprehension. *Journal of Experimental Psychology: General*, *135*(1), 1.