

Investigating the Link between Action
Language and Action Performance

Claire Louise Moody

PhD

Psychology

June 2011

Abstract

Proponents of embodied cognition claim that the meaning of language is not stored amodally but is grounded within modality-specific brain regions. A large body of work supports this view by demonstrating that action language processing elicits motoric activation and behaviourally interacts with action performance. The fMRI and behavioural experiments described in the following chapters aimed to address several gaps in our current understanding of the nature of these language-induced motoric representations. By manipulating particular aspects of action language such as hand use and physical effort, the fMRI data supports the hypothesis that language evokes the activation of very specific and detailed action representations. As the effort information could only be derived from the combination of word meaning across the sentence, it was shown that these effects are not simply driven by single action verbs but by the integration of several activated semantic networks. Furthermore, the regions that were activated by action language are those that are involved in action planning as opposed to action execution, highlighting that these action representations are of a cognitive and abstract nature. Behavioural experiments were conducted to evaluate the functional significance of these embodied motoric activations. Despite observing modality specific representations using fMRI, when action and language shared specific physical effort attributes, behavioural interaction effects were absent, indicating that motoric activity may not necessarily be required for the processing of action language. The role that the motor system plays in the comprehension of action language is unclear from the evidence presented, as methodological issues may have played a part in generating this null result. The conclusions made from this selection of experiments and the implications of this research within the wider literature are further discussed.

List of Contents

Abstract	2
Table of Contents	3
List of Tables	6
List of Figures	7
Acknowledgements	9
Declaration	10
Chapter 1. Introduction	
1.1 The Complexity of Action Understanding	13
1.2 The Representation of Meaning	15
1.2.1 Embodied cognition	15
1.2.2 Neural Representation of Meaning.....	17
1.3 The Representation of Action Information	19
1.3.1 Action Representation in Monkeys	21
1.3.2 Action representation in Humans	25
1.4 The Comprehension of Action Language	30
1.4.1 A Sensorimotor System for Action Language Understanding	33
1.4.2 The Role of the Motor System in Language Comprehension	35
1.5 Conclusion	38
Chapter 2. The Comprehension of Implied Physical Effort via Action Sentences	41
2.1 Introduction	41
2.2 Experiment	48
2.2.1 Method.....	48
2.2.2 Results	62
2.3 Discussion	68
Chapter 3. Hand Specific Representations in Action Language Comprehension	77
3.1 Introduction	77
3.2 Experiment	82

3.2.1 Method	84
3.2.2 Results	93
3.3 Discussion	98

Chapter 4. Interactions between Action and Language for Shared

Weight Features: Explicit Weight Ratings of Object Words.....	104
4.1 Introduction.....	104
4.2 Experiment 1	109
4.2.1 Method	111
4.2.2 Results	118
4.2.3 Discussion	124
4.3 Experiment 2.....	127
4.3.1 Method	131
4.3.2 Results	139
4.3.3 Discussion	143
4.4 General Discussion	145

Chapter 5. Interactions between Action and Language for Shared

Weight Features: Implicit vs. Explicit Interactions Effects.....	149
5.1 Introduction.....	149
5.2 Experiment 1 & 2.....	152
5.2.1 Method	152
5.2.2 Results: Experiment 1 (Explicit Task)	160
5.2.3 Results: Experiment 2 (Implicit Task)	169
5.2.3 Discussion	174
5.3 Experiment 3.....	176
5.3.1 Method	177
5.3.2 Results: Experiment 3	178
5.4 General Discussion	182

Chapter 6. Discussion

6.1 The Nature of the Representations that Action Language Engages	188
6.1.1 Specificity of Representations.....	188

6.1.2 A Common Abstract Representational System	189
6.2 Engaging the Classic Mirror Neuron System.....	192
6.2 What is the Significance of Language Induced Motor Activations?	194
6.3 The Relationship between Action and Language.....	198
6.3.1 Sub-threshold Activation.....	199
6.3.2 How “Shared” are Motoric Representations for Action and Language Tasks?	199
6.4 Future Directions.....	200
6.4 Conclusions.....	201
Appendices	204
Appendix 1: List of Stimuli Included in the Experiment Described in Chapter 2	204
Appendix 2: List of Stimuli Included in the Experiment Described in Chapter 4	206
Appendix : 3 Discussion of the Order x Congruency Interaction (Chapter 5, Experiment 1).....	207
References	209

List of Tables

Chapter 2

Table 1. Example Sentences for a Given Item.....	47
Table 2. Mean Log Frequency and Character Length for Sentences.....	50
Table 3. ROI information: Size (in voxels) of the Active Regions, Coordinates (MNI Coordinates in mm) and Maximum Intensity Values.....	66

Chapter 3

Table 1. Details of Go/No-go Cues.....	84
Table 2. Details of Sentence Stimuli.....	86

List of Figures

Chapter 1

Figure 1. Cortical organisation of the macaque motor system	25
Figure 2. Cortical organisation of the human motor system	27

Chapter 2

Figure 1. Mean imageability rating for each condition.....	52
Figure 2. Mean plausibility rating for each condition.....	53
Figure 3. Mean effort rating for each condition for the overall effort rating questionnaire, the hand/arm effort rating questionnaire and the leg effort rating questionnaire	54
Figure 4. Mean % selection of each body part for the sentences in each of the three conditions	55
Figure 5. Left premotor ROI	59
Figure 6. ROIs for the left IPL, the left PMTG, the pars opercularis, and the pars triangularis.....	60
Figure 7. Areas activated by hand/arm execution data, action language and the overlap in activity between the action execution and the action language	62
Figure 8. Voxels sensitive to the increase in implied physical effort in action sentences for the left premotor ROI, the LIPL ROI and the pars triangularis ROI.....	65
Figure 9. Average % signal change for each condition across participants....	66
Figure 10. Correlation between sensory-motor regions (IPL and premotor) and the LIFG, PMTG	68

Chapter 3

Figure 1. Hand specific action execution ROIs	90
Figure 2. Action planning ROIs	92
Figure 3. Whole brain analyses for each action condition vs. baseline.....	96
Figure 4. Whole brain analyses for each language condition vs. baseline.....	97
Figure 5. % signal change for right and left action performance/language in	

each of the general action planning ROIs 98

Chapter 4

Figure 1. Experiment 1: Stimulus details..... 112

Figure 2. Experiment 1: Apparatus 116

Figure 3. Experiment 1: Procedure 117

Figure 4. Experiment 1: Mean bias scores 120

Figure 5. Experiment 1: Mean response times..... 123

Figure 6. Experiment 2: Object stimulus details..... 134

Figure 7. Experiment 2: Verb stimulus details 135

Figure 8. Experiment 2: Apparatus 137

Figure 9. Experiment 2: Procedure 137

Figure 10. Experiment 2: Mean planning times..... 141

Figure 11. Experiment 2: Mean lift times 143

Chapter 5

Figure 1. Experiment 1 & 2: Stimulus details..... 154

Figure 2. Experiment 1: Design 157

Figure 3. Experiment 2: Design 158

Figure 4. Experiment 1 & 2: Procedure 160

Figure 5. Experiment 1 & 2: Item removal..... 161

Figure 6. Experiment 1 & 2: Reaction time range 162

Figure 7. Experiment 1: Mean planning times..... 167

Figure 8. Experiment 1: Mean lift times 168

Figure 9. Experiment 2: Mean planning times..... 172

Figure 10. Experiment 2: Mean lift times 173

Figure 11. Experiment 1 & 3: Illustration of the tube colour and tube
response-label assignment 177

Figure 12. Experiment 3: Mean planning times..... 180

Figure 13. Experiment 3: Mean lift times 181

Acknowledgements

It is my pleasure to acknowledge the overwhelming and unerring support I received from my supervisor Silvia Gennari during both my MSc and PhD, without whom the completion of this thesis would never have been possible. I would also like to extend sincere thanks to Gerry Altmann and to all members of our lab group who, with honesty, helped guide the ideas presented in this thesis and provided me with the confidence and motivation necessary to reach this end point.

Thanks must also be given to the members of my research committee Piers Cornelissen and Beth Jefferies for providing an important outside perspective and overseeing my progress. I am also indebted to all those at YNiC who took me under their wing when I was an undergraduate student and gave me the inspiration to carry out neuroimaging work as well as giving me the technical skills needed to do so. I must of course show my appreciation to all of my colleagues and office mates of whom there are too many to mention for helping and supporting me over the years.

And, finally I owe my deepest gratitude to my wonderful husband, who has provided the unending emotional support I have needed, and who by now probably knows my thesis as well as I!

Author's Declaration

I declare that the work in this dissertation was carried out in accordance with the Regulations of the University of York. The experiments described by the author are original and carried out under the supervision of Silvia Gennari at the University of York. The work was funded by the Economic and Social Research Council. Any views expressed in the dissertation are those of the author and in no way represent those of the University of York.

This research has not been previously submitted to the University of York or to any other University for examination. Part of the data collection from experiment described in Chapter 2 was carried out by Veronika Chuang, as part of her MSc project. Part of the data collection from the experiment described in Chapter 3 was carried out by Gina Humphreys, as part of her third year undergraduate project. However, the final data sets reported here included additional participants and all analyses were conducted separately.

The data from the experiment described in Chapter 2 is based upon a peer reviewed scientific article published by Claire Moody and Silvia Gennari:

Moody, C. L., & Gennari, S. P. (2010). Effects of implied physical effort in sensory-motor and pre-frontal cortex during language comprehension. *NeuroImage*, 49, 782–793.

This work was additionally presented at two conferences:

Talk: Moody, C. L., & Gennari, S.P. Physical Effort in Sentence Comprehension. Conference on human sentence processing, March 15th, 2008.

Poster: Understanding Physical Effort through Language. Moody, C. L., Chuang, V., & Gennari, S.P. Cognitive Neuroscience Society Annual Meeting, April 15th 2008.

Data from the experiment described in Chapter 3 was presented at two conferences:

Talk: Comprehension of Hand Specific Action Language. Moody, C. L., Humphreys, G., & Gennari, S.P. Experimental Psychological Society Meeting, 7th January 2008.

Talk: Hand Specific Representations in Language Comprehension. Moody, C. L.,
Humphreys, G., & Gennari, S.P. Conceptual Structure, Discourse and Language &
Embodied and Situated Language Processing Conference (CDSL ESPL),
September 17th 2010

Chapter 1

Introduction

1.1 The Complexity of Action Understanding

Due to evolutionary pressure, humans have developed an incredible ability to interact with a diverse array of different objects to ensure their survival. Not only have we developed limbs that physically enable the performance of precise object directed interactions, but we have also developed the cognitive capabilities that are necessary for accurately planning actions and for making the decision to act. Furthermore, the brain is able to retain detailed action information and organise it in a way that it can be easily accessed when needed at a later date. Therefore, the human brain is remarkably specialised in its ability plan, initiate and represent knowledge about a multitude of different actions, some of which may consist of a complex combination of features and may be highly context dependent.

Both online incoming sensory information and stored action information are required for the planning and performance of an action. When receiving “bottom up” sensory input the brain is able to extract any action relevant information and to calculate appropriate action plans based on the physical properties of objects in the environment. Stored “top down” contextually relevant information is also used in the formation of action plans as a result of learned positive associations between sensory stimuli and action outputs. On combining incoming and stored information, the most suitable body-part can then be selected and oriented so to best interact with the object using the optimal amount of physical force (this is essential for the accuracy of the action as small changes in force can have very different action outcomes). Finally, the brain is able to communicate this detailed action schema to specific muscles in order to initiate and control the action online.

We also combine incoming sensory and stored action information in order to understand the action events that we encounter. For example, when viewing an action performed by another individual we are able to recognise the action being performed (e.g., grasp, pinch), and we can infer the actor’s ultimate intentions using stored

knowledge about what actions are likely to be performed on an object (e.g., a knife is most frequently used for cutting). Furthermore, the context within which the action is taking place can aid action understanding (e.g., a chair is more likely to be sat on in a dining context but stood on when needing to reach high). We also encounter action events via the language we hear or read; this is essential for human communication as allows us to refer to actions that are not simultaneously occurring, for example actions in the past or future. This means that often, in order to understand the meaning of action language, we must map the words onto the appropriate action representations in the absence of the corresponding physical stimuli using experience based associative links. This is a complex process as words are essentially a set of arbitrary labels that are often semantically unrelated to the action itself, for example the phonology or orthography of the word “grasp” does not tell you anything about its meaning. Essentially, combining visual or linguistic input with top down stored knowledge and context we are able to successfully comprehend action information.

Understanding the systems that are involved in the calculation and execution of action plans, the sensory processing of incoming action information, and the understanding of action language has the potential to tell us much about the way in which the brain processes and retains conceptual information. If the same action system that is responsible for action planning and performance is additionally involved in processing sensory properties of actions and also in action language comprehension, then this gives us an indication that our own experience of performing actions shapes the way in which we store action meaning. On the other hand, if different systems are separately involved in action performance and action perception/language, then this would suggest that our action experience does not determine how action meaning is stored. Instead sensory and linguistic aspects of actions could be stored at a higher level in independent non-action systems.

Consequently, the purpose of this initial chapter is to give an overview of the theoretical and experimental evidence for and against the proposal that action meaning is represented in a distributed manner across several modality-specific systems including the motor system. Furthermore, the question of how action words are mapped onto meaningful representations during language comprehension will be addressed. Do we

actively reconstruct the action that is described by language using sensory-motor systems or is the meaning of action language represented in a separate lexicon? This discussion will further evaluate evidence that specific motor plans/schemas that are necessary for the performance of actions are partially reactivated both during action perception and action language comprehension, suggesting that language meaning maps onto motor representations.

1.2 The Representation of Meaning

1.2.1 Embodied Cognition

Traditional views assume that conceptual representations are non-perceptual and that meaning is stored in a amodal symbolic and disembodied way by redescribing the information and storing the features as lists in a system that is completely independent from modality-specific systems such as the motor system (Fodor, 1981, 2001; Newell & Simon, 1972; Pylyshyn, 1984). The relationship between these symbols and the perceptual mechanisms that produced them is completely arbitrary (L. Barsalou, 1999). However, despite their powerful nature there are several problems with amodal theories; firstly category specific deficits can occur when modality-specific brain areas are lesioned, for example damage to the visual system impairs knowledge related to categories that rely on visual properties such as animals, however categories that rely on motor features such as tools are unaffected (Warrington & McCarthy, 1987; Warrington & Shallice, 1984). This suggests that no one brain system houses semantic knowledge. Secondly, there is no direct evidence that these symbols actually exist and no mechanisms have been proposed to explain how the transformation from perceptual states to symbolic states occurs (L. Barsalou, 1999). Furthermore, meaning in amodal theories is explained by the interconnections between amodal symbols, however, if the symbols do not map back and ground themselves in the real world then it is difficult to explain how meaning arises (Pecher & Zwaan, 2005). Due to these issues many have rejected a symbolic theory of meaning in favour of a modality-specific theory, where concepts are stored in a more distributed manner. These embodied theories claim that

cognition is grounded within modality-specific systems that are themselves responsible for action and perception.

There is no one single account of the fundamental components of embodied cognition and this is reflected in the fact that there are various models that aim to explain how conceptual knowledge is grounded within modality-specific systems (L. Barsalou, 1999; Pulvermuller, 1999). However, all variants share the same basic principles, the most important being that our higher level cognition develops as a consequence of having motor and perceptual systems that allow us to move and interact with objects in the environment and perceive action stimuli. Due to these sensory-motor experiences, knowledge about action features will be stored within sensory and motor systems that are themselves responsible for action perception and performance. Concepts (including actions) are multi-modal in nature in that they represent properties from more than one modality; therefore according to embodied cognition their meaning is stored in a distributed manner across several modality-specific systems. For example, actions are not only defined by our knowledge of how they are performed, but also by their sensory features (visual motion, auditory and tactile) and by the language labels associated with them. Therefore, it is proposed that the motor system will represent kinematic properties of the actions, whereas sensory systems will represent the perceptual features relating to the action concept.

If action meaning is distributed, a mechanism for integrating the inter-modality information is necessary. Direct connections between individual neurons in sensory and motor systems are not possible as “the necessary powerful, direct cortico-cortical pathways are not present” (Pulvermuller, 1999). Instead, embodied theories often include an integration mechanism to inter-connect information between modalities and to enable the multi-modal re-activation of complete action concepts. Integration units and mechanisms have been given several different names including “convergence zones” (Damasio, 1989), “event codes” (Hommel, Müsseler, Aschersleben, & Prinz, 2002) and “perceptual symbols” (L. Barsalou, 1999) and their main function on encountering action information via one modality, is to simultaneously reactivate associated information in other modalities. Therefore, when accessing an action’s meaning, not only information about how to perform the action will be available but

associated visual, somatosensory, auditory and linguistic information will also be activated, thereby enabling access to the action's meaning as a whole. It has also been proposed that in addition to modality-specific integration units, we also have a unified higher level amodal semantic hub that is involved in cross-modality integration housed in the anterior temporal lobes (Lambon Ralph, Pobric, & Jefferies, 2009). Damage to this area disrupts semantic processing in a modality independent manner in conditions such as semantic dementia (Jefferies & Lambon Ralph, 2006). It is important to note that within the embodied framework this amodal integration region is not thought to represent conceptual information itself, instead it is simply a hub which links information that is stored in modality-specific regions.

The embodied cognition framework proposes that during action perception or action language comprehension we automatically mentally re-enact or "simulate" the action within the motor system, using many of the same neurons that we would use to perform the action itself (L. Barsalou, 1999, 2008; Gallese & Lakoff, 2005; Glenberg, 1997; Jeannerod, 2001). This automatic and rapid re-enactment is thought to be *essential* for the recognition and understanding of the action stimulus. The strong proponents of embodied cognition go a step further and claim that this re-enactment process is necessary not only to facilitate the recognition of the action, but also to aid the understanding of the action meaning, for example, to interpret not only the physical but also the psychological goal of the actor (Iacoboni, et al., 2005; Rizzolatti & Craighero, 2004). Integration units may well mediate access to a complex combination of associated action relevant semantic features incorporating prior knowledge of the objects in the scene and any relevant action context, thereby giving rise to the higher-level understanding of actions

1.2.2 Neural Representation of Meaning

Different regions of the human cortex are specialised for different types of modality-specific processes. Firstly, sensory regions such as the visual, auditory and somatosensory cortices process incoming information, whereas the motor system is responsible for outputting behaviour, when planning and executing actions. According to embodied cognition, each modality is also thought to be responsible for the

representation of modality-specific knowledge relating to the individual features of actions and objects for instance the motor system stores knowledge about how to perform actions (i.e., grasp kinematics), and the visual system stores knowledge about the visual features of actions (i.e., what a grasping action looks like). Modality specific information across brain regions is then closely linked up to form representational networks for specific actions (e.g., by combining the kinematic and visual features for a grasping action).

A very simple Hebbian mechanism is thought to account for the integration of stored information that is distributed across these modality-specific areas (Hebb, 1949; Heyes, 2001; Keyser & Perrett, 2004). Simply speaking, if two neurons are concurrently activated in a frequent manner, they will become functionally connected so that when one fires, the other will also fire. Relating this to the previous example, often when performing an action such as a grasp, one will not only experience the physical act of grasping, but will often experience concurrent sensory input, as will additionally observe the shape of the grasping hand. Due to the simultaneous activation of these different neuronal populations, the motor schema for grasping will become functionally linked to the visual information of the hand shape and together will form part of the grasping concept. Subsequently, when observing a grasp performed by another individual, the associated motor schema for grasping will also become activated in order to aid action understanding. Therefore, grasp-related visual and motoric features will be integrated together to form a “cell assembly” based on this correlational Hebbian principle. Other separate concepts may also become linked to the grasping concept for example the act of grasping will often be seen in conjunction with the objects that are being grasped such as a cup or ball. It is these distributed cell assemblies and the relationship between different cell assemblies that form meaningful representations of different object and action concepts.

This Hebbian learning principle can also be used to explain how words are mapped onto representations of meaning (Pulvermuller, 1999). It has been proposed that there are core language areas involved in representing words at a non-semantic level; these include posterior Broca’s area that stores articulatory representations for words, Wernicke’s area that stores auditory phonological word patterns and the visual word

form area that stores the orthographic representations of words. When we experience a word it is often in a multimodal context, for example when reading a word aloud we simultaneously recruit articulatory, orthographic and phonological representations. Due to this simultaneous activation, the Hebbian principle would predict that word-specific articulatory, phonological and orthographic activity patterns would become functionally connected and form a representational cell assembly for that particular word within perisylvian regions. Additionally, we often experience words in semantic context, for example during conversation a word such as ‘kicking’ may be in reference to the sensory perception of a kicking event. Therefore, it is thought that these arbitrary word labels gain meaning via association with semantic sensorimotor patterns of activity to form a wider cell assembly. After enough repetitions, when the word is again encountered in the absence of the kicking event, sensorimotor states relating to the kicking action will become reactivated through Hebbian connections and the meaning of the word will be accessed.

As these integrated cell assemblies are made up of several sensorimotor features, this means that when limited information is available, an object or action concept can still be activated. For example, in a visually noisy environment the associated banging sound processed in auditory areas will cause the automatic activation of all other hammer-related sensorimotor and linguistic features within different modality-specific areas to activate the full hammer concept and aid recognition. Evidence for this comes from the cross-modal priming literature where priming effects are observed irrespective of whether the prime and target are presented in the same modality or not (Schneider, Engel, & Debener, 2008; Vallet, Brunel, & Versace, 2010). Therefore, inter-modality connections allow each modality-specific region have a functional influence on the activity within other modality-specific regions for a particular semantic cell assembly, therefore motor regions can modulate processing in sensory regions and vice versa.

1.3 The Representation of Action Information

For many years actions were seen to be the product of a uni-directional processing sequence where information flowed from the perceptual system to the action system in a linear sequence. However, it is now thought that there are multiple routes

between perception and action (Rizzolatti & Matelli, 2003) and that the two systems are much better integrated than was previously thought with them having a close bidirectional relationship; the perceptual system can cause our action system to initiate object-appropriate action plans, and our action system can cause our perceptual system to attend to action relevant sensory properties of objects (Hommel, et al., 2002). This intersystem modulation is likely to be mediated by sensorimotor integration units, where to some extent these units can be thought of as modality-specific shared representations between action and perception/language.

Several behavioural studies have found that action performance or even action planning alone can facilitate or interfere with perceptual processing (Fagioli, Hommel, & Schubotz, 2007; Repp & Knoblich, 2007; Wohlschläger, 2000, 2001; Wuhr & Müsseler, 2001; Zwickel, Grosjean, & Prinz, 2007) and more specifically action performance can interact with action perception when the two modality-specific processes share certain action features (Craighero, Bello, Fadiga, & Rizzolatti, 2002; Craighero, Fadiga, Rizzolatti, & Umiltà, 1999; Hamilton, Wolpert, & Frith, 2004; Jacobs & Shiffrar, 2005; Miall, et al., 2006). Hamilton, Wolpert and Frith (2004) asked participants to watch videos of boxes being lifted by other individuals and to judge the weight of the boxes. Critically while performing the task participants themselves held a box that was either heavy or light. It was found that the same boxes in the videos were judged as being heavier when participants were holding the light versus the heavy box, and lighter when participants were holding the heavy vs the light box demonstrating that action performance can modulate action perception when the two modalities share a certain property such as weight. Similarly, Craighero and colleagues (2002) asked participants to prepare to make either a clockwise or anticlockwise grasp. Importantly the “go” signal was an image of a hand either in a clockwise or anticlockwise orientation and was therefore either congruent or incongruent with the planned action. It was found that times to initiate the grasp movement were faster on congruent than incongruent trials indicating that the pictured action interacts with the action plan resulting in longer/shorter reaction times.

Similarly, action perception has been found to influence action performance. One study demonstrated that the observation of compatible vs. incompatible finger

movement affected the speed at which a lifting/tapping finger movement was subsequently executed; when the observed finger movement was compatible with the executed finger response, reaction times were faster than when they were incompatible (M Brass, Bekkering, Wohlschläger, & Prinz, 2000). Furthermore, the observation of grasping actions towards either small or large objects has been shown to prime the execution of an action towards an object that has compatible size (Castiello, Lusher, Mari, Edwards, & Humphreys, 2002; Edwards, Humphreys, & Castiello, 2003). Therefore, the evidence suggests that action and perception can interact with one another in a bidirectional manner when they share action features, providing support for the existence of shared representations for action performance and action perception.

Objects alone can also influence action performance if they both share specific action affordances, for example, Edwards and colleagues (2003) found that observing a small/large object directed grasp primed the performance of a compatible grasp even if the object was presented alone without being acted on. Furthermore, it has been found that participants are faster to respond to an arbitrary cue such as object colour when the object itself has affordances that are compatible with the response hand for example when the handle is aligned with the response hand (Bub & Masson, 2009; Vainio, Ellis, & Tucker, 2007). In addition both the functional and volumetric properties of a pictured object can interfere with a response if it is either functionally or volumetrically related to the viewed object (Bub, Masson, & Cree, 2008). This suggests that all action affordances are a part of an object's meaning, therefore when the object alone is perceived, its associated motoric representations are automatically accessed to a high enough degree to interfere with action performance. Furthermore, these behavioural interactions suggest that the activation of motoric representations is an essential part of understanding the action stimuli.

1.3.1 Action Representation in Monkeys

Extensive work has been carried out to determine whether there is evidence in support of embodied cognition at the single neuron level. Due to the invasive nature of single unit recording, few studies have reported stimulus induced responses of individual neurons in the human brain, however, the monkey motor system has been

interrogated for its sensorimotor properties at the neuronal level. As the monkey brain is thought to share organisational properties with the human cortex, with a degree of caution we can extrapolate these findings to aid understanding of the human brain. It has been found that several brain areas involved in action planning are devoted not only to producing actions but also to the representation of action information. These areas include the dorsal (PMd) and ventral (PMv) premotor cortex and the inferior (IPL) and superior (SPL) parietal cortex (Barbas & Pandya, 1987; Rizzolatti, Fogassi, & Gallese, 2001). Different connections between the premotor and parietal cortex form action circuits (Lewis & Van Essen, 2000; Luppino, Murata, Govoni, & Matelli, 1999; Matelli, Camarda, Glickstein, & Rizzolatti, 1986; Petrides & Pandya, 1984; Tanne-Gariepy, Rouiller, & Boussaoud, 2002), two of which will be further discussed: the dorsolateral and the dorsomedial circuit.

Dorsolateral circuit. The dorsolateral circuit is comprised of the IPL (anterior intraparietal sulcus (AIP)) and the PMv (F5), and is primarily thought to be responsible for the mapping of an object's dimensional information such as shape and size (in the AIP) onto appropriate action plans specifically for grasping (in F5). See Figure 1 for a diagram of the macaque motor cortex. Physiological recordings from these areas in the macaque brain suggest that there are neurons with visual or motor properties and some "mirror neurons" displaying both visual *and* motor properties, responding both during the performance of a hand action and the observation of the same specific hand action (Fogassi, Gallese, Fadiga, & Rizzolatti, 1998; Fogassi & Luppino, 2005; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Gallese, Fogassi, Fadiga, & Rizzolatti, 2002; Murata, Gallese, Luppino, Kaseda, & Sakata, 2000; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996; Rizzolatti, et al., 2001; Rizzolatti & Luppino, 2001; Sakata, Taira, Murata, & Mine, 1995; Taira, Mine, Georgopoulos, Murata, & Sakata, 1990). Mirror neurons respond during the execution/perception of very specific types of object oriented hand actions for example tearing and grasping (Rizzolatti, et al., 1988) and when either F5 or AIP are temporarily inactivated, grasping actions (but not reaching actions) are impaired (Fogassi, et al., 2001; Gallese, Murata, Kaseda, Niki, & Sakata, 1994) thereby supporting the role of this circuit in the planning and execution of grasping actions.

As well as playing a role in visuo-motor transformations for action performance there is much evidence to suggest that mirror neurons play a higher level representational role. Firstly, they are not only sensitive to *visual* information but also to action sounds (Keysers, et al., 2003; Kohler, et al., 2002) suggesting that they multimodally represent entire action concepts. Furthermore, mirror neurons can also be influenced by the context of the action, for example, some mirror neurons will only respond when a hand/mouth is interacting with an object (as opposed to seeing the pantomimed hand/mouth action or the object alone) and a grasping neuron may only fire when a grasping action has a particular end goal such as putting the food in the mouth as opposed to putting it in a container (Fogassi, et al., 2005). Mirror neurons therefore represent the meaning of goal-directed actions and not simply low-level action or object features. Mirror neurons are not even necessarily driven by the perception of a physical action, for example, they fire in the same way when viewing an object that affords a particular action as when interacting with that same object (Murata, et al., 1997; Murata, et al., 2000). They have even been found to respond when an object-directed grasping action is known to be ongoing but is blocked from view (Umiltà, et al., 2001). This particular finding demonstrates that the monkey has a mental representation of the grasping event, as activity within these neurons is not simply being driven by incoming perceptual input. Taking all these findings into consideration, it appears that the dorsolateral circuit is involved in action performance as transforms sensory information into specific action plans, and more controversially may also play a higher level representational role, whereby sensory input is mapped back onto an individual's action schemas to enable the recognition and understanding of perceived actions.

Dorsomedial circuit. The second circuit is comprised of the SPL (medial intraparietal sulcus (MIP) and V6a) and the PMd (areas F2 and F7). Despite being less well studied than the dorsolateral circuit it has long been thought to play a functional role in the planning of reaching (Battaglini, et al., 2002; Caminiti, Ferraina, & Johnson, 1996; Johnson, Ferraina, Bianchi, & Caminiti, 1996; Marconi, et al., 2001) and grasping actions (Fattori, Breveglieri, Amoroso, & Galletti, 2004; Fattori, et al., 2001). Damage to V6a causes impairments in reaching and grasping and in orienting the wrist thereby

supporting the role of the SPL in action performance (Battaglini, et al., 2002; Battaglini, Muzur, & Skrap, 2003).

Neurons within this dorsomedial circuit also display representational mirror properties, as are active during action/object perception *and* action performance (Evangelidou, Raos, Galletti, & Savaki, 2009; Raos, Evangelidou, & Savaki, 2007; Tkach, Reimer, & Hatsopoulos, 2007) and therefore may be considered as part of the mirror system. However, this area not only responds to the observation/performance of ongoing actions, but also responds to action relevant information in an anticipatory manner (Cisek & Kalaska, 2004; Johnson, et al., 1996; Nakayama, Yamagata, Tanji, & Hoshi, 2008; Xiao, Padoa-Schioppa, & Bizzi, 2006). For example, when holding an action instruction in memory, neurons in this circuit will be activated even before the action is initiated, demonstrating that this region is capable of mapping arbitrary non-action cues onto specific action plans (Cisek & Kalaska, 2004; Johnson, et al., 1996). When F2/F7 is inactivated, despite being able to physically perform actions monkeys become unable to associate simple sensory signals with motor responses (Kurata & Hoffman, 1994; Passingham, 1988; Sasaki & Gemba, 1986), suggesting that this region is involved in representing the learned associations between visual input and motor output. The role of these neurons therefore goes above and beyond that of standard “mirror” neurons, as they are also able to activate action plans in an anticipatory manner, and in a sense “simulate” the anticipated action before it is performed based upon non-action arbitrary cues.

These two circuits are very similar in that they are involved in action planning and action representation, however there is a distinction in the type of sensory information that the two circuits utilise with the dorsolateral circuit recruiting action specific information from ongoing actions, and the dorsomedial circuit recruiting arbitrary action-associated cues in an anticipatory manner. Irrespective of these differences, the representational nature of these cells provides strong support for theories of embodied cognition as the same neurons that are responsible for action performance are additionally involved in the storage of action information. As these representations are shared for both action performance and action understanding, they may well account

for the bidirectional behavioural influence that action and perception have upon one another (Damasio & Meyer, 2008).

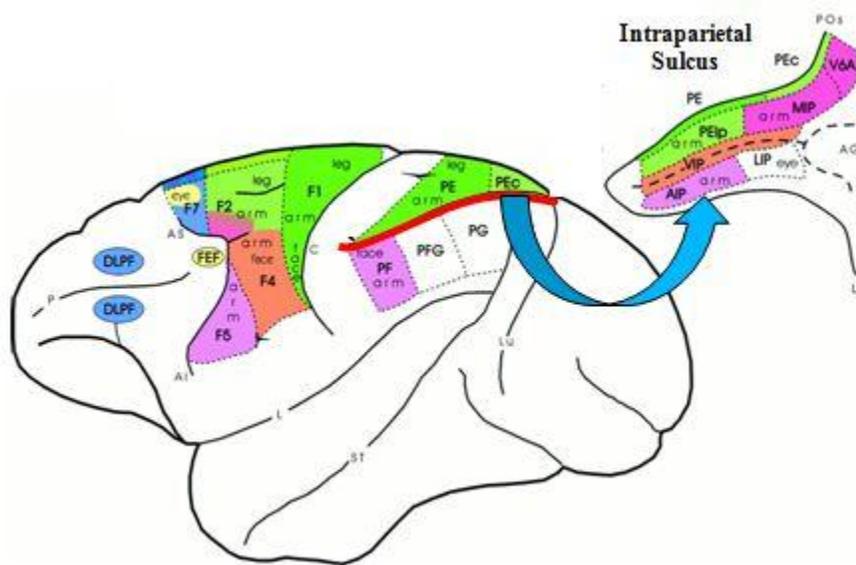


Figure 1. Cortical organisation of the macaque motor system. Left: lateral view with the intraparietal sulcus marked in red. Upper right: unfolded view of the intraparietal sulcus. Image taken from Rizzolatti & Luppino (2001).

1.3.2 Action Representation in Humans

Researchers have asked whether humans have a comparable system to that in the monkey cortex for the representation of action information, and if so, whether it is responsible for observed behavioural interactions between action performance and perception. Although single unit recording is the most direct measure of neuronal properties, the invasive nature of this procedure means that it can only be carried out in humans in very exceptional circumstances, therefore the existence of individual human mirror neurons has not yet been verified. However, several other measures have been employed including positron emission topography (PET), functional magnetic resonance imaging (fMRI), transcranial magnetic stimulation (TMS), and

magnetoencephalography (MEG) in order to assess whether any human brain areas contain populations of neurons that exhibit sensorimotor representational properties. The combination of these techniques can help to identify *where* populations of sensorimotor neurons are located and also *when* they are activated in order to further constrain embodied theories.

Functional imaging techniques, have consistently shown that several areas of the human cortex are activated both during action performance and action observation (Buccino, Lui, et al., 2004; Buccino, Vogt, et al., 2004a; Calvo-Merino, Glaser, Grezes, Passingham, & Haggard, 2005; Cross, Hamilton, & Grafton, 2006; Cross, Kraemer, Hamilton, Kelley, & Grafton, 2009; Filimon, Nelson, Hagler, & Sereno, 2007; Gazzola & Keysers, 2009; Grezes & Decety, 2001; Iacoboni, et al., 1999; Nishitani & Hari, 2000, 2002; Postle, McMahon, Ashton, Meredith, & de Zubicaray, 2008). Even the presentation of manipulable object stimuli in the absence of a physical action can activate this system (Beauchamp, Lee, Haxby, & Martin, 2002; Chao & Martin, 2000; Culham, Valyear, & Stiglick, 2004; Grafton, Fadiga, Arbib, & Rizzolatti, 1997; Kellenbach, Brett, & Patterson, 2003). Furthermore, the temporal pattern of activity within these sensorimotor regions is similar during action observation and execution demonstrating that it is not just the same areas that are engaged in both tasks, but they are engaged in a temporally similar manner (Nishitani & Hari, 2000, 2002). Studies using single pulse TMS to stimulate the primary motor cortex have shown increased activation in hand muscles (motor evoked potentials) when observing hand actions relative to non-action control conditions (Aziz-Zadeh, Maeda, Zaidel, Mazziotta, & Iacoboni, 2002; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Gangitano, Mottaghy, & Pascual-Leone, 2004; Patuzzo, Fiaschi, & Manganotti, 2003; Strafella & Paus, 2000; Urgesi, Candidi, Fabbro, Romani, & Aglioti, 2006) further suggesting that action observation excites the motor system to a high enough degree to mobilise the muscles themselves. This evidence has led researchers to conclude that humans have a sensorimotor system that is responsible not only for action performance but also for action perception and understanding.

The areas involved in action representation are predominantly housed within the motor system in areas that are specifically involved in the planning and performance of

actions: the IPL (BA 39 and 40), the SPL (BA 5 and 7), the ventral and dorsal premotor cortex (BA6) and also an area known as Broca's area just anterior to the premotor cortex in the left inferior frontal gyrus (BA44/45) (see Figure 2). Much debate exists as to whether Broca's area or the ventral premotor cortex in humans corresponds to the monkey mirror neuron area F5 (Morin & Grèzes, 2008; Preuss & Kaas, 1996), however, based on location and cytoarchitecture, the human sensorimotor system is very similar to that of the monkey sensorimotor system.

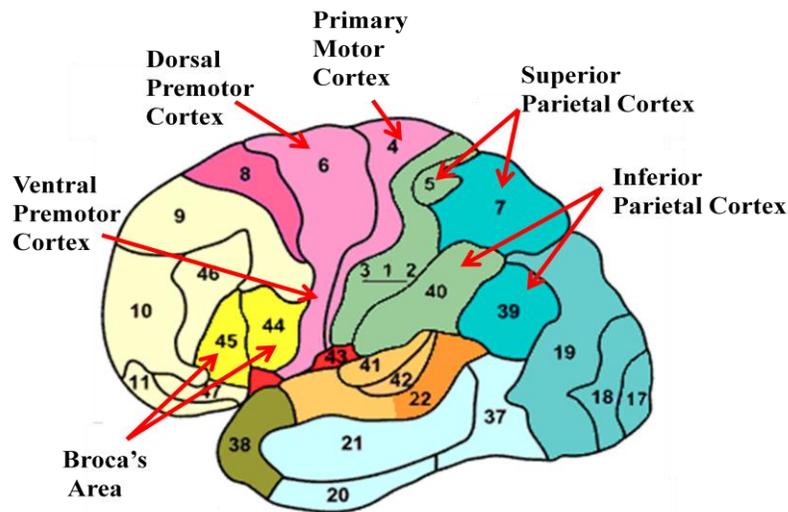


Figure 2. Cortical organisation of the human motor system. (Image taken from: <http://spot.colorado.edu/~dubin/talks/brodmann/brodmann.html>)

These human motor areas also show high level representational qualities, further suggesting that this human action system is also involved in understanding action-related sensory input. Like in the monkey, the equivalent human system is not only driven by action-related visual stimuli, but also by auditory stimuli such as crunching candy, ripping paper and clapping (Aglioti & Pazzaglia, 2010; Gazzola, Aziz-Zadeh, & Keysers, 2006; Hauk, Shtyrov, & Pulvermuller, 2006; Lahav, Saltzman, & Schlaug, 2007; Pizzamiglio, et al., 2005). The audiovisual properties indicate that these neuronal populations are multimodally integrated, whereby sensory-motor information across the

brain is linked. Furthermore, motor areas are active even in the absence of any sensory stimuli when actions are imagined (Ehrsson, Geyer, & Naito, 2003; Filimon, et al., 2007; Gerardin, et al., 2000; Jeannerod & Decety, 1995). This is an important finding as it demonstrates that rather than solely being driven by sensory stimuli this system is involved in mentally representing action information. This finding provides strong support for embodied theories which have proposed that access to action-related information involves a partial mental re-enactment of the action within the same neural substrate that is responsible for the performance of that action.

If, as embodied cognition would predict, we have shared representations for action performance and action perception, those shared neuronal populations should not only be sensitive to the perception of a specific action feature but should also be responsible for the execution of that action feature. For example, neurons that represent grasping actions should be involved specifically in performing hand actions compared to actions involving other body parts. The premotor cortex (and perhaps also the parietal lobule: see Buccino, et al., 2001) is thought to have a somatotopic representation whereby different populations of neurons represent actions involving different body-parts (Godschalk, Mitz, Duin, & Burga, 1995; Kurata, 1989; Leyton & Sherrington, 1917; Penfield & Rasmussen, 1952). Several studies have found that the same body-part specific regions are not only involved in the performance of an action using a particular body-part but also when processing action stimuli relating to that body-part. This effect has been found for action observation (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Buccino, et al., 2001; Postle, et al., 2008), action imagery (Ehrsson, et al., 2003), and action sounds (Gazzola, et al., 2006; Hauk, et al., 2006) thereby supporting the role of the sensorimotor system in the detailed representation of action information.

The embodied framework also purports that our bodily interactions with the environment strongly influence how action and object information is represented. It can therefore be predicted that the shared action representations within the human sensorimotor system are dependent upon experience. It has been found that when viewing actions performed by other animals (Buccino, Lui, et al., 2004) or humanly impossible movements (Candidi, 2007; Costantini, et al., 2005) the human sensorimotor

system is less active than for natural human actions, the explanation being that non-conspecific actions or impossible actions are not part of our motor repertoire and therefore cannot be understood using our motor schemas. Furthermore, practised musicians and experts in dance and martial arts are found to have more premotor and parietal activity when processing the movements that they are expert in compared to non-experts, suggesting that they have a more elaborate motor representation of these movements stored within the human sensorimotor system (Calvo-Merino, et al., 2005; Haslinger, et al., 2005). Similar results come from studies that have taught participants new movements (Buccino, Vogt, et al., 2004b; Cross, et al., 2006) or trained them in interacting with novel objects (Kiefer, Sim, Liebich, Hauk, & Tanaka, 2007), thereby ruling out the possibility that the differences are due to participants having more visual experience of others performing these movements. As a person's action experience for a particular movement determines how that movement is later represented, this strongly suggests that our motor experience shapes the organisation of knowledge in the brain and demonstrates that the human sensorimotor system is highly flexible and experience dependent.

It is clear from the similarities in the neuroanatomy and functional properties of the monkey and human brain that action meaning is stored in a comparable way across species. There is even evidence to suggest that humans have distinct dorsomedial and dorsolateral action circuits just like the monkey. When participants are asked to perform, imagine, or observe hand actions the AIP and BA44/PMv of the dorsolateral circuit are activated (Binkofski, et al., 1999; Buccino, et al., 2001; Creem-Regehr, Dilda, Vicchilli, Federer, & Lee, 2007; Filimon, et al., 2007; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Molnar-Szakacs, Iacoboni, Koski, & Mazziotta, 2005). Furthermore, lesions or repetitive TMS of the dorsolateral circuit result in disturbances to the coordination of finger movements needed for grasping but reaching was not affected (Binkofski, et al., 1998; Davare, Andres, Cosnard, Thonnard, & Olivier, 2006; Tunik, Frey, & Grafton, 2005). On the other hand lesions to the SPL of the dorsomedial circuit have been shown to cause inaccurate or slower reaching (Danckert, Goldberg, & Broderick, 2009; Ferro, 1984) and have been linked to a condition called optic ataxia where object directed reaching is impaired (Buxbaum & Coslett, 1997; Karnath &

Perenin, 2005). In addition single pulse TMS to the areas in this circuit causes a facilitation of the reach movement (Busan, et al., 2009). Other studies have found that the dorsomedial circuit represents learned non-standard associations between one or more arbitrary sensory stimuli such as colour and action (Chouinard, Leonard, & Paus, 2005; Grefkes, Ritzl, Zilles, & Fink, 2004; Petrides, 1997) and furthermore that this activation can occur during a delay period between the cue and the initiation of the movement in an anticipatory fashion (Beurze, De Lange, Toni, & Medendorp, 2007, 2009; J. Connolly, Andersen, & Goodale, 2003; Medendorp, Goltz, Crawford, & Vilis, 2005). This evidence suggests that the human sensorimotor system is very similar to the monkey system as it made up of functionally distinct action circuits that are specialised for certain action processes. Due to the different properties of these action circuits they may play different roles in the representation of actions, for example the dorsolateral circuit may well be involved in understanding ongoing actions via the mapping of sensory information onto existing grasp-specific action plans, whereas the dorsolateral circuit may be involved in more abstract action representation by linking arbitrary cues (such as language) onto action plans in an anticipatory manner.

In summary, humans like monkeys have a very similar network of sensorimotor brain areas that is capable of representing the meaning of actions in great detail at the conceptual level. These findings support theories of embodied cognition as action meaning is represented in a detailed manner within this low-level modality-specific motor system and is highly experience dependent. The motor representations that are used in both action performance and action perception/understanding may well account for the behavioural interactions as described above.

1.4 The Comprehension of Action Language

We not only experience actions via sensory perception in the real world but we also experience actions via language. Action language makes up a large proportion of our human communication and enables us to effortlessly convey and comprehend information about events that are not necessarily currently ongoing (for example events in the past and future). Therefore, as action language understanding is such a significant and uniquely human ability, it is important that we understand the mechanisms that

support it. Action language comprehension is a complex process as the relationship between words and meaning are arbitrary, in that the phonology or orthography of words are not semantically related to the meaning of the word. Therefore to understand language we must map words back onto meaningful representations often in the absence of the action itself and its related context. If, as embodied theories suggest, action meaning is represented within the motor system, it can be predicted that action language recruits these motoric representations during comprehension in the same way as in action perception, and that described actions are re-enacted within the same neuronal populations that are involved in actually performing the action.

Many studies have investigated whether there are shared representations for action performance and action language (Glenberg & Kaschak, 2002; Taylor, 2008; M. Tucker & Ellis, 2004; Zwaan & Taylor, 2006). One landmark study found that when the direction of response (e.g., towards/away from the body) is compatible with the direction implied by an action sentence (e.g., “open/close the drawer”), participants are behaviourally faster to make a sensibility judgement to the sentence than when the sentence and response direction are incompatible (Glenberg & Kaschak, 2002). Similarly, when participants are asked to read a sentence that implies physical rotation (e.g., “He turned down the volume”) sensibility judgements were quicker when the response direction and the sentence rotation direction was the same, but only at the point in the sentence where the direction was disambiguated (Taylor & Zwaan, 2008; Zwaan & Taylor, 2006). This interaction effect suggests that both the action and the language task are recruiting the same direction-specific motor schema.

Interaction effects have also been found for single word studies for example people are faster to say that a word describes a natural/manmade object when their response involves an action (either precision or power grip) that was congruent as opposed to incongruent with how the object itself would be grasped (M. Tucker & Ellis, 2004). Words denoting physical or spatial properties that are printed on a to-be-grasped object such as “long/short”, “place/lift” “large/small” and “near/far” (Gentilucci, 2003; Gentilucci & Gangitano, 1998; Gentilucci, Gangitano, Benuzzi, Bertolani, & Daprati, 2000; Glover & Dixon, 2002) or even words that imply size differences such as “grape/apple” (Glover, Rosenbaum, Graham, & Dixon, 2004), cause kinematic errors

during the initial stages of the action that are related to the specific action dimension that was manipulated (for example reading “grape” led to a smaller grip aperture than reading “apple”). Furthermore, reading words relating to specific body parts can interfere with the performance of actions that require the same body part, for example Sato and colleagues (Sato, Mengarelli, Riggio, Gallese, & Buccino, 2008) found slower hand responses to hand verbs than foot verbs during a semantic task. In addition, responses that are either functionally or volumetrically related to the action affordances of an object word are faster than for unrelated action responses (Bub, et al., 2008; Masson, Bub, & Newton-Taylor, 2008; Masson, Bub, & Warren, 2008). Therefore, when action and language share an action feature, this causes a behavioural interaction thereby suggesting that the activation of motor representations is critical for understanding the meaning of language.

Action performance is made up of two main stages, firstly the planning stage whereby all action-related information is collated and transformed into the most appropriate action plan, and secondly the execution stage whereby the action is initiated and controlled online. By separating out the planning and movement stages of the action, behavioural studies have provided evidence as to the stage at which this interaction between action and language occurs. For example, in the studies by Glover and colleagues (Glover & Dixon, 2002; Glover, et al., 2004) the semantics of words printed upon to-be-grasped objects only affected hand aperture during the initial stages of the action, the effects diminished as the action progressed. Similar results were found by Masson, Bub and Cree (2008) who by simultaneously presenting an action cue (text colour) and an object word, forced participants to plan an appropriate action while processing the word meaning. It was found that when the object described by the word and the planned action shared either a functional or volumetric property (e.g., when in response to “calculator” a functional poking action or a volumetric whole hand grasp was performed), participants were faster to initiate the action than if no action properties were shared between the object and the action. This suggests that temporally speaking, action language recruits action representations that are stored at the level of action planning but does not interfere with online control mechanisms during action execution.

Therefore based on this behavioural data, action and language are thought to be much more closely integrated than was once thought, with each having an influence upon the other in a bidirectional manner during the action planning stage. However, the behavioural data alone cannot specify the level at which these language interactions occur, for example, whether they are mediated by abstract high level processing systems such as those involved in decision making or instead instantiated in lower-level perception and action systems as the embodied literature would predict. Furthermore, behavioural data does not provide us with a complete picture as to how these links between action and language manifest themselves within the brain. The grounded cognition framework would predict that our motor experience in the real world shapes the way in which we store action knowledge, resulting in action concepts being housed within the motor system. If action language understanding is also embodied, it can be predicted that during comprehension action representations within modality-specific motor regions will be recruited and that action language will not depend upon independent amodal representations.

1.4.1 A Sensorimotor System for Action Language Understanding

Unlike in studies of action observation and imagery, activation of the motor system during language comprehension has been more difficult to identify, however, several studies using neuroimaging techniques have found effects of action language in the sensorimotor system. For example, when asked to silently name tool pictures or to read action words/sentences participants' sensorimotor circuits become activated (Chao & Martin, 2000; Culham, et al., 2004; Desai, Binder, Conant, & Seidenberg, 2009; Grabowski, Damasio, & Damasio, 1998; Grafton, et al., 1997; James & Maouene, 2009; Martin, Wiggs, Ungerleider, & Haxby, 1996). Furthermore, TMS stimulation of the primary motor cortex results in greater arm motor evoked potentials (MEPs) when reading action versus non-action words (Oliveri, et al., 2004) demonstrating that action language effects can even filter down to the muscles themselves.

At a more specific level, when participants listen to action verbs (for example lick, pick, kick) or action sentences (for example "I bite an apple", "I grasp a knife", "I kick the ball") relating to the face, arm or leg, somatotopically distinct regions of the

premotor cortex are activated (Hauk, Johnsrude, & Pulvermüller, 2004; Tettamanti, et al., 2005). This language induced activity spatially overlaps with those areas that are engaged during the performance of foot, finger and tongue actions, i.e., areas responsible for leg actions were more active for leg verbs than either face or arm verbs (Hauk, et al., 2004). Other studies failed to find somatotopic motor language effects (e.g., Postle, et al., 2008), however, this may have been due to the choice of task (lexical decision tasks do not require access to action semantics) or to the way in which the regions of interest were defined. It has also been argued that rapid language induced motor activity may not reflect comprehension, but may instead be a bi-product of Hebbian associations that is not required for action language understanding. It is not just literal action sentences that have been found to elicit somatotopic activity within these areas, metaphorical sentences relating to different effectors have also been found to elicit these effects for example “he grasped the idea”, and “he kicked the bucket” (Boulenger, Hauk, & Pulvermuller, 2008) demonstrating that the action representations within the motor system may be fairly abstract and flexible. However, these effects for metaphorical sentences have not been found in other studies where only the items in their literal context activated the sensorimotor system (Aziz-Zadeh, et al., 2006; Raposo, Moss, Stamatakis, & Tyler, 2009). Other studies have used TMS stimulation of the motor cortex in order to identify body-part specific language effects. When a body-part specific region is stimulated participants are found to be faster to make a lexical decision to a verb that is related to that body-part compared to verbs related to other effectors (Pulvermuller, Hauk, Nikulin, & Ilmoniemi, 2005). Furthermore, motor evoked potentials recorded from body-part specific muscles are larger when a sentence refers to an action that would require that same muscle in action performance (Buccino, et al., 2005).

Much action detail is represented in the sensorimotor system even beyond the body-part. It has been shown that the bilateral IPL is sensitive to the type of information presented in hand-action verbs, for example more activity was found when reading verbs at a subordinate semantic level (“to wipe”) compared to verbs at a more abstract level (“to clean”) (van Dam, Rueschemeyer, & Bekkering, 2010). Therefore regions involved in the performance of hand actions are sensitive to the specificity of the action

content of the language, the more specific the verb is and the more action detail it contains, the more extensive an action representation can be activated within the sensorimotor system. Similarly, sensorimotor areas are sensitive to the action properties of words, as a greater neural response is seen when reading about manipulable objects that can be “used” (e.g., pen) and involve more fine-grained action features compared to object words that simply have volumetric properties (in that they can be moved but not used e.g., “clock”) (Rueschemeyer, van Rooij, Lindemann, Willems, & Bekkering, 2010). In summary, there is evidence to suggest that the sensorimotor system is not only involved in the recognition of perceived actions, but is also involved in the comprehension of action language as stores conceptual representations of action meaning that are required for language understanding. In the same way that the action system can produce a multitude of diverse actions, it can also represent information about actions at an extremely detailed level, and this detailed information is activated on encountering action language.

1.4.2 The Role of the Motor System in Language Comprehension

Although the motor system is activated during action language comprehension, this does not necessarily mean that these sensorimotor regions are necessary for processing the semantic information, as it could be argued that meaning is understood via amodal symbols in a disembodied way. The additional motor system activity could simply be a bi-product of associative Hebbian connections (Mahon & Caramazza, 2008) or post-lexical processes such as imagery. By looking in more detail at the time course of action language activity, behavioural and neuropsychological data, we can learn more about the role that the motor system plays in action language comprehension.

If language recruits action representations at a post-comprehension processing stage (e.g., imagery) rather than for understanding the action content of the language, it can be expected that activation of the motor system will be fairly slow (greater than 500ms: see Papeo, Vallesi, Isaja, & Rumiati, 2009). However, if motor regions are critically involved in processing the meaning of action language, and if this occurs directly via the fast spreading of activity through Hebbian connections, then they should be automatically engaged very early in time within the first 200ms. Papeo and

colleagues (2009) presented participants with action and non-action verbs and then applied TMS stimulation over the primary motor cortex. They found a difference between action and non-action words only when TMS was applied 500ms after the stimuli (but not at 170 and 350ms). This suggests that the interaction between action and language only occurs at a later processing stage, after which the meaning of the language will already have been accessed, and that this area is not involved in comprehending the verb. In contrast Pulvermüller and colleagues (2005) using MEG provided participants with spoken face or leg words and found rapid activity within body-part specific areas where the face area was active at 142-146ms, and the leg area at 170ms. Similarly processing action verbs has been found to affect overt motor performance within 200ms of word onset (Boulenger, et al., 2006), therefore this speedy interaction between action language and action performance also manifests itself behaviourally. The timing of language induced access to motor representations is controversial, but there seems to be some evidence for their early recruitment. This suggests that sensorimotor areas are critically involved in the semantic processing of action language rather than simply playing a role in other non-semantic post-lexical processes.

However, early activity is not concrete proof that the human motor system is essential for the understanding of action language, as it has also been argued that rapid language induced motor activity may not reflect comprehension, but may instead be a simple bi-product of inter-region Hebbian associations. Therefore, despite motoric activation, it is still possible that action meaning is processed in an amodal system independent from sensorimotor areas. Studies of patients with particular neurological problems can offer further evidence that the sensorimotor system is necessary for action language processing. Neurodegenerative Motor Neurone Disease has been found to specifically targets areas of the nervous system that are involved in action production, therefore studies have investigated the effects that this action system disorder has on the ability to use and understand action language. This disease has been found to impair the ability to produce and comprehend action verbs compared to nouns, demonstrating that action oriented words are perhaps more dependent upon these motor structures (Bak & Hodges, 2004; Bak, O'Donovan, Xuereb, Boniface, & Hodges, 2001). Other studies of

patients with left or right frontal lesions have shown the same verb specific effects (Daniele, Giustolisi, Silveri, Colosimo, & Gainotti, 1994; Kemmerer & Tranel, 2003; Neininger & Pulvermüller, 2003; Shapiro & Caramazza, 2003).

Further neuropsychological evidence comes from patients who have ideomotor apraxia. These patients retain knowledge about the function of tools but cannot imitate actions or perform actions when instructed. They are still able to grasp and manipulate tools based on their visual information but learned knowledge of how to interact with them for their use is impaired. These patients nearly always have lesions to the left inferior and superior parietal cortex and/or premotor cortex – regions thought to house action representations (Haaland, Harrington, & Knight, 2000). It is not only action performance that is impaired in these individuals but their language abilities are also found to be altered, for example they have difficulties in understanding action based metaphors such as “he hit the nail on the head” (McGeoch, Brang, & Ramachandran, 2007). Also in tests of apraxia the action command is a verbal one demonstrating that these patients cannot understand the meaning of language instructions. Again this demonstrates that in order to understand action language the activation of associated motor schemas is necessary. As neurological disorders affecting the motor system impair not only action performance but also action language processing, this suggests that the action representations within the human sensorimotor system play a fundamental functional role in understanding action language. This supports an embodied perspective, as suggests that there is no independent language module where meaning is extracted, instead the meaning of action language is represented in the action system itself.

Alongside neuropsychological data, behavioural data also provides additional evidence to suggest that the motor system is essential for understanding action language. As described earlier, several studies have found behavioural interactions between action performance and the comprehension of action language when they share a specific a spatial feature such as action direction or orientation (Glenberg & Kaschak, 2002; Taylor & Zwaan, 2008; Zwaan & Taylor, 2006) or a kinematic feature such as grip size (Gentilucci & Gangitano, 1998; Gentilucci, et al., 2000; Glover & Dixon, 2002; Glover, et al., 2004). This suggests that rather than having separate regions responsible for

action performance and action language understanding, they to some extent rely on the same neural mechanism. When additionally taking into consideration findings from neuroimaging where functional overlap between action language and performance occurs within motoric areas, and the neuropsychological literature where damage to motor areas impairs action language processing, this suggests that this shared mechanism exists within the motor system.

In summary, the data suggests that understanding the meaning of action stimuli requires access to action knowledge that is stored within action planning areas in the parietal and premotor cortex. More specifically action language comprehension (a process that requires an extra mapping step from the arbitrary word form onto meaning) also recruits action-specific representations, suggesting that lexical meaning is dependent upon modality-specific brain areas and not on an amodal system exclusively. Furthermore, neuropsychological and behavioural data emphasise the necessary purpose of motor activations for action language comprehension, thereby supporting embodied cognition where action meaning is stored within modality-specific systems and is recruited by language during comprehension.

1.5 Conclusion

Despite the vast number of studies that have aimed to clarify the role of the sensorimotor system in language comprehension there are many unanswered questions that merit further investigation. Firstly, language relating to different body-parts appears to recruit somatotopically distinct regions of the premotor cortex. But what other details are preserved in the motor schemas that are recruited, for example, is the sensorimotor system sensitive to the specific left/right hand that is described in language, or to the degree of physical effort that is described in a sentence? And are any motoric activations revealed by fMRI capable of influencing the behaviour of participants when these detailed dimensions are manipulated? Furthermore, it is not clear what type of action representation is being recruited by language, although some studies have identified overlapping activity between action language and action performance in areas that have been implicated in action planning, it is not yet clear whether the language induced activity is associated with action execution or action

planning, as no studies to date have separately assessed the two action components and interrogated them for their language properties. Experiments described in the following chapters aim to shed some light upon these remaining questions, and to further advance our knowledge of the role of sensorimotor structures in action language comprehension using a range of neuroimaging and behavioural techniques.

Chapter 2

The Comprehension of Implied Physical Effort via Action Sentences

2.1 Introduction

The behavioural and neuroimaging evidence discussed in the introductory chapter, indicates that not only are there shared representations between action performance and action perception, but also between action performance and action language. These shared representations are thought to be housed within the motor system in the posterior parietal cortex, the premotor cortex and the pars opercularis (BA44) of the left inferior frontal gyrus (LIFG), all areas that are recruited both during action performance and when processing perceptual and linguistic aspects of action stimuli (e.g., Chao & Martin, 2000; Gazzola, et al., 2006; Grezes & Decety, 2001; Hauk, et al., 2004; Hauk, et al., 2006; Tettamanti, et al., 2005). Motor areas are therefore thought to represent higher level action meaning, not only storing knowledge regarding the mechanics of how to perform the action, but also representing the conceptual meaning of the action. It is access to this action meaning that is necessary for the understanding of perceived action events and arbitrary action language labels. Some proponents of embodied cognition have even gone as far as to suggest that when reading action language we partially re-enact the action, recruiting many of the same neurons as would be required to actually perform the action (L. Barsalou, 1999; Gallese & Lakoff, 2005; Glenberg, 1997; Jeannerod, 2001).

Of interest for this study is the nature of the shared representations that are required for action performance and action language comprehension. If it is true that we precisely re-enact the actions that are described to us through language, and that action language is not understood by an amodal mechanism, it can be predicted that at least some of the same neurons will be recruited when performing a particular action and when comprehending action language that relates to that same specific action. As reviewed in the introduction, several studies that have employed neuroimaging and

behavioural techniques have found action specific behavioural interactions or spatial overlap within the brain for action performance and action language when they share particular features such as action direction (Glenberg & Kaschak, 2002; Taylor, Lev-Ari, & Zwaan, 2008; Zwaan & Taylor, 2006), size (Glover, et al., 2004), or body part (Buccino, et al., 2005; Hauk, et al., 2004; Pulvermuller, Hauk, et al., 2005; Tettamanti, et al., 2005). Although these findings support embodied cognition in that language recruits specific action representations during comprehension, there are still several questions that need to be addressed.

The present study asks two main questions: Firstly, does the level of specificity that is represented in the motor system and recruited by action and language extend beyond the level of the body part to reflect the physical effort that is involved in the performance of an action? If so this would provide support that action language retrieves action information to a level of detail that was previously unknown. Secondly, do these neural overlaps for action and language exist not only for single action-related words but also for action-related sentences, where the meaning of several words across a sentence must be combined in order for the physical effort meaning to be understood?

The Specificity of the Action Representations Recruited by Language

Actions have several features, with body part being just one of these features. One other action feature that is controlled by the motor and premotor cortex in action performance is physical effort, i.e., the amount of force that the muscles generate when performing a particular action. During action performance, the exertion of a very precise amount of force is very important for achieving a successful action outcome; consider picking up an egg, too little force and it will slip from your hand, too much force and you will crush the egg between your fingers. Therefore, force is an important action parameter that requires a large degree of control.

The primary motor cortex plays a important role in generating physical force as it is closely connected to muscles via the spinal cord, and it has been shown both in monkey single unit recording (Evarts, 1968; Evarts, Fromm, Kroller, & Jennings, 1983; Maier, Bennett, Hepp-Reymond, & Lemon, 1993; Thach, 1978; Wannier, Maier, & Hepp-Reymond, 1991) and when imaging the brains of human subjects (Cramer, et al.,

2002; Dai, Liu, Sahgal, Brown, & Yue, 2001; Dettmers, et al., 1995) that that primary motor neurons are activated to a higher degree the greater the force exerted.

Furthermore, TMS induced lesions of the human primary motor cortex disrupt participants ability to accurately scale grip force (Berner, Schönfeldt-Lecuona, & Nowak, 2007; Keisker, Hepp-Reymond, Blickenstorfer, Meyer, & Kollias, 2009; Nowak, Voss, Ying-Zu Huang, & Rothwell, 2005; Schabrun, Ridding, & Miles, 2008) suggesting that the primary motor cortex is necessary for the control of force output during action performance.

Furthermore, cells in areas implicated in action planning (premotor regions) have also been found to show sensitivity to the effort required by an action. Again, single unit recording in monkeys (Hendrix, Mason, & Ebner, 2009; Hepp-Reymond, Hüsler, Maier, & Qi, 1994; Hepp-Reymond, Kirkpatrick-Tanner, Gabernet, Qi, & Weber, 1999; Werner, Bauswein, & Fromm, 1991) and neuroimaging in humans (Dai, et al., 2001; Dettmers, et al., 1995) have identified populations of neurons in both the ventral (PMv) and dorsal (PMd) premotor cortex that increase as the production of force increases. Additionally, TMS induced lesions of the PMv impairs the ability to scale the grip force when the predicted weight of the object unexpectedly changes (Dafotakis, Sparing, Eickhoff, Fink, & Nowak, 2008). This evidence suggests that the premotor as well as the primary motor cortex participates in the planning and execution of force specific actions.

Closely related to physical effort is object weight, as the heavier an object is the more force is required to interact with it. Unlike features that are visually apparent such as shape and size where there is a one-to-one mapping between the visual information and the grasp kinematics needed to interact with an object, with weight there is often no direct relationship between the object's visual features and the force that is needed to lift it. Therefore, knowledge of object weight must be learned through our experiences of interacting with different objects. We can learn general rules about objects that allow us to estimate the weight of never-before-lifted objects, for example, we learn that different materials are different in weight, in that objects made from glass are likely to be heavy and those made from cork are likely to be light, and that bigger or "full" objects are likely to be heavier than smaller or "empty" objects (Gordon, Forssberg, Johansson, &

Westling, 1991). Through repeated exposure with familiar items, we can store very specific and accurate weight representations based on our experience of the force that is needed to lift them.

Our ability to retain weight-specific representations for familiar objects is shown by the fact we scale our grip forces differently for familiar and novel objects, whereby we anticipate the upcoming weight for a familiar object but less so for a novel object (Gordon, Westling, Cole, & Johansson, 1993). This demonstrates that on viewing a to-be lifted object we are able to access its associated weight related information and use this to plan a weight specific action to guarantee an accurate lift. When the object is novel there is less information available regarding the weight of the object and a less accurate action plan is formed. In the same way that the visual appearance of an object and its weight are linked, participants have been shown to quickly learn to use arbitrary cues such as colour or sound to predict the upcoming weight of an object (Ameli, Dafotakis, Fink, & Nowak, 2008; Cole & Rotella, 2002). The dorsal premotor cortex may well be involved in associating cues with weight-specific action representations, as when it is temporarily inactivated by repetitive TMS the ability to scale grip forces based on learned arbitrary cues is impaired (Chouinard, et al., 2005). Repetitive TMS to areas involved in action execution, more specifically the primary motor cortex did not impair performance on this task suggesting that it is action planning areas that are involved in the sensorimotor transformations.

Several studies have found evidence that perception of weight information recruits weight specific action representations. Hamilton and colleagues (de C Hamilton, Wolpert, Frith, & Grafton, 2006) asked participants to lift a light box, a heavy box, or no box, and shortly after, while still performing the action, to observe videos of differently weighted boxes being lifted. They found that the weight of a lifted object would bias the weight judgement of a similarly weighted object if perception and action share the same weight-specific neural mechanism. They then aimed to identify the source of the weight induced bias effect. On an individual subject level a regression analysis was performed to find brain voxels where the magnitude of the psychophysical bias (mean box weight rating when lifting a heavy box minus the mean box weight rating when lifting a light box) covaried with the magnitude of a bias contrast in the

imaging data (voxels that responded more when lifting a heavy box than when lifting a light box). Significant correlations arose in a network of action and visual areas that have been implicated in processing action stimuli including the IFG, central sulcus, intraparietal sulcus and the extrastriate body area thereby suggesting that the motor system houses weight-specific action representations that are activated in the same way in both action perception and action performance. Similarly it has been found that MEPs in hand muscles are larger when viewing an actor lifting a heavy compared to a light object even when the two objects were visually the same (Alaerts, Senot, et al., 2010; Alaerts, Swinnen, & Wenderoth, 2010). This data indicates that when observing a hand action, not only are hand areas of the motor cortex activated, but they are activated to an effort specific degree depending on the kinematic properties of the stimulus.

In summary, there is some evidence to suggest that in order to understand action stimuli and more specifically action language, we not only recruit body part specific plans but we recruit those plans to an effort specific degree, in the same way that we would if we were to perform an action. However, only few studies have identified these subtle effort effects, therefore, the current experiment aims to further investigate neural effort specific effects for language.

Does Language Induced Motor Activity Reflect Sentence Comprehension?

In previous studies that have investigated language induced body part specific motor activation, the body part information is conveyed via a single verb rather than by the sentence as a whole, for example in a sentence such as “I bite an apple” whereby the critical body-part information is conveyed solely via the word “bite” (Tettamanti, et al., 2005). As physical effort is such a subtle action feature that depends on both the type of action being performed and the properties of the object, it is often necessary to convey this information across several words in a sentence. To then reconstruct the force information, the meaning of the words across the sentence must then be recombined during comprehension. Take a sentence such as “the delivery man is pushing the piano”, here the word “pushing” conjures up a very general image of a pushing action, however when it’s meaning is combined with the meaning of the word “piano” a much more detailed action picture is painted. Now we know how the hands are likely to be

oriented and critically how much physical effort must be applied in order for the action to be successfully carried out. A very different pushing action would be involved if the object were to be something smaller and lighter like a chair. Therefore, the second question that this study aims to address is whether the activity within motor areas can occur when action meaning is derived from the combination of the words across a sentence.

The mapping of arbitrary action words onto meaningful representations within the motor system is thought to occur via hebbian connections (Hebb, 1946). These connections associate the word's orthographic, articulatory and phonological representations with a sensorimotor semantic representation thereby forming a meaningful cell assembly for a particular word (Pulvermüller, 1996). What is not clear is whether language induced activity in the motor system extends beyond the level of individual words and reflects the overall meaning of the combination of the words across a sentence. For the meaning of two or more words to be integrated across a sentence, this may involve the mutual influence of one word's cell assembly upon the other for the understanding of the whole sentence to occur. The second aim of this study is therefore to identify whether any language induced effort modulations within the motor cortex exist when the force information can only have been as a result of combining word meaning across the sentence.

Current Study

In the present event-related fMRI study participants read object-directed hand action sentences such as those in Table 1 that conveyed either high or low degrees of physical effort (verbs: *shake, throw, fling, stack, put, pull, pour, carry, lift*). A control condition was also included where the action verbs were replaced with non-action mental or perceptual verbs (e.g., *forget, notice, glance, wait, detest, hate, dislike, pleased, worried, enjoy*). The activity generated by these three effort conditions was then compared. Critically, in order to understand the effort content of these sentences the meaning of the noun and verb has to be integrated as the sentence is unfolding. As the same verb is included in both the low and the high effort conditions, it alone does not convey any differences in effort across the two action sentence types. Similarly,

although different nouns are included in the low and high effort sentences, they alone cannot be driving the differences in perceived effort once compared to the control condition that includes the same object words. Therefore, when comparing across all three sentence types, understanding the differences in physical effort depends upon online semantic integration of the noun and verb. To ensure that the sentences were perceived to be different in physical effort and that they were equally plausible the sentences underwent pre-tests.

Table 1

Example Sentences for a Given Item

Condition	Example sentence
No effort	The delivery man has forgotten the piano
Low effort	The delivery man is pushing the chair
High effort	The delivery man is pushing the piano

If action sentences that convey detailed action properties such as physical effort recruit very specific action schemas during comprehension, and if we integrate the meaning of all words across a sentence in order to calculate action meaning, then it can be predicted that the brain regions involved in hand action performance should be increasingly active as the effort content of the sentence increases. More specifically we expect to see these effects in a network of regions that has previously been implicated in both action performance and action perception/action language comprehension. This network includes the premotor cortex, the pars opercularis of the LIFG (BA44) and the posterior parietal cortex.

As well as observing increases in activity in regions that are specific to the action modality, increases in non-action executive regions that are perhaps involved in mediating the sentential integration process were also expected. When combining word meanings across a sentence their semantic representations must be maintained in

working memory long enough for the word specific semantic networks to have an influence upon one another. The ventrolateral prefrontal cortex especially in the left hemisphere is implicated in working memory processes for sentence comprehension (e.g., Caplan & Waters, 1999; Fiebach, Rissman, & D'Esposito, 2006). Furthermore, sentence comprehension may require a semantic control/selection mechanism to select and integrate the information provided by the word's active semantic networks. The left ventrolateral prefrontal cortex, especially the pars triangularis/BA45 of the LIFG, is thought to be involved in selecting between competing active representations whereas more anterior ventrolateral prefrontal areas (BA47) have been implicated in the controlled access to semantic representations (Badre & Wagner, 2002, 2007; Thompson-Schill, Bedny, & Goldberg, 2005; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997). As these prefrontal executive systems may be interacting with sensorimotor regions to mediate semantic integration, they may too show an increase in activity across the three conditions as a bi-product of their interconnections with the motor system.

If it is the case that BA45/47 plays a key role in semantic integration, it would be necessary for information to flow between BA45/47 and each sensorimotor region. Therefore, it can be further predicted that activation in the left premotor cortex and LIPL will be better correlated with BA45/47 than with a comparison region (left posterior middle temporal gyrus). This correlation analysis will shed some light on the nature of the relationships between the regions within this network, and the role played by BA45/47 if it is found to be sensitive to effort.

2.2 Experiment

2.2.1 Method

Participants

Seventeen right-handed native English speakers were tested (12 female, 5 male; mean age 25, age range 20-42 years). One participant was excluded due to poor task performance and sleep.

Materials

There were 57 items with three versions of each item: high effort, low effort and no effort resulting in a total 171 stimulus sentences (see Appendix 1 for a full list of stimuli). Low and high effort sentences were identical, except for the object that determined the effort content of the sentence (see Table 1). The no effort sentences were identical to the low and high effort sentences, except non-physical verbs replaced physical action verbs. As there were double the number of object words (from the high and low effort conditions) as there were control stimuli, the no effort control condition contained half the objects from the high effort condition and half the objects from the low effort condition. All sentences had simple subject-verb-object structure, except for 8 cases where there the verb required an extra phrase specifying an action goal (e.g., “the worker is pouring cereal *into the bowl*/sand *into the bucket*”). The sentence structure was the same across conditions for a given item, therefore, any between condition differences could not be explained by variations in sentence structure or length. The verbs (e.g., forget and push) and nouns (e.g., chair and piano) were matched for log frequency and word length across the conditions (COBUILD Corpus: 20 million words). Some items also included adjectives to issue the reader with detailed action information (e.g., carrying a *Greek* statue), these too were matched for length and log frequency across conditions. Comparisons for mean length and log frequency values across the three conditions are included in Table 2. There were no significant differences across conditions for log frequency or character length.

Table 2

Mean Log Frequency and Character Length for Sentences (Standard Deviation in Parentheses)

Word type	Condition	Log Frequency	Character Length	Sentence Example (Bold text refers to the portion of sentence of interest)
Verb	No effort	4.47 (0.55)	11.19 (3.69)	The housewife is admiring the thick quilt
	Low and high effort	4.49 (0.56)	10.67 (1.26)	The housewife is hanging the thick quilt/thin vest
Noun	No effort	3.77 (0.63)	5.53 (1.62)	The housewife is admiring the thick quilt
	Low effort	3.86 (0.71)	5.61 (1.73)	The housewife is hanging the thin vest
	High effort	3.82 (0.61)	5.75 (1.66)	The housewife is hanging the thick quilt
Adjective	No effort	4.60 (0.59)	4.46 (1.05)	The housewife is admiring the thick quilt
	Low effort	4.47 (0.57)	4.87 (1.25)	The housewife is hanging the thin vest
	High effort	4.73 (0.51)	4.93 (0.70)	The housewife is hanging the thick quilt
Sentence	No effort	-	38.21 (7.93)	The housewife is admiring the thick quilt
	Low effort	-	38.00 (7.09)	The housewife is hanging the thin vest
	High effort	-	37.84 (6.85)	The housewife is hanging the thick quilt

N.B. Character length for the verb is for the whole verb phrase e.g. “is admiring”

Stimulus sentences were pre-tested for physical effort, plausibility and imageability to ensure that the actions described by the sentences differed in physical effort across the three conditions but not in plausibility or in imageability. A further body part rating study was also conducted to ensure that the actions described all involve the hands and arms and to find out whether the involvement of other body parts differed across the three conditions, and if so how. Pre-test ratings were collected via an online questionnaire. For each questionnaire the sentences were divided into three lists, each of which contained one version of each of the 57 items, either *no effort*, *low effort* or *high effort*, while maintaining an equal number of sentences from each condition in each list. Each participant rated the items in one of these lists and entry into a prize draw was offered to encourage participation. Those who participated in the rating studies did not take part in the main experiment

Imageability ratings. Previous research has highlighted differences in the way that words are processed based on their imageability (Chiarello, Shears, & Lund, 1999; Sabsevitz, Medler, Seidenberg, & Binder, 2005; Strain, Patterson, & Seidenberg, 1995; Wise, et al., 2000). Therefore, to ensure that the imageability is equal across the three conditions in the present study, 61 participants were asked rate each of the sentences for imageability on a scale from 1 to 7. Most previous studies have been concerned with the imageability of single words, however, in the present study as the stimuli consisted of whole sentences and that the sentential context within which a word is embedded is likely to influence its meaning and imageability, participants were asked to rate the imageability of whole sentences. Due to the abstract nature of the verbs in the no effort condition, it was expected that these sentences would be rated as significantly less imageable than the action sentences. However, no differences were expected between the low effort and the high effort conditions. A one-way ANOVA confirmed these predicted results. See Figure 1 for a graph of the means across the three conditions. There was a significant main effect of condition ($F(2, 110) = 136.5, p < .001$; Welch's F statistics are reported due to inhomogeneity of variance) and post hoc tests (with Bonferroni correction) revealed that this was due to a large difference between the no effort and the two action conditions (both $p < .001$). Importantly no differences were found between the low effort and the high effort condition ($p > .05$).

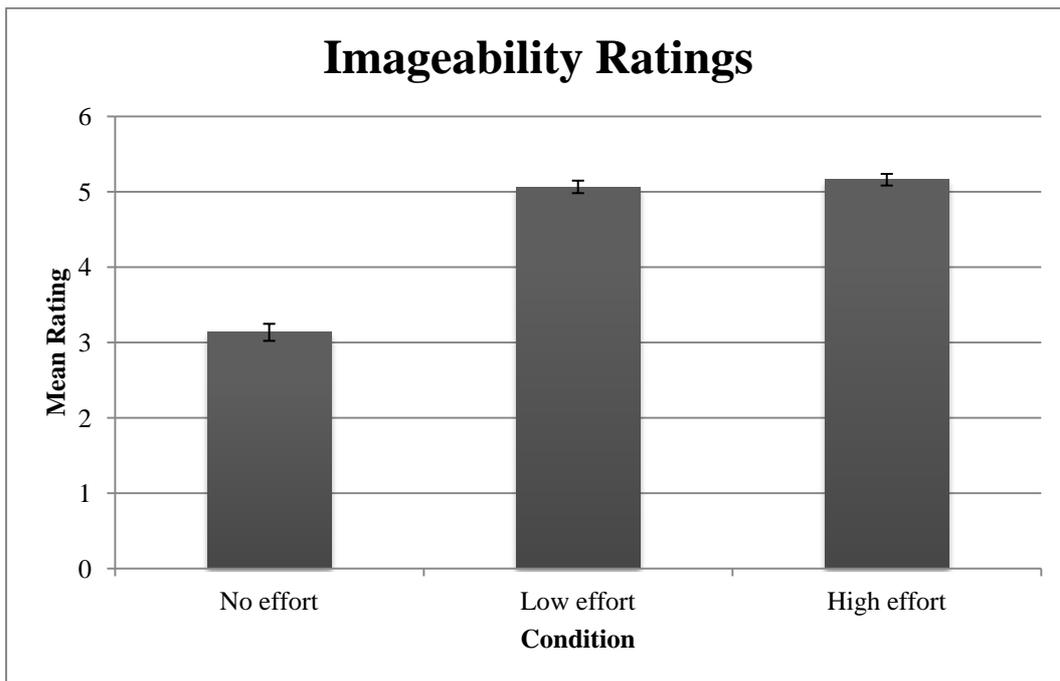


Figure 1. Mean imageability rating for each condition (bars represent standard error).

Plausibility ratings. In a similar way to imageability, semantic plausibility can affect the way in which we process language (Baumgaertner, Weiller, & Buchel, 2002; Rayner, Warren, Juhasz, & Liversedge, 2004; Traxler & Pickering, 1996). Therefore, to ensure that plausibility did not differ across conditions 55 participants were asked to indicate on a scale from 1 to 5 “how plausible is the action or state described by the sentence?”. A one-way ANOVA revealed that there was no significant main effect of condition ($F(2, 110) = 2.04, p < .05$; Welch’s F statistics are reported due to inhomogeneity of variance). See Figure 2 for a graph of the means across the three conditions.

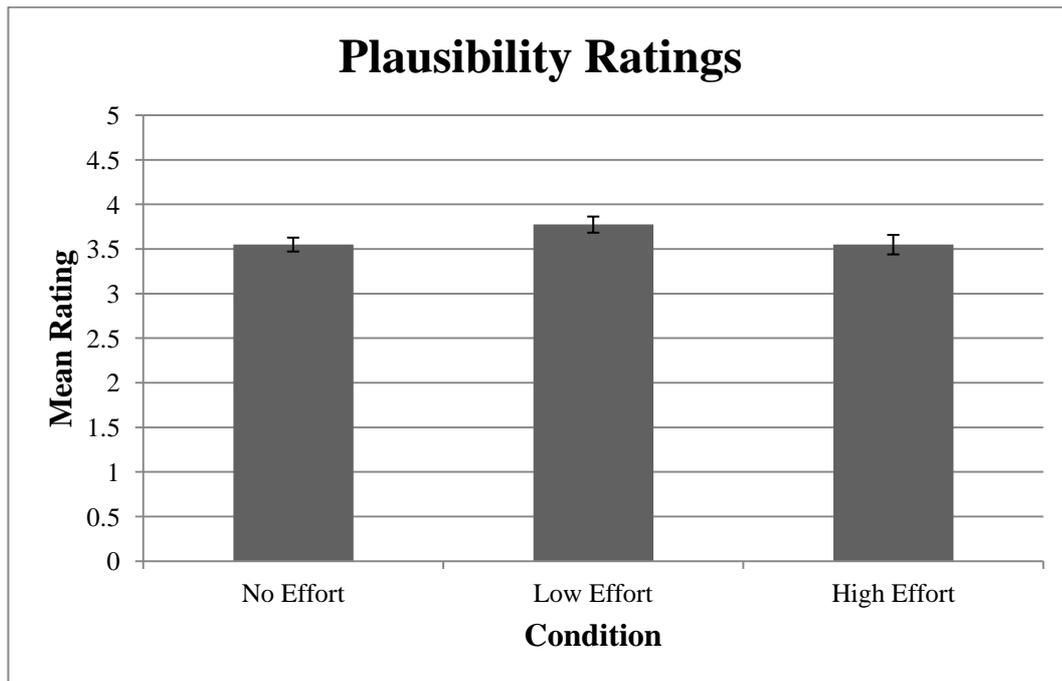


Figure 2. Mean plausibility rating for each condition (bars represent standard error).

Effort ratings. Three different questionnaires were constructed to assess the differences in physical effort across the three conditions. One questionnaire assessed the overall effort of the sentences (irrespective of the body part used) and asked 109 participants to indicate on a scale from 1 to 7 “how much physical effort is involved in the action or state being described by the sentence?”. The other two questionnaires specifically asked 68 and 44 participants “how much physical effort is being exerted by the person’s “hands and arms” or “legs” respectively. In all three questionnaires there was a significant ($p < .001$) main effect of condition (overall effort: $F(2, 79.15) = 417.32$; hand/arm effort: $F(2, 81.16) = 477.02$; leg effort: $F(2, 88.08) = 206.80$; Welch’s F statistics are reported due to inhomogeneity of variance). Post hoc tests (with Bonferroni correction) revealed that there were significant differences between the no effort and low effort condition, between the no effort and high effort condition and between the low effort and high effort conditions ($p < .001$ in all cases). The effort content of the sentences therefore differs across each of the three conditions in the expected direction. See Figure 3 for a graph of the means across the three conditions for each of the questionnaires.

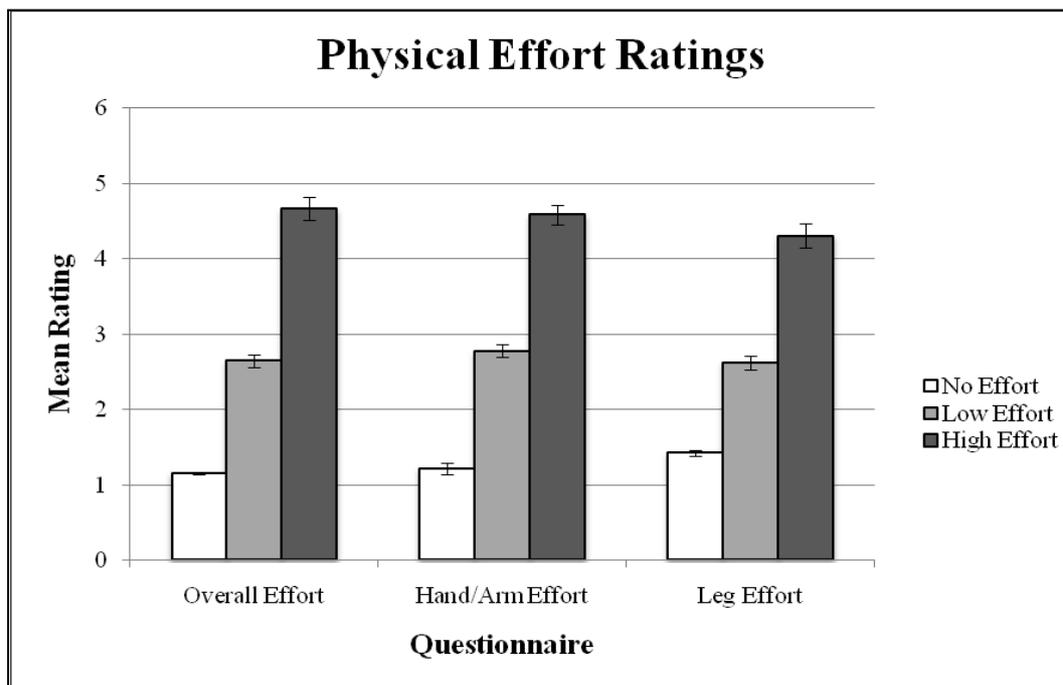


Figure 3. Mean effort rating for each condition for the overall effort rating questionnaire, the hand/arm effort rating questionnaire and the leg effort rating questionnaire (bars represent standard error).

Body part ratings. A further 43 participants were asked to indicate “what body parts are involved in the action described by the sentence?” and the options included “hand”, “arm”, “torso”, “leg” and “none”. As participants could select more than one body part for each sentence the results were analysed as the percentage of participants who chose each body part for each sentence. See Figure 4 for a graph of the results. A univariate ANOVA identified a main effect of body part ($F(3,672) = 317.6, p < .001$). Post hoc tests (with bonferroni correction) revealed that both hands and arms were selected significantly more often than torso and legs ($p < .001$ in all cases). There was also a main effect of effort condition ($F(2, 672) = 1101, p < .001$). Post hoc tests (with Bonferroni correction) indicated that % selection was higher in the low effort compared to no effort sentences, and for the high effort condition than the low and no effort conditions (all $p < .001$). A significant interaction was also found between body part and effort condition ($F(6, 672) = 74.51, p < .001$). This interaction occurred because the difference between % selection in the low and high conditions for hands and arms was minimal and almost

at a ceiling level for both body parts, whereas legs and torso were selected much more often in the high than the low effort condition.

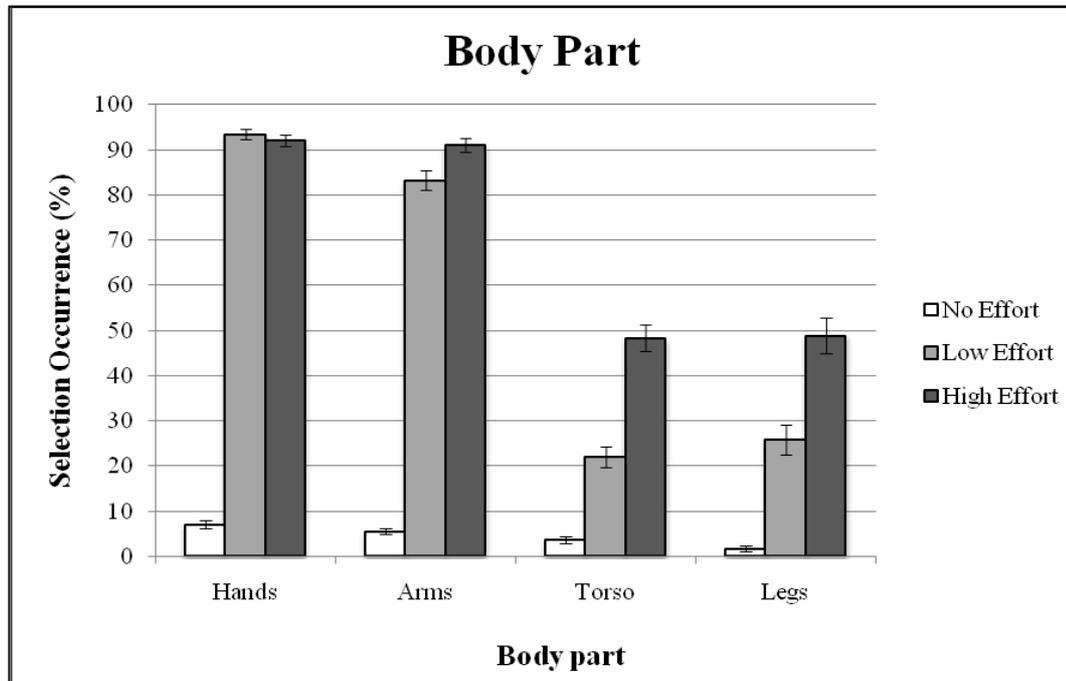


Figure 4. Mean % selection of each body part for the sentences in each of the three conditions (bars represent standard error).

Pretest summary. These pretests ensure that the items in each condition differed only in physical effort and not in plausibility and imageability; any differences in the main experiment can therefore only be attributed to this effort factor. All sentences were found to involve the hands and arms, and physical effort specifically for the hands and arms was perceived to increase across the three conditions. However, it was also found that more body parts were likely to be involved and to a higher degree as the effort content of the sentence increases. The implications for experimental interpretation will be assessed in the discussion.

Procedure

Reading comprehension task. In an event-related design, participants read the stimulus sentences, and then in around 19% of the trials they answered yes/no comprehension questions with their left hand (for example “did the delivery man forget the piano?”). These were catch trials designed encourage participants to

process the sentence meaning and to gain a measure of participant attention. The sentences were presented on a black background for 2 s in white lower case 40pt font with random inter-trial times (which averaged 4.54 s with a range of 2 to 22 s). Sentence presentation was randomised, however each experimental condition (no effort, low effort, high effort) followed the other conditions equally often. During inter-trial times a cross was presented on the screen. Participants were asked to process the meaning of the sentence and to respond as quickly and accurately as possible when a question appeared. Questions always referred to the preceding sentence and were written in capital letters for easy identification. To order the events and to produce a schedule where the maximum efficiency was obtained (in order to be able to effectively parse out individual hemodynamic responses during data analysis) a program named optseq was used (<http://surfer.nmr.mgh.harvard.edu/optseq/>).

Action execution task. Participants viewed 8 blocks of red or blue '@' symbols (block duration 16 s). Within each block stimuli were presented every 2 seconds for a duration of 200ms. Participants were asked to hold a cylindrical pad in each hand throughout the experiment and squeeze the pads hard when the red symbol appeared using a power grip, but not to squeeze them when the blue symbol appeared. The task therefore involved muscles in both the hand and arm and lasted 256 s in total. This execution task took place after the reading comprehension task so not to alert the participant to the importance of the action content of the sentences.

Data Collection Parameters

A 3T GE Signa Exite MRI scanner was used to collect both functional data and high level structural images. Functional images were obtained using a gradient-echo EPI sequence (TR 2000ms, TE 50ms, flip angle 90°, matrix 64 x 64, field of view 24cm) with 30 axial slices of thickness 3.5mm. Functional images excluded the cerebellum and in some participants inferior portions of the temporal lobe.

Data Analysis

First-level and higher-level analyses were separately carried out for each task using FEAT (fMRI Expert Analysis Tool) Version 5.91, part of FSL (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl). Pre-processing steps included motion correction (Jenkinson 2002); slice-timing correction, brain extraction, spatial

smoothing using a Gaussian kernel of FWHM 8mm, and high-pass temporal filtering (Gaussian-weighted least-squares straight line fitting, with $\sigma=25.0s$). Time-series analysis was carried out using FILM with local autocorrelation correction (Woolrich 2001). A boxcar model of the timeseries detailing the onset and duration of each event was created. This was then convolved with a hemodynamic response function (gamma function). Each event was modelled as beginning at the onset of each stimulus presentation and lasting for 2 s.

Several between condition contrasts were computed. For the language data each of the three conditions were firstly compared to the baseline in a whole brain analysis – where participants were instructed to fixate a cross (i.e., no effort > baseline: 1, 0, 0; low effort > baseline: 0, 1, 0; high effort > baseline: 0, 0, 1). A contrast calculating a general increase in activity across the conditions was also calculated (no effort < low effort < high effort ; -1, 0, +1) within pre-defined regions of interest (ROIs). This linear contrast does not necessarily stipulate that there needs to be a significant difference in activity between each of the conditions (no effort < low effort *and* low effort < high effort), only that there be a general increase from no effort to high effort. Therefore, the % signal change for contrast sensitive regions was extracted for each participant and ANOVAs were performed to assess whether between condition significant differences occurred.

For the action execution data, a contrast was computed in a whole brain analysis to identify those areas that were significantly active for the performance of a bilateral hand/arm action while removing any non-action activity related to simply holding the pad and to seeing the action cue (squeezing > no squeezing). The functional images were registered to each individual participant's high resolution structural space and to standard MNI space using FLIRT (Jenkinson, Bannister, Brady, & Smith, 2002; Jenkinson & Smith, 2001). All higher level group analyses used random effects statistics (Gaussianised T/F) and applied cluster correction ($p < .05$), where the size of the clusters was determined by a predetermined Z value that varied across each region (Worsley, Evans, Marrett, & Neelin, 1992). A cluster correction was applied as it is thought to be more sensitive to the true signal than the very stringent voxel-wise correction (Smith & Nichols, 2009).

Region of interest analysis. A whole brain analysis revealed no sensitivity to the linear contrast for effort when correcting for multiple comparisons – analyses

within smaller regions of interest were therefore essential to obtain a less stringent p threshold. A series of four region of interest analyses were conducted to test predictions regarding the sensitivity of the left premotor cortex, the left inferior parietal lobule (LIPL) and the two regions of the LIFG: the pars opercularis and the pars triangularis to the effort content of the sentences. Due to the different response properties of these motor areas, the ROIs were defined in slightly different ways. All ROIs were created in standard space.

The left premotor ROI was defined by several criterion. It was predicted that hand/arm action language activity would overlap with areas involved in the performance of actions using the hand/arm, therefore, the left premotor ROI included voxels that were activated by the action execution task (see Figure 5, green region). However, as this execution region was very large and included regions that were not of interest in the current experiment e.g., primary motor cortex, and to ensure that our results could be related to other action language studies, only voxels that were close to coordinates that have previously been implicated in processing action sentences were included. The average coordinates for activity elicited by hand action sentences as reported by Tettamanti and colleagues (2005) and Aziz Zadeh, Wilson, Rizzolatti and Iacoboni (2006), was calculated and 20mm was added in the x , y and z direction to allow for any variation caused by the brain averaging procedure or by individual differences in the neural representations of hand/arm action. This resulted in a region of cortex in the left premotor cortex as shown in blue in Figure 5. (x : -10 to -50; y : 16 to -24; z : 71 to 31). To ensure that this coordinate space included only the voxels that were active for the action execution task, the execution and coordinate images were overlapped and the common voxels made up the left premotor ROI (shown in red in Figure 5).

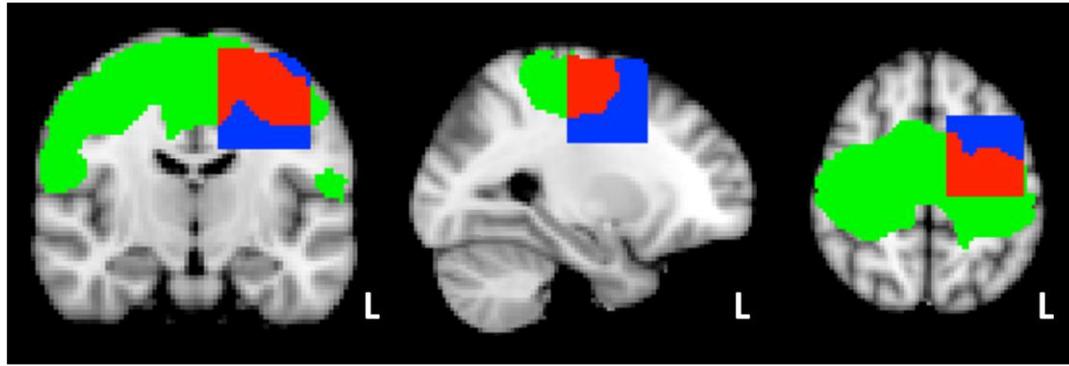


Figure 5. Left premotor ROI (red): common voxels for hand/arm action execution data (green) and the coordinate space defined by activity from other studies Tettamanti et al., 2005 and Aziz-Zadeh et al., 2006 (blue). The ROI (in red) is displayed in three views (from left to right: coronal, sagittal, transverse, coordinates (mm) -26, -14, 52).

The LIPL ROI was defined in a similar way. As few studies have found reliable effects in the LIPL for processing hand/arm action sentences (only Tettamanti, et al., 2005), the region was defined anatomically using the probabilistic map for the anterior supramarginal gyrus from Harvard-Oxford cortical structural atlas (integrated into FSL: <http://www.fmrib.ox.ac.uk/fsl/fslview/atlas-descriptions.html>). As for the left premotor ROI it was predicted that language activity in the LIPL would overlap with activity associated with action execution in the left hemisphere, therefore to ensure that the anatomical LIPL ROI only included voxels that respond during action execution, the common voxels between the two were identified. The resulting LIPL ROI is shown in Figure 6 in yellow. As it was not expected that the LIFG would be involved in action execution, the pars opercularis and the pars triangularis were defined solely using FSL's integrated atlas masks. These masks are shown in Figure 6 in green (pars opercularis) and red (pars triangularis).

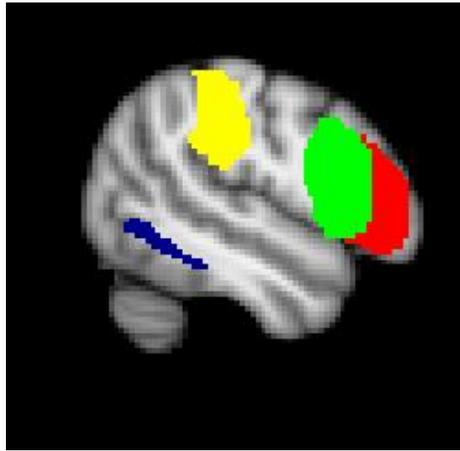


Figure 6. ROI image of the left IPL (yellow), left PMTG (blue), and the LIFG (*pars opercularis* (green), *pars triangularis* (red)). The image is shown in the sagittal view (*x* coordinate (mm): -50).

As it was predicted that each of the four regions would be increasingly active as the implied effort increases across the three sentence conditions, voxels demonstrating this trend were identified (contrast: no effort: -1; low effort: 0; high effort: +1). The analysis used a corrected cluster analysis ($p = .05$), cluster size: left premotor $Z > 2.4$, LIPL $Z > 2.5$, *pars triangularis* and *pars opercularis* cluster size: $Z > 2.3$) (Worsley, et al., 1992).

A significant linear trend within an ROI does not necessarily indicate that there is a significant difference in the amplitude of activity between the three conditions, therefore, further analyses were conducted to reveal the size of these differences within those voxels that contributed to the linear trend. Voxels that were significantly active for the physical effort contrast at the group level for each ROI were converted back into the functional space for each individual, and for those voxels that were sensitive to effort for that participant (in a whole brain uncorrected analysis), the % signal change for the three conditions was calculated using FeatQuery (part of FSL's FEAT software package: <http://www.fmrib.ox.ac.uk/fsl/feat5/featquery.html>). A repeated measures ANOVA was then conducted on this data to identify whether the signal across conditions was significantly different. The average signal change across participants for each of the ROIs is shown in Figure 9. Results from all post hoc tests are 2-tailed unless otherwise stated.

Correlation analysis. It was predicted that the strength of the correlation between different sensorimotor regions may vary across the effort sensitive brain regions. More specifically it was proposed that the pars triangularis may be involved in the integration of signals from more posterior effort sensitive sensorimotor regions. To assess whether this was the case the activity across the whole time course of the experiment for the LIPL and left premotor cortex (regions that are sensitive to implied effort) was correlated with the activity in the pars triangularis and with a comparison region. The left posterior middle temporal gyrus (LPMTG) was chosen as the comparison region as has similar response properties to the pars triangularis in that it has previously been implicated in the processing of language (e.g., tool words: Johnson-Frey, Newman-Norlund, & Grafton, 2005) but not in action performance. Furthermore, the LPMTG was found to be sensitive to effort in the current study in a whole brain analysis (the activation level did not reach significance in a cluster corrected analysis ($Z = 2.3, p < .05$), however activity was present in an uncorrected analysis with a high p significance value ($p < .005$)).

Active voxels from the group ROI analyses were converted back into each individual participant's functional space and those voxels that were sensitive to the effort condition for that participant at an uncorrected ($p < .05$) level were selected for the pars triangularis, the left premotor cortex, the LIPL and the LPMTG. As no LPMTG ROI analysis was carried out at the group level and as the LPMTG was not active for the effort contrast in a corrected whole brain group analysis, the voxels that were active in a whole brain analysis at an uncorrected ($p < .05$) level were selected for further analysis. Within the ROIs for each individual subject, the mean timeseries across active voxels obtained from the raw filtered functional data was calculated. Correlations were then performed between the sensorimotor regions (left premotor and LIPL) and the *pars triangularis* and LPMTG. These correlation coefficients were then compared across subjects. Of particular interest was whether there were any differences in the relationship that the sensorimotor regions had with the LIFG and LPMTG as this may indicate that these two regions play different roles in the action network.

2.2.2 Results

Overlap between Action Performance and Action Language.

A large region was found to be active for the performance of hand/arm squeezing action (cluster correction: $z = 2.3, p < .05$). The activity spanned bilateral primary motor, premotor, somatosensory, parietal, and cingulate cortices as well as the right IFG (see green area of activity in Figures 5 and 7). Reading action language (activity for high and low effort conditions compared to baseline) also activated several areas across the cortex (see blue activity in Figure 7), including the pars opercularis and pars triangularis of the LIFG, bilateral middle frontal gyrus (MFG) and superior frontal gyrus (SFG), bilateral superior and middle temporal gyrus, bilateral inferior and superior parietal lobe, bilateral cingulate gyrus and bilateral precuneus (cluster correction: $z = 2.3, p < .05$). As expected, activity for the action language and action performance task overlapped in several areas including the bilateral premotor cortex (anterior precentral gyrus, middle frontal gyrus, medial frontal gyrus), postcentral gyrus. Therefore, as predicted by previous studies, action language activates a similar network of areas that are involved in action performance specifically for hand actions.

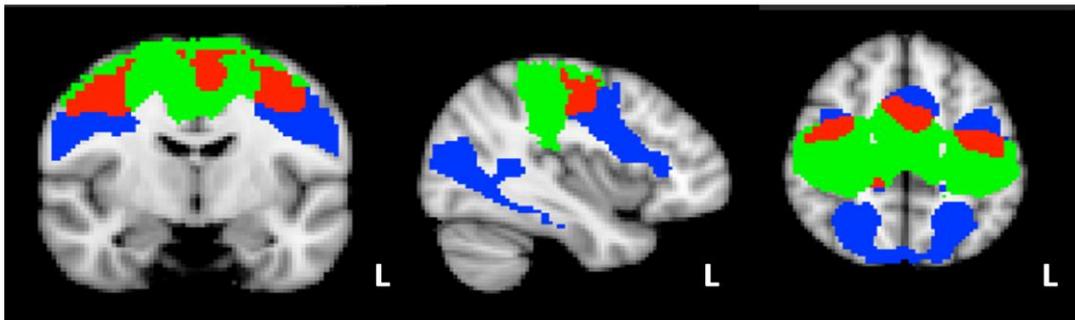


Figure 7. Areas activated by hand/arm execution data in green, action language in blue (combined activation for contrasts: *low effort* > baseline, *high effort* > baseline) and the overlap in activity between the action execution and the action language in red. Contrasts in this whole brain analysis are corrected for multiple comparisons. The overlapping activity is displayed in red in three views (from left to right: coronal, sagittal, transverse, coordinates (mm) -38, -8, 48).

Region of Interest Analyses

Group level analyses were carried out within specific predefined ROIs to identify whether the predicted regions are sensitive to the implied physical effort in the sentences. This group level effort specific activity within each ROI was then used as a mask and was converted into each individual's functional space. For those voxels within each mask that were sensitive to physical effort at the individual level (in a whole brain uncorrected analysis, $p < .05$), the % signal change was extracted for each condition and was averaged across participants. A repeated measures ANOVA was then performed across conditions for each region and a graph of the results is shown in Figure 9.

Left premotor ROI. A cluster of dorsal premotor (BA 6) voxels in the MFG and extending into the SFG were found to be sensitive to the physical effort implied by the sentences. See Figure 8 (top panel) for images of the active region (cluster correction: $Z = 2.4$, $p < .05$) and Table 3 for coordinate information. At the individual level a significant main effect of condition was found ($F(2, 30) = 14.45$, $p < .001$). Planned contrasts (orthogonal Helmert contrast used) showed that the low effort and high effort conditions exhibited higher activity than the no effort condition ($F(1, 15) = 21.76$, $p < .001$) and that the high effort condition showed significantly higher activity than the low effort condition ($p < .05$, one-tailed). The difference between the high effort and low effort condition is reported as one tailed due to the effect being marginal in a two tailed analysis ($p = .07$). It was felt that a one-tailed analysis was justified due to the clear directional prediction that the high effort condition would elicit more activity than the low effort condition in areas that are also involved in action execution. Therefore, there is an increase in activity in the left premotor cortex as the effort implied in the sentences increases.

LIPL ROI. A cluster of voxels centred in the LIPL (BA 40) were found to be sensitive to the physical effort content of sentences. See Figure 8 (middle panel) for images of the active region (cluster correction: $Z = 2.5$, $p < .05$) and Table 3 for coordinate information. A slightly higher Z -threshold was used for defining the cluster size in the LIPL than for the left premotor ROI. A smaller region of activity was expected for the LIPL as no language activity was seen in this area in the whole brain analysis. No effort sensitive voxels were seen when a smaller threshold was used. At the individual level a significant main effect of condition was found (F

(1.27, 19.00) = 42.87, $p < .001$, Greenhouse-Geisser correction applied). Planned contrasts (orthogonal Helmert contrast used) showed that there was significantly higher signal change in the low effort and high effort condition than the no effort condition ($F(1, 15) = 29.00, p < .001$), and that there was significantly higher signal change for the high effort condition than the low effort condition ($F(1, 15) = 4.47, p = .05$). Therefore, the LIPL is increasingly active as the effort implied in an action sentence increases.

LIFG ROIs. Two ROI analyses were performed in the LIFG. It was found that the pars opercularis demonstrated no sensitivity to the effort contrast (cluster correction: $Z = 2.3, p < .05$). This was even true in a separate analysis where no correction was carried out ($p < .05$). A further analysis was conducted to identify whether the pars opercularis was more active for action than non-action sentences (no effort < low effort + high effort; -2, +1, +1) and it was not found to be active in either a corrected (cluster correction: $Z = 2.3, p < .05$) or an uncorrected ($p < .01, p < .05$) analysis. The implications for this result will be discussed later.

The pars triangularis ROI on the other hand was active for the physical effort contrast. See Figure 8 (bottom panel) for images of the active region (cluster correction: $Z = 2.5, p < .05$) and Table 3 for coordinate information. At the individual level a significant main effect of effort condition was found ($F(1.41, 21.07) = 20.76, p < .001$). Planned contrasts (orthogonal Helmert contrast used) showed that the low effort and the high effort condition elicited more activity than the no effort condition ($F(1, 15) = 25.53, p < .001$), and the high effort condition elicited more activity than the low effort condition in the expected direction ($F(1, 15) = 5.94, p < .05$). Therefore, a frontal region that is not part of the “action network” was found to exhibit sensitivity to the physical effort content of action sentences.

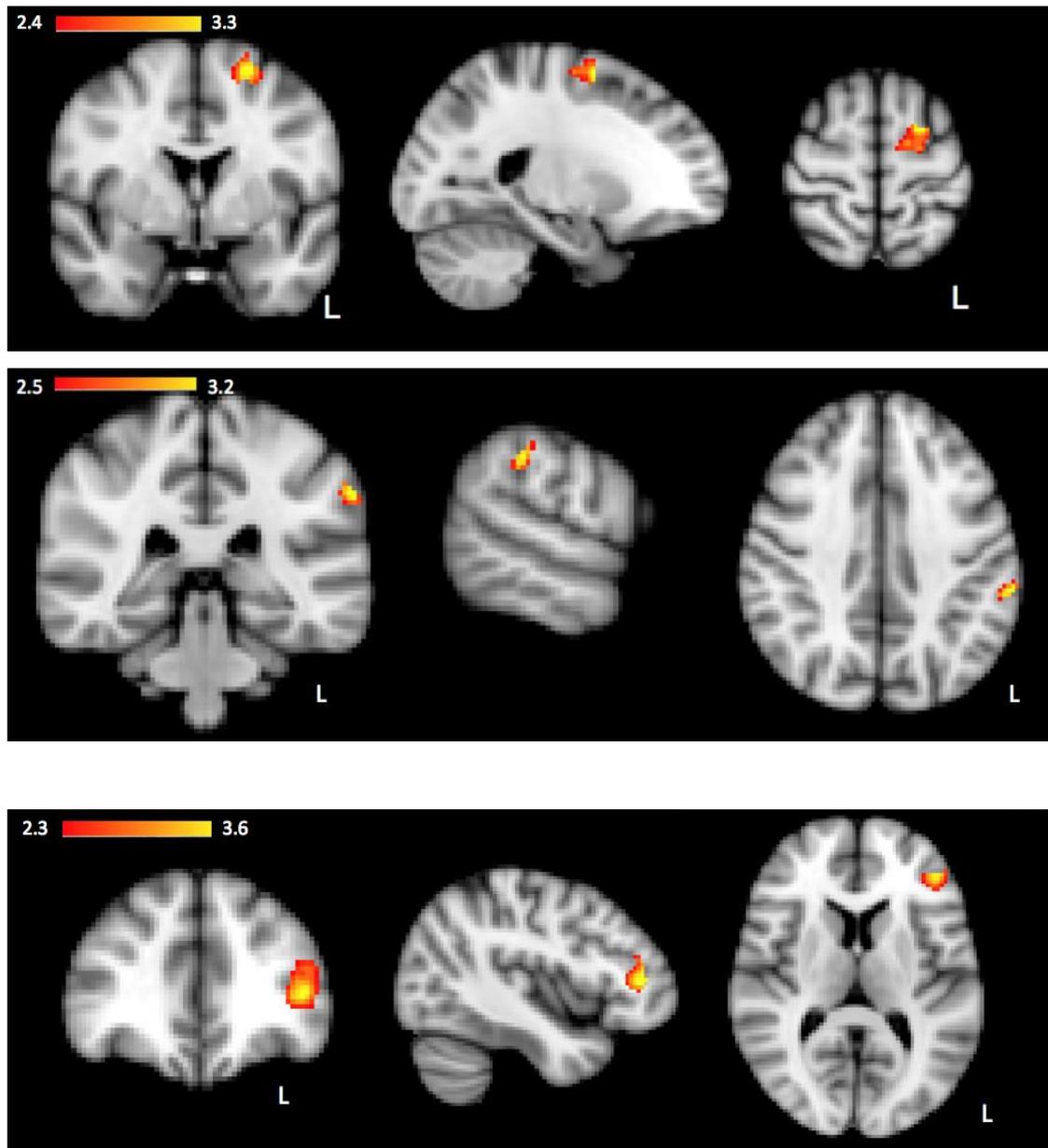


Figure 8. Voxels sensitive to the increase in implied physical effort in action sentences for the left premotor ROI (top), the LIPL ROI (middle) and the pars triangularis ROI (bottom). The activity is displayed in three views (from left to right: coronal, sagittal, transverse).

Table 3

ROI information: Size (in voxels) of the Active Regions, Coordinates (MNI Coordinates in mm) and Maximum Intensity Values

ROI	No Voxels	Maxium Intensity (z value)	Coordinates		
			x	y	z
Dorsal premotor	162	3.33	-22	0	62
IPL	52	3.21	-60	-34	38
Pars triangularis	168	3.57	-42	40	8

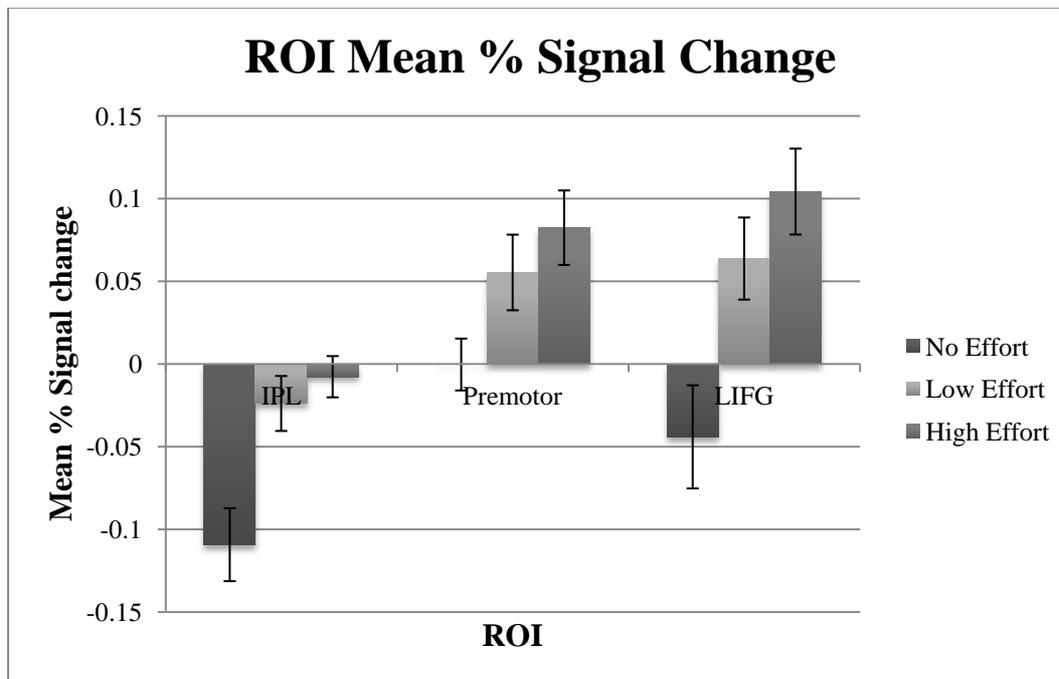


Figure 9. Average % signal change for each condition across participants (bars represent standard error).

Correlation

For each individual participant the mean time course of activity within two effort sensitive sensorimotor regions (left premotor, LIPL) were correlated against 2 “anchor” regions (pars triangularis, LPMTG). See the Methods section for more

details about how these ROIs were defined and Figure 10 for a graph of the mean correlation coefficients across pairs of regions. It was thought that the relationship between sensorimotor regions and each of the anchor regions may differ if a frontal region such as the pars triangularis is involved in semantic integration and a more posterior region like the LPMTG is not. The correlation coefficients for pairs of regions were subjected to a repeated measures ANOVA with anchor region (pars triangularis, LPMTG) as factor 1 and all other regions (LIPL, left premotor, LPMTG/pars triangularis when not anchor region) as factor 2. It was found that there was a main effect of anchor region ($F(1, 15) = 11.19, p < .01$) demonstrating that the *pars triangularis* was significantly more correlated with the sensorimotor regions than the LPMTG. Planned comparisons confirmed that both the left premotor ROI ($F(1, 15) = 8.47, p > .05$) and the LIPL ROI ($F(1, 15) = 8.30, p < .05$) were significantly better correlated with the pars triangularis than the LPMTG. There was no main effect of sensorimotor region ($F(1, 15) = 1.62, p > .05$) indicating that the left premotor cortex and LIPL are both equally correlated with anchor regions. Furthermore, there was no interaction between the anchor regions and the sensorimotor regions ($F(1, 15) = 1.15, p > .05$) indicating that the differences in correlation coefficients for the two anchor regions was constant across the two sensorimotor areas. Further planned comparisons (using an orthogonal contrast) demonstrated that the pars triangularis was related in the same way to the LPMTG as it was to the two sensorimotor regions ($F(1, 15) = .31, p > .05$). However, the LPMTG was less correlated with the activity in the sensorimotor regions than it was with the pars triangularis (although marginally so: $F(1, 15) = 3.54, p = .08$). These results suggest that the two anchor regions play different roles when comprehending action sentences and provide additional support for the role of the LIFG in semantic regulatory functions. The implications of these results will be further considered in the discussion.

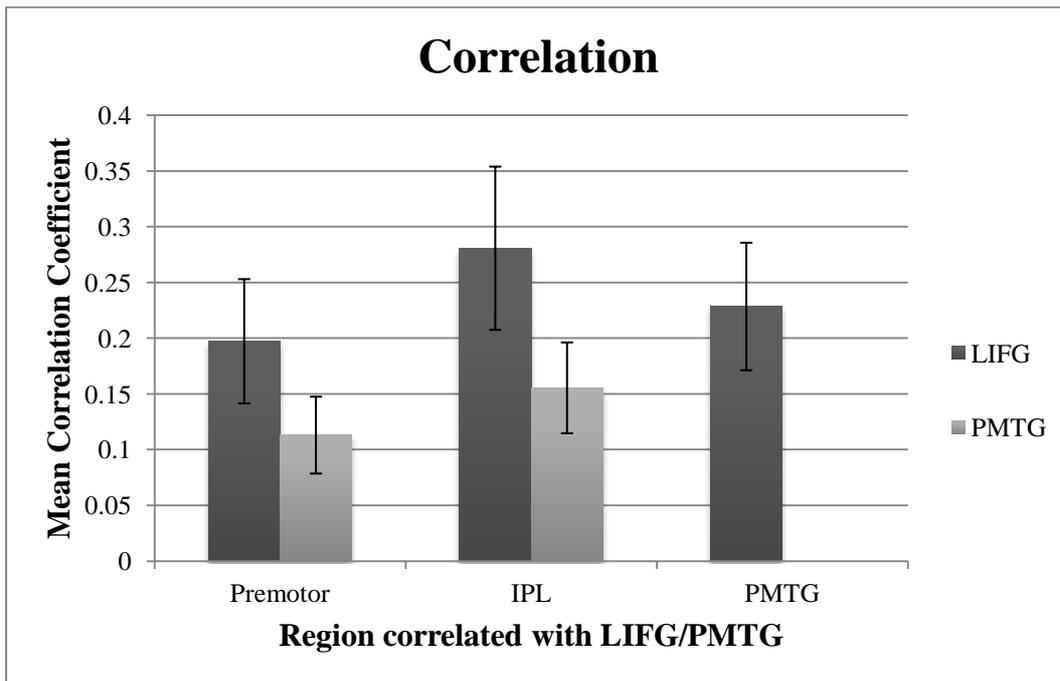


Figure 10. Correlation between sensory-motor regions (IPL and premotor) and the LIFG, PMTG (bars represent the standard error).

2.3 Discussion

Effort Sensitivity within the Motor System

In this experiment participants read hand/arm action sentences that described the exertion of different amounts of physical effort, and later were asked to perform bilateral squeezing actions with the hand/arm. Importantly, comprehension of the physical effort information required the integration of the object and action word meanings. It was predicted that those areas that are active both during the comprehension of action language and during the performance of hand/arm actions would additionally be sensitive to this effort information as conveyed by the whole sentence, and more specifically, that the more effort implied in the sentence, the more activity would be observed in regions that accommodate these shared representations. Analyses within several regions of interest supported this prediction as two left hemisphere sensorimotor regions, the LIPL and the left dorsal premotor cortex were not only activated by action language and action performance, but were also more active as the effort implied in the sentence increased.

The coordinates of effort sensitive voxels in the parietal and premotor cortex are very similar to coordinates that have previously been found to be activated by hand action stimuli. The premotor region of interest was defined using coordinates from two other studies that found hand action sentence activity (Aziz-Zadeh, et al., 2006: -30, -6, 46; Tettamanti, et al., 2005: -30, -2, 56), therefore the coordinates of the peak active voxel in the current study (-22, 0, 62) were very similar to these previous studies. Furthermore, the peak voxels were also very similar to those reported by Hauk and colleagues (2004) for hand action verbs (-22, 2, 64) demonstrating that those regions that have previously been implicated in the comprehension of hand action language are also sensitive to the effort implied by hand action sentences. Fewer studies have reported consistent left parietal activity for hand action language (with no parietal activity reported in some studies: Aziz-Zadeh, et al., 2006; Hauk, et al., 2004), however the coordinates recorded here (-60, -34, 38) are similar to those reported by Tettamanti and colleagues (2005) for the comprehension of hand action sentences (LIPL: -62, -26, 36). Many premotor and parietal regions have previously been implicated in representing action information, however, in the current investigation only certain subdivisions within the premotor and parietal cortex were found to be sensitive to effort. Further exploratory parietal ROIs were investigated (but not reported above) in the right posterior supramarginal gyrus, bilateral anterior supramarginal gyri, and bilateral superior parietal lobules (SPL) using the Harvard-Oxford cortical structural atlas (integrated into FSL: <http://www.fmrib.ox.ac.uk/fsl/fslview/atlas-descriptions.html>). Also the premotor coordinate mask was flipped into the right hemisphere and was interrogated for its effort properties. In these additional ROIs no clusters of effort sensitivity were found suggesting that very specific motor regions are involved in the representation of physical effort information, the significance of which must be further elaborated upon.

As described above, several studies have consistently found that action information engages the PMd (e.g., Aziz-Zadeh, et al., 2006; Hauk, et al., 2004; Tettamanti, et al., 2005). In monkeys, the PMd is thought to be part of a dorsomedial action circuit (along with the medial intraparietal sulcus in the SPL) that is involved in mapping arbitrary stimuli onto associated action plans (Cisek & Kalaska, 2004; Johnson, et al., 1996). As the PMd was activated in the current study

and was sensitive to effort, this suggests that the type of premotor representation that was activated was one that was formed by arbitrary associations between stimuli and actions. This is compatible with the argument that the weight of objects must be learned through experience as there is no consistent direct visual-to-motor mapping between the visual features of a stimulus and its weight. Arbitrary non-weight related visual features must therefore become associated with a weight specific action plan and it may well be that the dorsal premotor cortex is involved in this process. A study conducted by Chouinard and colleagues (2005) provides evidence that the PMd plays a role in the representation of weight information. Participants firstly learned associations between the weight of an object and a colour and subsequently performed a lifting task while repetitive TMS was applied either to the PMd or to the primary motor cortex. It was found that when stimulation was applied to the PMd (compared to the primary motor cortex), participants were unable to scale their grip force based upon the colour cues, suggesting that this region is responsible for linking arbitrary cues such as colour with weight specific action plans.

The IPL on the other hand is an area that is part of the dorsolateral action circuit in the monkey cortex along with the PMv. This circuit contains neurons with mirror properties and is thought to be specialised in performing visuomotor transformations. However, rather than associating arbitrary visual stimuli with action plans, it is thought to directly match the action-relevant physical properties of the stimuli such as size and shape onto an appropriate grasping action plan. It is therefore involved in the standard mapping of object features onto grasp specific action plans (Fogassi, et al., 1998; Fogassi & Luppino, 2005; Gallese, et al., 1996; Gallese, et al., 2002; Murata, et al., 2000; Rizzolatti, et al., 1996; Rizzolatti, et al., 2001; Rizzolatti & Luppino, 2001; Sakata, et al., 1995; Taira, et al., 1990). The activity in the IPL may therefore reflect processing of the grasp component of many of the actions described (e.g., in “dragging”, “pulling”, “throwing”) and due to the increasing effort across the sentences where a stronger grip would be required for heavier objects, higher activity is elicited.

Interestingly, the pars opercularis, an area thought by some to be the homologue of monkey mirror area F5 displayed no sensitivity to the effort implied in the sentence. At a more general level, further exploration revealed that this area responded in the same way to action and no action sentences demonstrating that this

area is unlikely to be involved in processing action stimuli specifically. It has been suggested that this area may be involved in processing language more generally and is only seen to be active for action sentences in these previous studies due to verbalisation of the stimuli or due to the use of a non-language baseline (De Zubizaray, Postle, McMahon, Meredith, & Ashton, 2010; Hashimoto & Sakai, 2002). As in the current investigation the no action control sentences were well matched to the action sentences for linguistic variables such as length and frequency, this may well explain why activity in this area did not show any specificity for sentences with action content.

Body Part Recruitment

As well as involving more effort in the muscles of each individual effector, actions involving more force also recruit additional body parts. In fact the actions described by the high effort sentences were judged as being more likely to include the legs and torso as well as the arms compared to the actions described in the low effort and no effort sentences. Is it possible that this additional body-part recruitment is what is causing the increase in activity across the three sentence types rather than the physical effort? The premotor cortex is thought to have a somatotopic organisation, whereby different regions are responsible for actions that are performed using different body-parts. If this is the case then for those actions that recruit additional body-parts, a more widespread area of activity should be observed. In contrast, when greater force is required for the performance of an action, based upon neurophysiological data, the amplitude of the activity for that body-part specific area should occur. As in the current experiment a difference in the amplitude of response was found across the three sentence types, this suggests that this effect is generated by the increase in force rather than the recruitment of extra body parts. Even if the number of body parts can partially explain this effect, this would still support the prediction that when reading action language we recruit very specific action representations even down to the number of body part representations that are activated.

Influence of Task

In order to answer the comprehension questions correctly, it was necessary for participants to attend to the meaning of the sentences, therefore when reading the

sentences participants were actively processing information described to them in the language. The results of this experiment therefore are not automatic as such, in contrast to those studies that report motor activation for passive reading tasks (Hauk, et al., 2004; Tettamanti, et al., 2005). Results from passive reading tasks have been used to provide evidence for embodied cognition in that semantic representations within the motor system are activated even when no attention is diverted to the action information suggesting that there are strong links between action words and their motor representations. However, the comprehension questions in the present study did not refer explicitly to the weight of the objects in the sentence or to the physical effort that the protagonist was exerting. Furthermore, when participants were later asked whether they knew the purpose of the experiment, nearly all were naive to the action content of the sentences or to the effort manipulation. Therefore, as sensitivity to effort in the motor system was seen when no additional attention was paid to the effort content of the sentence, this suggests that effort specific motor schemas are automatically recruited by action language. In previous experiments, detailed action information is conveyed using single words, and motor activity represents strong associative connections between these verbs and an action plan. In contrast in the current study these automatic activations occurred even when the effort information required the combination of word meaning across the sentence. Therefore, it is not simply that action *words* are associated with action plans, but action meaning is automatically derived from whole sentences are linked to very specific action plans in the motor system.

Hand Specificity

Previous experiments find that action language activity is left lateralised (Aziz-Zadeh, et al., 2006; Rueschemeyer, et al., 2010; Tettamanti, et al., 2005), and activity in current experiment follows this pattern whereby all three effort sensitive regions were located in the left hemisphere. This suggests that the left hemisphere may be specialised for the representation of actions as understood through language, but specialised in what way? There are two possible reasons for this lateralised effect, firstly the left hemisphere may be more highly activated in this language task as it is the language dominant hemisphere in right-handed individuals. Alternatively, it may be that the left hemisphere is activated in a more action-specific as opposed to language general manner. The contralateral hemisphere is thought to

control hand action execution, therefore if hand-specific (left vs. right) action information is also represented in the contralateral hemisphere, then action language describing unilateral actions may primarily induce dominant hand representations in this contralateral cortex (in this case the left hemisphere for the right-handed subjects). To rule out the dominant hand theory, the task would need to include sentences relating to both the left and the right hand to identify whether this leads to a contralateral pattern of motor activity.

Effort Sensitivity in a Non-Motor Region

Sensitivity to physical effort information was also seen in a non-action frontal area – the pars triangularis in the LIFG. As this area is not involved in action performance, it is unlikely that it plays a special role in representing action information. A correlational analysis between the two effort sensitive sensorimotor areas (left premotor cortex and LIPL), the LIFG and a comparison region (LPMTG) was performed to try and shed some light on the role of this frontal area in this task. Whereas the LPMTG is thought to be a sensory area that has in the past been associated with the representation of action motion information (Johnson-Frey, et al., 2005), the LIFG is thought to play less of a role in the representation of modality-specific semantic information, and instead is thought to play a higher level regulatory function, being responsible for selecting and accessing relevant semantic information (Badre & Wagner, 2002, 2007; Thompson-Schill, et al., 2005; Thompson-Schill, et al., 1997). The data supports this assignment of roles as it was found that in contrast to the LPMTG whose activity was less well correlated with the other sensorimotor regions than the LIFG, all sensorimotor regions (including the LPMTG) appear to be equally correlated with the LIFG. It may well be that during the language task the LIFG is involved in collating active semantic information that is fed forward from different sensorimotor regions, and is then able to select and integrate the context appropriate information to arrive at the correct interpretation of the linguistic input. This mechanism may well mediate the influence that the multiple active cell assemblies (representing information for different concepts) have upon one another. This integratory function is especially important for sentence processing where the meaning of individual words must be rapidly combined online, especially in the current study where the comprehension of effort information requires the semantic integration of the noun and verb.

However, why would this region be more highly activated as the effort content of a sentence increases? The correlational analysis suggests that there are strong connections between sensorimotor regions and the pars triangularis. Due to these strong connections and the fact that both areas are engaged during this language task, the effort induced modulations in action-specific sensorimotor areas may well be fed forward as a bi-product to other connected areas including the pars triangularis. The absence of pars triangularis activity in previous studies may well be due to the fact that action effects have been driven by single word stimuli and have not required the integration of words across a sentence in order for the understanding of subtle action features such as physical effort. An alternative explanation for the recruitment of the pars triangularis is that the event frequency or semantic complexity may differ across the three sentence types. For example, high effort actions may be less frequent than low effort actions in real life (you are much more likely to experience a “chair pushing” event than a “piano pushing” event) which may result in greater processing demands. However, the sentences in the current experiment were equally plausible which may rule out the effect of frequency on differences between the three sentence conditions. Furthermore, high effort actions are often semantically more complex than low effort actions. For example, pushing a piano would take more time, more physical space and would require multiple action components (e.g., adjusting the movement to go around corners, uphill etc) than a low effort action. Comprehension of higher effort action sentences may therefore require greater cognitive control to process the many competing associated semantic representations. As the pars triangularis has previously been associated with the regulation of competing semantic variables (Badre & Wagner, 2002, 2007; Thompson-Schill, et al., 2005; Thompson-Schill, et al., 1997), this may explain why it is recruited in an effort specific manner. As complex semantic factors are an inherent characteristic of more effortful actions, the current experiment can only speculate as to why the pars triangularis is activated.

Conclusion

The current findings go beyond that of previous studies by showing that we not only activate detailed body part specific action representations when reading action language, but we activate these representations to an effort specific degree. The representations that we activate are therefore very detailed and specific

providing support for theories of embodied cognition. Furthermore, this study demonstrates that action specific representations are not simply activated by single word stimuli but can result from the combination of word meanings across a sentence and therefore truly reflect action language processing. As frontal regions responded in the same way as sensorimotor regions, this provides support that together with the LIFG, the motor system plays an important role in the comprehension of action sentences.

Despite shedding some light on the nature of the representations that are shared between action and language, there are still several gaps in our knowledge that were not addressed in the current experiment. The language activity (irrespective of effort) did not fully overlap with the action performance activity (see Figure 7). This suggests that when understanding action language we do not fully “simulate” the described action as if we were performing it. Therefore, it is important to further investigate the nature of the action representations that language recruits: Do language induced activations reflect access to more general and abstract action planning representations, or do we additionally recruit those areas required for action execution? Furthermore, what detailed information is further retained, for example do motor activations reflect the hand specific information i.e., left vs. right? The study described in the following chapter aims to clarify these issues and to further investigate the mechanisms responsible for action language understanding.

Chapter 3

Hand Specific Representations in Action Language Comprehension

3.1 Introduction

Embodied cognition predicts that in order to understand action language, we partially “simulate” the associated action using some of the same regions that are involved in the performance of that action (L. Barsalou, 1999, 2008; Gallese & Lakoff, 2005; Glenberg, 1997; Jeannerod, 2001). In support of this claim, it has been found that body part specific regions of the motor system are activated when reading action language (Buccino, et al., 2005; Hauk, et al., 2004; Pulvermuller, Hauk, et al., 2005; Tettamanti, et al., 2005) and that they are activated to an effort specific degree (see chapter 2), suggesting that language recruits very detailed action representations that would also be required for the performance of the same specific action.

However, unanswered questions still remain regarding the nature of the representations that are shared between action and language. For example, in the study described in Chapter 2 (see Figure 7), action language and action performance did not activate exactly the same areas. Despite there being an area of common activation, language activity extended further anteriorly and action activity extended further posteriorly. Similar results were found by Hauk and colleagues (2004) where body part specific activity in both action and language were similar but only overlapped minimally. This suggests that when comprehending action language, we do not “simulate” the described action in exactly the same way as if we were performing it; instead the region of common activity involves only certain action regions. The study described in this chapter aims to further investigate the nature of the representations that are recruited by language.

To what Extent do we “Simulate” Actions when Reading Action Language?

Actions are made up of two main components, firstly an action planning component where action-relevant sensory stimuli in the environment are mapped onto appropriate schemas for action. For example, on observing a cup, the stored knowledge of how to use a cup and the physical properties of that particular cup such

as its shape and size that are required for grasping will be mapped onto a specific grasping schema. The extraction of an object's action affordances is thought to occur automatically (Bub & Masson, 2009; Bub, et al., 2008), however this mapping process may be further facilitated by high level goals and desires, for example, greater attention to action features and faster mapping onto the action plan may occur if the actor is thirsty (Cheng, Meltzoff, & Decety, 2007). These action plans are highly abstract as they neither reflect perception nor action; instead they are an intermediate integratory stage between the two, responsible for high level sensorimotor associations. Secondly, actions have an execution stage whereby the planned action is initiated and controlled online via sensory feedback. The current study aims to identify whether language recruits more abstract representations that are confined to the planning stage of actions, or whether the representations are more detailed by additionally including those structures that are involved in action execution as would be the case if the action was actually performed. As previous studies (such as in Chapter 2) did not separate the planning and action stages in the action performance task, it is therefore unclear as to what action component the region of overlap between action and language represents. The current experiment aims to further investigate this issue to shed light upon the meaning of these language induced activations.

It is widely thought that shared representations between action and language occur at the action planning stage rather than at the stage of action execution. For example, the Theory of Event Coding has proposed that “the stimulus representations underlying perception and the action representations underlying action planning are coded and stored not separately, but together in a common representational medium” (Hommel, et al., 2002). Intuitively, the mere fact that we are able to plan actions, observe actions and comprehend action language without simultaneously performing the action indicates that shared representations are likely to exist at the level of planning rather than execution. Behavioural evidence suggests that simply preparing to perform an action can interfere with perception when the two tasks share a specific feature (Bub, et al., 2008; Craighero, et al., 1999; Glover & Dixon, 2002; Glover, et al., 2004; Muesseler & Hommel, 1997).

Planning has long been thought to take place in the premotor and parietal cortex as these areas have direct neuronal links to the primary motor cortex (M1) and

spinal cord (Dum and Strick, 1991; Barbas & Pandaya, 2004; Muakkassa & Strick, 1979) and consequently have the potential to influence the movements we execute. In order to isolate those areas implicated in action planning, researchers have previously inserted a delay between the presentation of an action cue and the execution of an initiated action, in order to capture activity that is related to action preparation without any contamination of action execution. These studies have shown that these fronto-parietal regions are implicated in action planning in both monkeys at the single neuron level (Cisek & Kalaska, 2004; Nakayama, et al., 2008; Thoenissen, Zilles, & Toni, 2002) and in humans using imaging techniques (Richter, Andersen, Georgopoulos, & Kim, 1997; S. Simon, et al., 2002; Thoenissen, et al., 2002; I. Toni, et al., 2002b). Based upon this evidence it is likely that these premotor and parietal planning regions are involved in the representation of action information, and it may well be that action language additionally recruits these representations.

There is also evidence to suggest that action perception/language recruits areas that are not activated during action planning but are specifically engaged during action execution in M1. Several studies have shown that in tasks where participants are asked to imagine themselves performing actions (Lotze, et al., 1999; Porro, et al., 1996; Roth, et al., 1996; Tomasino, Fink, Sparing, Dafotakis, & Weiss, 2008) or to observe actions (Hari, et al., 1998; Järveläinen, Schürmann, & Hari, 2004), the same population of M1 neurons is active as when performing those same actions. This suggests that during action imagery/observation we precisely re-enact the action, involving not only those areas involved in planning but also those that are involved in execution. However, these results are not necessarily clear cut as some studies report imagery-related activity in the premotor and parietal cortices but not in M1 (M. Deiber, et al., 1998). Furthermore, whereas some action language studies have provided evidence for arm/leg verb induced activity in M1 (Hauk, et al., 2004; James & Maouene, 2009), others did not find the same somatotopic results in M1 (Aziz-Zadeh, et al., 2006; Tettamanti, et al., 2005). Evidence that there are sensorimotor mirror neurons in M1 also suggests that this area is capable of representing action information – the same information that could potentially be recruited by action language comprehension (Tkach, et al., 2007).

Many studies have also found that TMS stimulation of M1 during action observation (Alaerts, Senot, et al., 2010; Alaerts, Swinnen, & Wenderoth, 2009; Alaerts, Swinnen, et al., 2010; Aziz-Zadeh, et al., 2002; Borroni, Montagna, Cerri, & Baldissera, 2005; Brighina, La Bua, Oliveri, Piazza, & Fierro, 2000; Clark, Tremblay, & Ste-Marie, 2004; Fadiga, et al., 1995; Gangitano, Mottaghy, & Pascual-Leone, 2001; Gangitano, et al., 2004; Patuzzo, et al., 2003; Strafella & Paus, 2000; Urgesi, et al., 2006) or action language comprehension (Buccino, et al., 2005; Candidi, Leone-Fernandez, Barber, Carreiras, & Aglioti, 2010; Oliveri, et al., 2004) causes significantly larger/smaller MEPs in muscles that would be required for the performance of the same specific action, or facilitates/impairs processing of words that relate to the same body part (Gerfo, et al., 2008; Pulvermuller, Hauk, et al., 2005). This suggests that M1 houses shared representations that are used in both action performance and action understanding. However, it is not known what generates these effects in M1, it may be that the action-perception interactions occur upstream from M1 in secondary motor areas that are responsible for motor planning, with stimulus driven increases/decreases in activity being filtered up to M1 via dense cortical interconnections (Alaerts, Senot, et al., 2010; Fadiga, Craighero, & Olivier, 2005).

It is therefore unclear as to what the shared activity for action language and action performance represents. This study therefore aims to clarify whether when reading action language we accurately simulate the action within the same regions that are involved in both the planning *and* execution of the action, as we would if the action were to be performed, or alternatively whether shared representations are more abstract and involve only those regions involved in action preparation.

Hand Specificity

In order to identify the specific action components that are involved in the comprehension of action language, a task that will elicit a specific pattern of activity across the motor system in action performance is required, so that the same pattern can be investigated in language comprehension. In this case the task requires participants to perform and to read about hand-specific actions. When preparing to perform an object-directed action, based on the properties of the objects in the scene and the current availability of the limbs, you must choose whether to use your left or

right arm (or both). There is evidence to suggest that when viewing a picture of an object the action affordances of the object including the hand-specific information is accessed. Several behavioural studies have found that participants are faster to perform a right/left handed action when the orientation of an object is spatially compatible with the response hand (i.e., faster to press a left than a right key when seeing an object with the handle on the left) suggesting that the hand-specific object affordances were activated on seeing the image (Bub & Masson, 2009; J. Phillips & Ward, 2002; Tipper, Paul, & Hayes, 2006; M Tucker & Ellis, 1998; Vainio, et al., 2007). These alignment effects were stronger for more graspable objects (Symes, Ellis, & Tucker, 2007) and when attention was drawn to the action features of the object (Bub & Masson, 2009) suggesting that the shared representations between action and language are action specific. The current experiment aims to further investigate these hand-specific interactions and to identify whether these shared representations are stored in the motor system, and if so, whether they are located in those regions involved in action planning or those regions additionally involved in action execution.

Hand-specific Activity in M1

M1 has long been thought to play an important role in the control of limbs on the contralateral side of the body (e.g., Cisek, Crammond, & Kalaska, 2003; Tanji, Okano, & Sato, 1988). This action execution area has also been implicated in the representation of hand-specific information. In an experiment where single pulse TMS was applied to right and left M1, Aziz-Zadeh and colleagues (2002) found greater MEPs in hand muscles after the observation of actions involving the contralateral hand compared to the ipsilateral hand (see also Fadiga, et al., 1998) supporting the role of the primary motor cortex in the representation of hand specific information. If M1, an area responsible for action execution, additionally plays a major role in the representation of hand-specific information, it can be expected that during the comprehension of action language referring to a specific hand, contralateral M1 will be engaged.

Hand-Specific Activity in the Premotor Cortex

A more complex relationship for left and right hand actions exists within secondary motor planning areas such as the dorsal premotor cortex whereby neurons that respond preferentially to actions performed with a particular hand can be found, however they exist in smaller numbers than in M1 (13% v.s. 85%) (Tanji, et al., 1988). Instead most neurons respond to both left *and* right hand actions responding to a slightly greater degree for contralateral actions (Cisek, et al., 2003; Kermadi, Liu, & Rouiller, 2000). Furthermore, fMRI data in humans suggests that a contralateral pattern of activity is found in M1 but not in other motor areas including the premotor cortex (Dassonville, Zhu, Ugurbil, Kim, & Ashe, 1997; Hanakawa, Honda, Zito, Dimyan, & Hallett, 2006; Horenstein, Lowe, Koenig, & Phillips, 2009). Therefore, as premotor neurons in both the left and right hemispheres are involved in the representation of both left and right hand actions and that lateralised hand representations are not as well established in premotor areas as in M1, a contralateral pattern of activity was not necessarily expected.

However, it was thought that other patterns of activity may occur in this action planning region. Previous studies have shown that action representations within sensorimotor areas are influenced by the degree to which a participant has experience of performing a specific action. For example, more activity is seen in these areas for the observation of human (Buccino, Lui, et al., 2004) and biomechanically performable actions (Candidi, 2007; Costantini, et al., 2005) and for those actions that a participant is expert in performing (Beilock, Lyons, Mattarella-Micke, Nusbaum, & Small, 2008; Calvo-Merino, et al., 2005; Cross, et al., 2006; Haslinger, et al., 2005; Kiefer, et al., 2007) suggesting that increased experience results in the establishment of a more elaborate action representation. (Beilock, et al., 2008). As humans have much more experience of performing actions using the dominant hand, it may be expected that within these sensorimotor regions there is a more elaborate representation and therefore more activity when right-handed participants plan and perform actions using their right vs. left hand.

2.2 Experiment

In the current experiment, in order to assess the specificity of the action representations recruited by hand-specific language, participants were asked to both

read about and to perform left and right hand button presses (see Table 1). In previous experiments that have assessed the overlap between action and language the kinematics of the executed action were often different from the kinematics of the actions that were described in the language. For example, in the effort study (Chapter 2) participants were asked to squeeze a pad in the action execution task, a very different action to those described by the language for example “the delivery man is pushing the piano”, an action that does not require any squeezing. In addition, in the language task the activity was averaged across sentences that described very different actions (such as “the delivery man is pushing the piano” and “the child is throwing the rock”). Due to these issues it is difficult to conclude from previous studies that the same specific neural population is involved in both the performance and the comprehension of an action. Therefore, stronger conclusions can be made with the current design regarding the specificity of the hand action representations that are recruited in language, as participants performed and read about the same specific actions.

Activity during hand specific action performance and action language comprehension was then separately assessed within those areas that are involved in action planning and action execution. In order to dissociate the execution and planning components a go-no-go task was used, where participants planned an action but refrained from executing it. The identification of these no-go trials enabled the isolation of the two different action components (see methods for further details about the definition of these ROIs). Once the planning and execution areas had been identified, they were then interrogated for their hand specificity in both action performance and in action language to see whether any similar patterns were observed. It was predicted that if we simulate actions in great detail and recruit the exact same neural areas as are required for the performance of the action, then the same contralateral hand-specific pattern of activity should be seen across the two tasks in action execution areas. If however, language recruits abstract planning representations only, then it is expected that a similar pattern of activity across the two tasks will only be found in action planning areas – in this case a non-contralateral pattern of activation relating to the dominant hand.

2.2.1 Method

Participants

18 participants were recruited for the experiment, all were right-handed native English speakers (14 female, 4 male; mean age 21, age range 19-23 years).

Materials

The experiment had two sections, a go/no-go action performance task and a language comprehension task. The stimuli in each task were divided into 2 main conditions: right hand action performance/language and left hand action performance/language. Additionally, in the language task questions were inserted and in the action performance task no-go trials were inserted. All stimuli were presented centrally on a black background.

In the action performance task, participants were given action/no-action cues consisting of pairs of letters in red uppercase 50pt text (e.g., “RR”, “XR”). In total 200 action stimuli were presented, 160 “go” trials and 40 “no-go” trials (see Table 1). The go trials instructed participants to press either one or two buttons using either the right or the left hand. For the baseline, “HH” was presented in white 50pt text. This baseline stimulus was chosen so when compared to stimuli in the experimental conditions, any lower level effects of viewing complex letter stimuli would be reduced and the critical response components would be more easily identified.

Table 1

Details of Go/No-go Cues.

Cue	Trial Type	N	Cue Instruction
“RR”	Go	40	Press two buttons with the right hand
“RX”	Go	40	Press one button with the right hand
“LL”	Go	40	Press two buttons with the left hand
“LX”	Go	40	Press one button with the left hand
“XR”/“XL”	No-go	40	Do not perform a button press

In the language comprehension task sentences were presented in white 30pt text. All sentences were written in the first person narrative (e.g., “*I am pressing...*”) to encourage the activation of the participant’s own motor plan during language comprehension. Each sentence described left/right hand button presses using either one or two fingers. In total 160 action sentences were presented and occasionally after the sentence presentation a question appeared (see Table 2). To encourage participants to process the sentence meaning and to maintain their attention, the phrasing of the sentence was varied, for example, when describing one button press with the left hand participants could read one of 4 different sentences (see Table 2). The length in characters of the sentences varied from 27-47 (mean length 37.25), however to ensure that the sentences were all matched across each condition the same structure was used in the left and right conditions, where the only thing that differed was the hand that was referred to (“right” vs “left”). Therefore, psycholinguistic variables such as length and frequency should not have influenced the results as were equal across conditions. As some of the sentences were too lengthy to fit on one line, all sentences were divided and presented on two lines. For the language baseline, a string of 37 X’s were presented (to match the average character length of the sentences), so again when compared to the experimental conditions any effects of viewing complex letter strings would be reduced and any activity relating to action sentence processing would be more easily identified.

Table 2

Details of Sentence Stimuli.

Hand action	Cue	N	
Right: Two fingers	“I’m pressing both buttons with my right fingers”	10	
	“I’m pushing two buttons on the right”	10	
	“I’m pushing two right buttons”	10	
	“On the right, I’m pressing two buttons”	10	=40
Right: One finger	“I’m pressing the button with my right finger”	10	
	“I’m pushing one button on the right”	10	
	“I’m pushing one right button”	10	
	“On the right, I’m pressing one button	10	=40
Left: Two fingers	“I’m pressing both buttons with my left fingers”	10	
	“I’m pushing two buttons on the left”	10	
	“I’m pushing two left buttons”	10	
	“On the left, I’m pressing two buttons	10	=40
Left: One finger	“I’m pressing the button with my left finger”	10	
	“I’m pushing one button on the left”	10	
	“I’m pushing one left button”	10	
	“On the left, I’m pressing one button”	10	=40
Questions	“LL?”	8	
	“LX?”	9	
	“RR?”	10	
	“RX?”	7	=34

Procedure

As the action and language task included the same conditions and numbers of stimuli, a similar schedule of events was used for each task lasting 960s (schedule created using Optseq: <http://surfer.nmr.mgh.harvard.edu/optseq/>). The 40 no-go trials in the action task were substituted for question trials in the language task, however as on 5 occasions the no-go trials occurred in succession, they were

replaced with only one question trial in the language task schedule. A further question trial was removed to ensure there were an equal number of yes and no responses (resulting in 18 questions per answer type).

Go/no-go task. Participants were presented with action or no-action cues lasting 500ms. Cues from different conditions were randomly intermixed in an event-related design therefore participants could not predict the upcoming stimulus. Inter-trial intervals were occasionally inserted between trials and ranged from 0-30s (average 2.81s) to allow for the haemodynamic response to return to normal.

The cue instructed participants to press buttons with the right or left hand using either one or two fingers as quickly as possible. If the cue began either with an "R" they pressed one/two buttons on the right and if the letter pair began with an "L" they pressed one/two buttons on the left. If one of these letters were present this indicated that one button was to be pressed ("LX" / "RX"), and if two of these letters were presented this indicated that two buttons were to be pressed ("LL" / "RR"). These one and two button trials were not separately analysed, as for the current study only information about left and right hand action performance was of interest. However, these one/two button trials were included to increase the variability in the actions and force participants to actively plan. If only simple left and right hand actions were included this may have resulted in very little action preparation and would have reduced the chances of capturing action planning activity. No-go trials were also included; these trials consisted of the same letters as the go trials but in reverse order (e.g., "XR" instead of "RX"). On these trials participants were told not to press any buttons. These trials were used to define areas involved in action planning (see data analysis section). Participants underwent a practice session before they took part in the real experiment with 28 trials from each action condition (14 left, 14 right) and 4 no-go trials.

Language task. Participants were presented with sentences each lasting 2000ms and were asked to read the sentences for meaning. Again an event-related design was used where the sentences from each condition were intermixed and therefore could not be predicted. Inter-trial intervals ranged from 0-30s (average 2.96s). Question trials (also lasting 2000ms) were inserted after 34 of the sentences (21.25% of trials). The questions were the same cues that were used in the go/no-go task for example "RR?". Participants had to indicate whether this question cue

corresponded to the meaning of the previous sentence using a left hand button press (index finger for yes and middle finger for no). If, for example, the sentence read “I’m pushing two buttons on the right” participants were required to answer yes if the following question was “RR?”. In order to perform well on this task participants had to read the sentences carefully for their hand-specific action meaning, therefore it ensured that participants were actively processing the language and maintaining their attention throughout the experiment. Participants received 5 practice trials (two of which included questions). Fewer practice trials were included in the language than the action task as the language task was relatively easier than the action performance task.

Data Collection Parameters

A 3T GE Signa Exite MRI scanner was used to collect both high resolution structural images and functional images. Functional images were obtained using a gradient-echo EPI sequence (TR 2000ms, TE 50ms, flip angle 90°, matrix 64 x 64, field of view 24cm) with 38 axial slices of thickness 3.0mm. The resulting voxel size was 3.75cm x 3.75cm x 3cm. Functional images excluded the cerebellum and in some participants inferior portions of the temporal lobe. A T1 flair image was also obtained in order to facilitate the registration between the high resolution structural and functional data.

Data Analysis

Both first level and higher level analyses were carried out for the language and the action task separately using FEAT (FMRI Expert Analysis Tool) Version 5.91, part of FSL (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl). Several pre-processing steps were undertaken including motion correction (Jenkinson 2002); slice-timing correction, brain extraction, spatial smoothing using a Gaussian kernel of FWHM 8mm, and high-pass temporal filtering (Gaussian-weighted least-squares straight line fitting, with $\sigma=25.0s$). Time-series analysis was carried out using FILM with local autocorrelation correction (Woolrich 2001). A boxcar model of the timing of events was created involving the onset and length of each stimulus event, which was then convolved with a haemodynamic response (gamma) function. For both action and language data the event was modelled at the onset of the stimulus presentation with action trials lasting 500ms and language trials lasting 2000ms.

Several contrasts were run between the different conditions in the action and the language task. For the action data all actions together (irrespective of hand) were compared to baseline (Action > B) and right and left hand actions were also compared against one another to find those areas that are specifically involved in performing left or right hand actions (R > L, L > R). A further contrast was calculated for the action performance data to isolate those areas in the no-go trials that are involved in response inhibition/planning compared to baseline (N > B). For the language data, a contrast was calculated whereby all sentences together (irrespective of hand), were compared to baseline (Language > B). These contrasts were calculated using both voxel-wise and cluster correction. For the language task the question trials were modelled separately to account for the participant's motor response but this data was not analysed. See Figures 3 and 4 for an image of each of these whole brain analyses (voxel corrected, $p < .05$)

Two ROIs were defined, firstly for the hand-specific action execution clusters of activity, and secondly for action planning clusters of activity. These regions of interest were taken into the coordinate space of each participant's brain and the % signal change (from baseline) within each of these regions for left/right hand action performance and left/right hand language was then calculated to assess whether there were any similarities in activity across the action performance and action language task.

ROIs for hand-specific action execution. Based on previous evidence it was predicted that regions involved in right and left hand action execution may also be involved in the representation of hand-specific action information. In order to test this prediction, ROIs that were specifically involved in the performance of right hand (R > L) and left hand actions (L > R) were separately identified in a cluster corrected analysis. This resulted in a contralateral pattern of activity whereby right hand actions activated the left hemisphere and left hand actions activated the right hemisphere. As action execution is comprised of both execution and planning components, by subtracting left from right and right from left action performance, this should cancel out any general planning activity that is shared. However, to ensure that this execution ROI did not include any areas involved in hand-specific action planning processes, any voxels that were also activated by the no-go trials were removed and activity in any additional regions that were not of interest (e.g.,

subcortical regions) was also removed. To focus in on language effects, only those execution areas that overlapped with general language activity were further analysed (Language > Baseline from a cluster corrected analysis).

The resulting ROIs therefore represented those regions involved in both the execution of a hand-specific action and in general language comprehension. These ROIs included the contralateral pre- and post central gyrus (primary motor cortex (BA 4) and somatosensory cortex (BA 2)) where the right hemisphere is responsible for left hand execution and the left hemisphere is responsible for right hemisphere execution (see Figure 1). A medial area, the paracentral lobule was also found to be activated for both contralateral execution and language, an area that is also known as the SMA and has often been found to be involved in the execution of actions (e.g., Goldberg, 2010).

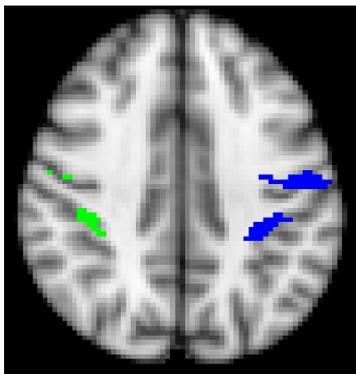


Figure 1. Hand specific action execution ROIs. Coloured regions refer to the left hand-specific ROI (green) and the right hand-specific ROI (blue).

Identifying action planning areas. One of the hypotheses to be tested in this experiment is that those areas involved in representing action plans would be the areas that are additionally involved in understanding action language. In order to test this prediction, brain areas involved in the preparation of hand actions were identified. The no-go trials were used to identify planning areas separately from execution, as on these trials participants are encouraged to access action plans based upon the directional information in the cue (as these cues included “R” or “L” information) but to refrain from executing the action.

To ensure that participants were planning the action on these no-go trials several measures were taken. Firstly, the no-go trials were relatively rare (20%) compared to the go trials (80%), therefore participants expected a go cue and were used to performing an action on seeing a cue. This made it difficult for participants to refrain from performing a hand-specific action on seeing a no-go cue. Secondly, the no-go cues were visually similar to the go cues as contained the same letters, and therefore the same hand-specific information (go: “RX” vs no-go: “XR”). Therefore, on seeing these no-go cues participants would find it difficult not to access a hand-specific action plan and to subsequently execute it. Furthermore, participants were also told to perform the cued actions very quickly and if possible while the action cue was still on the screen (within 500ms) meaning that participants would automatically be inclined to perform a cue related action as quickly as possible within the allotted time window. The combination of these factors: the relative proportion of go to no-go cues, the visual similarity of the go and no-go cues and the short time window for response all contributed to participants accessing an action plan when they viewed the no-go cues. To ensure that participants were actually planning the action on the no-go trials, the number of errors (where the action was mistakenly executed) was calculated. If participants on occasion actually performed the action, this would be evidence that they are planning the action and find it difficult to inhibit its execution. Also if on error trials, where participants accidentally perform an action, the hand used is always consistent with the “R” or “L” in the cue, this would provide evidence to suggest that participants are automatically transforming the hand-specific information in the no-go cue into an action plan.

ROIs for general action planning. To define the planning ROIs the common regions of activity for the action performance trials (irrespective of hand) and the no-go trials were identified. As both of these tasks should share an action planning component, any commonly activated voxels should represent those regions specifically involved in action planning. At the same time those voxels that are involved in other processes that are not shared across the two tasks will be removed such as inhibition, a process that is likely to be recruited in the no-go trials but not in the action performance trials. The general action planning ROIs identified using this method are very similar to planning regions identified in other studies (J. D. Connolly, Goodale, Cant, & Munoz, 2007; Deiber, 1996; Richter, et al., 1997;

Schumacher, 2007; S. R. Simon, Meunier, M., Pieltre, L., Berardi, A.M., Segebarth, C. M., Boussaoud, D., 2001; I Toni, et al., 2002a).

Using this action planning mask only those voxels that were additionally sensitive to language (irrespective of hand) were included. See Figure 2 for an image depicting the general planning regions of interest. The inhibition, language and action performance masks that were used to create these ROIs were all derived from voxel-wise corrected group analyses (using a less stringent cluster correction resulted in too widespread an area of activity to perform ROI analysis therefore a voxel-wise corrected analysis was used to focus in on the most responsive voxels). Four separate ROIs were identified bilaterally in the premotor (BA 6) and posterior parietal cortex (BA 40). More specifically, the premotor ROIs include the middle frontal gyrus, extending into the inferior frontal gyrus and the parietal ROIs include the inferior parietal lobule extending into the anterior intraparietal sulcus (aIPS). It is important to note that the position of these regions is relatively anterior in the premotor cortex and posterior in the parietal cortex compared to the action execution ROIs .

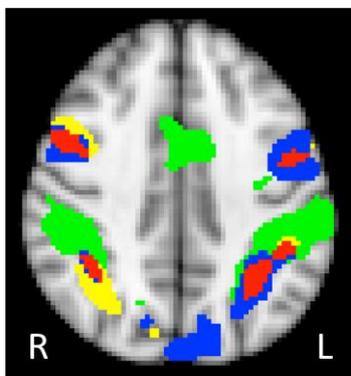


Figure 2. Action planning ROIs. Coloured regions refer to inhibition activity for no-go trials (yellow), action performance activity (green), language activity (blue) and the ROI formed from the overlapping activity (red).

ROI analysis. The ROIs were then treated as masks and were converted into the functional space of each individual participant. The average parameter estimate across the ROIs for each condition was extracted and converted into % signal change

relative to baseline using FeatQuery, part of FSL's FEAT software package (<http://www.fmrib.ox.ac.uk/fsl/feat5/featquery.html>). In each ROI the % signal change for right/left sentences and right/left actions were then extracted to identify whether there were any similarities in activity for right and left hand actions across the action and the language task and if so what ROI type yielded such a result. Any ROI types demonstrating a similar effect across the two tasks can be considered as containing hand-specific representations that are recruited in the same way by both action performance and action language.

3.2.2 Results

Behavioural Data

Action task. The time taken for participants to perform the instructed action and the number of errors made were measured. Participants responded on average in 636ms, and despite there being a trend for faster response times for the right compared to the left hand no differences were found in reaction time ($t(17) = -1.43$, $p > .05$). For the action trials a response was classed as an error if participant either failed to make a response or responded using the wrong hand, if participants responded with the wrong number of fingers this was not classed as an error, as we were interested only in the distinction between left and right handed actions. On average participants made an error on 3.06% of action trials. A Wilcoxon Signed-Rank tests was performed on the frequency of errors comparing right and left hand actions. Despite there being a trend for higher error rates on right handed actions, no reliable differences were found between the frequency of errors for left hand ($Mdn = 2$) and right hand ($Mdn = 2$) action conditions ($z = -.637$, $p > .05$).

As one participant did not adhere to the no-go rule on no-go trials, their data was removed from any further analysis of this inhibition data (however as this participant performed well on the action trials, their data was used in the analysis of left and right action trials). Of the remaining 17 participants, the numbers of errors on nogo trials were calculated, with errors being defined as those nogo trials where an action was incorrectly performed. On average, errors on no-go trials were relatively low and were made 2.5% of the time. Furthermore, almost all errors (94%) were consistent with the directional letter in the cue (i.e., if the cue was XR the right button was most likely to be erroneously pressed, and if the cue was XL the

left button was most likely to be erroneously pressed). As participants sometimes performed an action on no-go trials this suggests that the context of the task caused them to activate an action plan, and that they found it difficult to suppress the desire to execute the planned action. Furthermore, as the hand that is used to erroneously perform the action is so consistent with the directional letter in the nogo cue, this is strong evidence to suggest that the activated plan is hand-specific. This is strong evidence to suggest that participants are actively planning a cue-specific action during these no-go trials and therefore justifies the use of the nogo trials for the identification of action planning areas. As errors were relatively few, these error trials were not removed from further analysis.

Language task. Due to experimenter error, no responses were recorded from one participant. For the remaining 17 participants, on average participants responded correctly on 90.7% of the question trials and the mean reaction time for the responses was 2605ms. These reaction times are long suggesting that the task was difficult, and therefore encourages participants to read the sentences for their meaning in order to perform the task correctly.

ROIs

The whole brain analyses that were used to create each ROI can be found in Figures 3 (action task) and 4 (language task) (voxel correction, $p < .05$). The ROIs derived from the group analyses were transformed into each individual's functional space and the % signal change relative to baseline for each of the conditions of interest was calculated.

Activity within hand specific action execution ROIs during action language comprehension. The language activity within these hand-specific execution areas was assessed in order to identify whether there were any contralateral activity patterns as there was in action performance. No significant differences in % signal change were seen between right and left action language in the left or right hemisphere motor, parietal or medial ROIs (left motor: $t(17) = -1.85, p > .05$, right motor: $t(17) = -1.16, p > .05$, left parietal: $t(17) = -1.08, p > .05$, right parietal: $t(17) = -.683, p > .05$, left medial: $t(17) = -1.97, p > .05$, right medial: $t(17) = -.941, p > .05$). The hand specific pattern of data as seen in action performance is therefore not seen when comprehending hand specific action language within these execution areas.

Activity within action planning ROIs for action language and performance.

Paired t-tests were performed on each of the regions between right and left hand action performance and right and left hand action language. It was predicted that a dominant hand effect would be seen for both action and language if both tasks recruit hand-specific planning representations. Firstly, in the action task, % signal change was higher for right hand actions than left hand actions in both hemispheres (left hemisphere: $t(17) = -4.86, p < .001$, right hemisphere: $t(17) = -2.80, p < .05$). Additionally, for both the left and the right premotor cortex greater % signal change was found for right than left hand sentences in the language task (left hemisphere: $t(17) = -2.58, p < .05$, right hemisphere: $t(17) = -3.34, p < .01$). Therefore, a similar dominant hand effect was observed in both the action and language task in the premotor cortex irrespective of hemisphere.

In the left parietal cortex significantly higher % signal change was seen for right than left actions in both the action language ($t(17) = -3.18, p < .01$) and action performance tasks ($t(17) = -2.51, p < .05$). However, in the right parietal cortex significantly higher % signal change for right than left actions was seen in the language task ($t(17) = -3.00, p < .01$) but was not found in the action task despite there being a trend for greater right than left hand % signal change ($t(17) = -1.23, p > .05$). Therefore, the IPL is showing a similar pattern of results for both the action and language task in the left hemisphere but less so in the right hemisphere. See Figure 5 for graphs summarising these results.

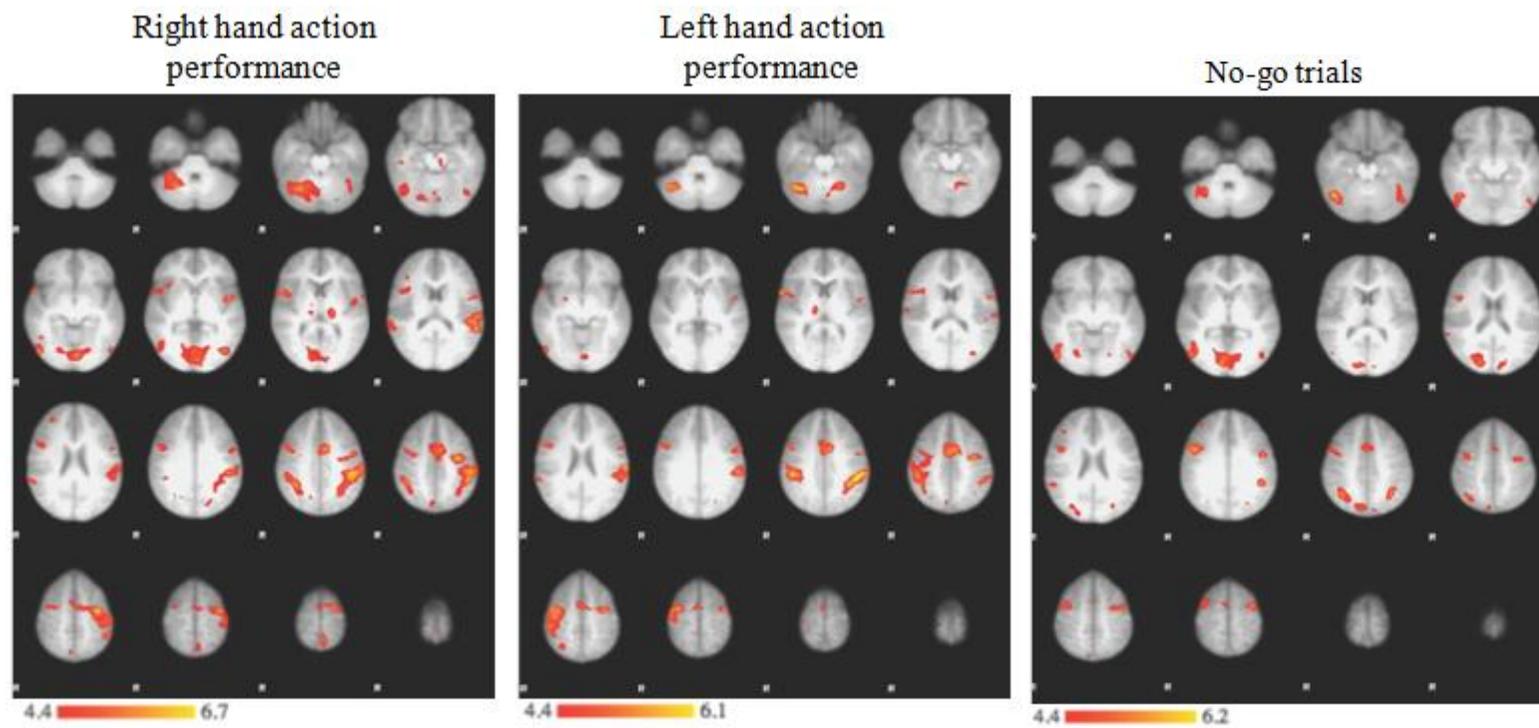


Figure 3. Whole brain analyses for each action condition vs. baseline (voxel corrected, $p < .05$)

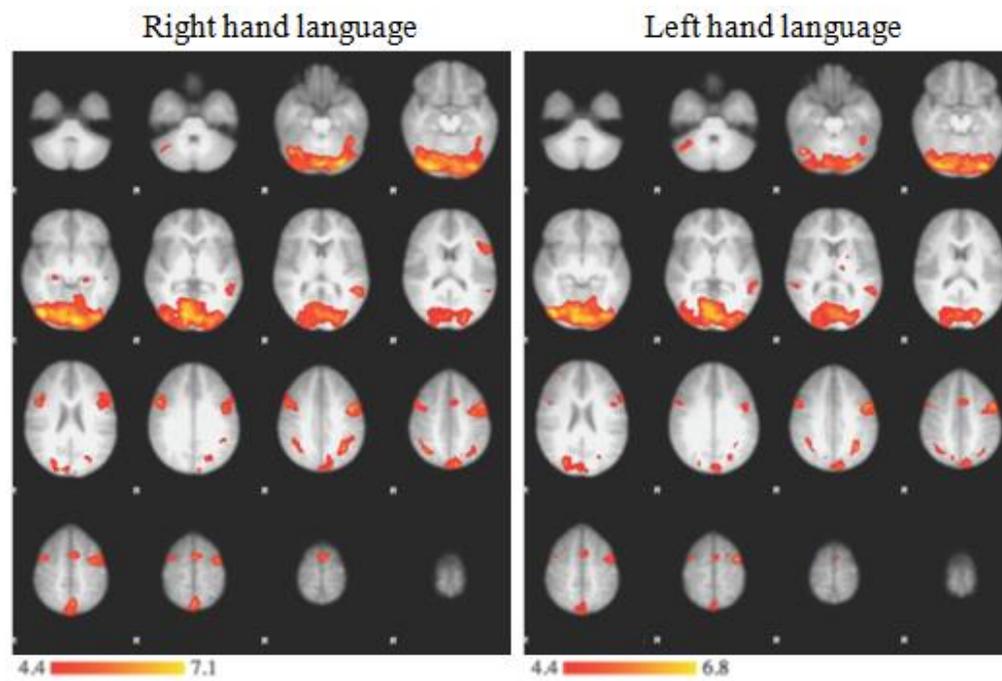


Figure 4. Whole brain analyses for each language condition vs. baseline (voxel corrected, $p < .05$)

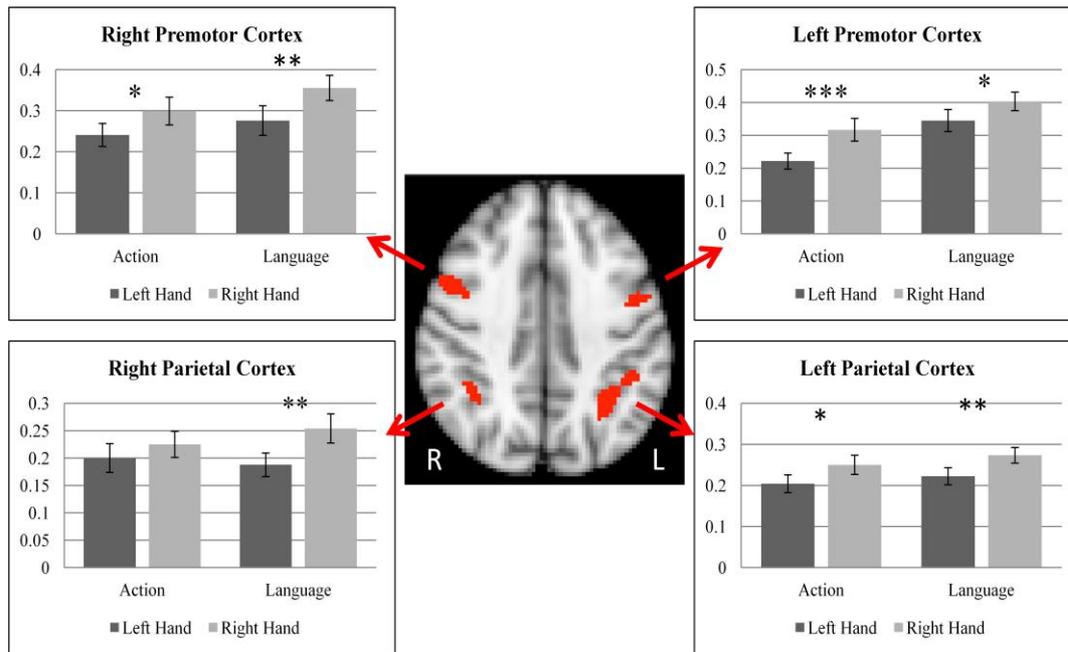


Figure 5. % signal change for right and left action performance/language in each of the general action planning ROIs (* $p < .05$, ** $p < .01$, *** $p < .001$; bars represent standard error).

3.3 Discussion

The study aimed to investigate the nature of the representations that are recruited by action language during comprehension, and to assess the extent to which we “simulate” the actions that we read about. Participants were asked to perform left and right hand button presses and read sentences that described the same left and right hand button presses. Hand-specific activity for the action and language task was then assessed within several carefully defined ROIs where action and language activity overlapped. By identifying ROIs that are either responsible for action planning or for action execution the type of representation that is shared by action and language could be assessed.

Language Activity in Action Execution Regions

Activity for left and right hand action sentences within regions that are responsible for the execution of actions was assessed. It was firstly predicted that if we accurately simulate the actions we read about, hand-specific contralateral activity

should occur in execution areas such as the primary motor cortex for action language in the same way that it does in action performance. This prediction was not supported, as although there was some overlap in activity more generally for action and language in the primary motor, parietal and medial regions, a contralateral pattern of activity for hand-specific actions was not seen in language as it was in action performance. This suggests that action language does not recruit these execution areas in a hand-specific way, and therefore that hand-specific information that is required for action language comprehension is not represented within execution areas.

Activity in Action Planning Regions

It was also predicted that if hand-specific information is represented in a more abstract and general way, then those areas that are responsible for action planning (including the premotor and parietal cortex) would display equivalent activation patterns in the action performance and action language task for left and right hand actions. Those regions of the premotor and parietal cortex that were more generally activated during action planning (irrespective of hand) were assessed for their hand-specific properties in the action language and performance tasks to see whether activation patterns matched for left/right hand actions. It was firstly predicted that there would be a dominant hand effect in action performance and this prediction was supported in all four general planning ROIs. This demonstrates that motor representations are highly influenced by action experience as suggested by many other studies (e.g., Beilock, et al., 2008; Buccino, Lui, et al., 2004; Calvo-Merino, et al., 2005). Furthermore, this dominant hand effect was also seen in the action language task whereby more activity was observed for right hand than left hand sentences. These results provide strong support for embodied cognition as not only do we more prominently represent the dominant than the non-dominant hand in action performance, but these hand-specific representations are also recruited in the same way when processing hand specific-action language. This suggests that action language recruits very detailed hand-specific action representations and supports the argument that we simulate the actions we read about using at least some of the same brain areas as we would use to perform the action.

So are participants fully re-enacting the action information when reading action language? It was predicted that if participants fully simulate the action that

they are reading about then both planning and execution regions would be activated in the same way during action performance and action language processing for hand-specific language. However, if on the other hand actions are only partially simulated then only certain action components would be engaged. As similar hand-specific patterns of activity were found only in areas involved in action planning, this suggests that when reading action language we do not fully activate all action components that are required for the performance of that action in order for comprehension to occur. Instead, only the activation of more abstract action representations that are stored in areas responsible for action planning are required for the performance of the action – we therefore only partially simulate the actions we read about.

What Type of Representation is recruited During Action Language Comprehension?

It is clear from the results that the planning ROIs are involved in processing hand-specific language information in the current experiment. However, what type of representation is housed in these planning areas and why is it required for action language comprehension? These planning regions are located more anteriorly (for the premotor region) and more posteriorly (for the parietal region) than the execution regions and are thought to represent information in a much more abstract and schematic way. Previous experiments have shown that the rostral PMd is less involved in action performance and is instead thought to play more of a cognitive role in action planning, as is active for higher order processing functions such as the formation of visuo-motor associations and response selection (Boussaoud, 2001; Johnson, et al., 1996; Picard & Strick, 2001; S. Simon, et al., 2002). Therefore, during the comprehension of a hand-specific action sentence, we activate representations that are very specific, but are at the same time fairly abstract and schematic in nature.

Language is itself a relatively abstract process as requires the mapping of arbitrary word forms onto action meaning. The comprehension of action language therefore relies upon the ability to map sensory input (in the form of a spoken or written word) onto specific information that is related to the action being described. From the evidence provided in the current experiment, this language-action mapping appears to take place in general action planning areas that are thought to play a role in more abstract cognitive processes. The meaning of language is therefore not

dependent on those structures that are required for the execution of an action, but instead relies upon higher-level association areas where action meaning is represented. In chapter 1, a distinction was made between the ventral and dorsal premotor cortex whereby the ventral premotor cortex is thought to be responsible for standard mappings between a physical object's dimensions and an appropriate action plan – no learning is required for this process to occur (Fogassi, et al., 1998; Fogassi & Luppino, 2005; Gallese, et al., 1996; Gallese, et al., 2002; Murata, et al., 2000; Rizzolatti, et al., 1996; Rizzolatti, et al., 2001; Rizzolatti & Luppino, 2001; Sakata, et al., 1995; Taira, et al., 1990). On the other hand the dorsal premotor cortex is responsible for matching arbitrary stimuli with action plans based upon learned associations (Chouinard, et al., 2005; Cisek & Kalaska, 2004; Johnson, et al., 1996). As action language is essentially an arbitrary stimuli that must be associated with its action meaning, then this may well explain why action language activates the dorsal premotor cortex. Furthermore, as the rostral PMd is thought to be responsible for higher level cognitive action functions such as the formation of visuo-motor associations than action performance itself, this may explain why language recruits specific information in this area, as it is itself a product of these visuo-motor associations.

Does Activity in General Planning Regions Really Reflect a Dominant Hand Effect?

Despite finding more activity in general planning regions for the right dominant than the left non-dominant hand, as only right-handed participants were tested in the current study the conclusion that this is an effect of the dominant hand is not as concrete as it could be. For example, if left handers were also to participate in this experiment the reverse effects within general planning regions would be predicted, whereby more activity for left hand actions and language than right hand actions and language would be found. This would certainly be an informative study, however, any experimental interpretation is complicated by the fact that many left handed individuals have experience of performing actions with their non-dominant right hand based on constraints imposed by society (e.g., handshakes are usually performed with the right hand). The current study therefore cannot rule out other reasons for this right hand effect, however, based on the extensive research that has shown that the premotor cortex is influenced by action experience it is possible that experience with the dominant hand is the cause.

Left Hemisphere Superiority for Action Language Processing

Interestingly, in the current experiment the amplitude of activity was no higher in the left hemisphere than the right hemisphere. This is surprising in light of data from other experiments (including the experiment described in chapter 2) where action language activity is more prominent in the left hemisphere. Some have suggested that left hemisphere activity in action language tasks is because often only unilateral dominant hand actions are described which may activate the contralateral left hemisphere (R. Willems, Hagoort, & Casasanto, 2010). The current experiment provides contrary evidence, as suggests that the dominant hand is better represented than the non-dominant hand in both the left *and* the right hemisphere within action planning areas therefore contradicting these previous findings. It would therefore seem from the current experiment, which included language relating to both left and right hand actions, that hand-specific information is represented much more bilaterally, and that previous findings of left hemisphere speciality is therefore unlikely to be due to language relating to the dominant hand.

Conclusion

The evidence provided by the current experiment suggests that we don't re-enact the actions that we read about in all the same brain areas as are required for the performance of the action. Only very particular action representations are recruited by action language – those involved in very abstract stages of action planning in the rostral PMd. However, this does not mean that we do not recruit detailed action information when reading action language, as the representations that are stored in these general planning regions are highly specific to the action that is performed in terms of the amplitude of activation. Therefore, embodied theories are partially correct in that in order to understand action language we activate some of the same hand-specific action representations that are also recruited for action performance, however, we do not accurately simulate the action as such throughout the motor system. Instead we partially re-enact the action requiring only representations stored within those regions involved in abstract action planning. Action language understanding is therefore somewhat removed from action performance as does not involve areas associated with action execution. It instead relies upon higher-level

cognitive regions that are capable of establishing sensorimotor associations in order to relate action language to its meaning.

One important issue has yet to be addressed by the experiments presented so far, in that the functional role of those regions that are commonly activated by action performance and action language has not been investigated. Despite the specific nature of the representations that language recruits, this does not necessarily mean that the representations are involved in the comprehension of the action language *per se*, they may instead reflect post-sentential processes such as imagery, or may even be related to some other function that is shared between action and language that is distinct from action semantics. To shed more light on the role of language induced motor activations, behavioural data is necessary to assess not only whether action and language interact with one another when they share certain features, but also whether these interactions occur during *only* the planning stage of the action as would be predicted by the present results. Experiments in the following chapters aim to address these issues.

Chapter 4

Interactions between Action and Language for Shared Weight Features: Explicit Weight Ratings of Object Words

4.1 Introduction

The fMRI experiments described so far in chapters 2 and 3 provide support for cognitive embodiment, whereby action language recruits very detailed action representations that are specific to the hand used (chapter 3) and are activated to a specific degree depending on the physical effort implied (chapter 2). These results suggest that during action language comprehension, very precise action information is accessed – the same specific information that is activated during the performance of that action.

Do Motor Activations Reflect Comprehension?

Evidence supporting the existence of shared neural representations for action and language has almost all been provided by fMRI (Boulenger, et al., 2008; Hauk, et al., 2004). Its high spatial resolution makes it a powerful tool, as it can reveal activity that is common across different tasks (such as action performance and action language) when they share specific features. However, despite showing that action language activates motor representations, it is difficult to conclude from these studies that this activity reflects comprehension of the action meaning of a sentence. It may be that semantic understanding requires other non-sensorimotor brain structures such as the temporal pole where there is evidence to suggest that amodal representations exist (e.g., Lambon Ralph, et al., 2009). If this is the case then the motor system activation may instead reflect post-comprehension processes such as imagery (Papeo, et al., 2009). Language induced motor activity could also reflect spurious and disorganised associative activity between actions and linguistic labels that are formed as a bi-product of learned Hebbian associations (Mahon & Caramazza, 2008). It is possible that this type of activity does not contribute to the understanding of language and that this meaning extraction occurs elsewhere.

One way to determine that motor activity is not due to post-comprehension processes is to show that it occurs early i.e., shortly after the onset of the stimulus

when comprehension occurs, rather than later once the meaning of language has already been extracted. MEG, a technique that measures the magnetic signals generated by populations of neurons on a millisecond by millisecond basis has been used to show rapid body-part specific motor activity in response to action language within 200ms (Pulvermuller, Hauk, et al., 2005). This suggests that we automatically recruit stored action representations when comprehending action language, and therefore suggests that any motor system activity is not caused by post-comprehension processes. However, conflicting results have been obtained using TMS; when measuring motor evoked potentials (MEPs) in the hand after motor cortex stimulation, enhanced MEPS were found for action compared to non-action verbs only when stimulation exceeded 500ms and not during earlier time points (170ms, 350ms) (Papeo, et al., 2009). This suggests that our recruitment of the motor system during language comprehension is relatively late and is therefore not involved in initial access to semantic meaning.

There is also evidence to suggest that motor activity does not reflect spurious action-language associations and actually relates to the comprehension of meaning. When the premotor cortex is stimulated, faster lexical decisions are observed for manual compared to non-manual verbs (R. M. Willems, et al., 2011). Additionally, when body-part specific regions of the motor cortex are stimulated lexical responses to words relating to the same body-part are faster than for other body-parts. As the activation of the motor system affects language processing, this suggests it is involved in understanding the meaning of words. Overall, the conflicting results demonstrate that the role of the motor system in the comprehension of action language is far from clear, further evidence is therefore required to determine whether or not the motor system plays an important role in action language comprehension.

Evidence for *behavioural* interactions between action performance and action language is an important and direct way of ascertaining whether this is the case. If language induced motor activations are simply a redundant bi-product of the comprehension process and are not involved in action language comprehension, then the performance of an action should not influence the comprehension of language and vice versa, therefore interactions between the two tasks would not be predicted. However, if motor activations are associated with the comprehension of action

language, then you would expect that the performance of an action would influence the comprehension of action language, and therefore interactions between the two tasks would be predicted. Any evidence for behavioural interactions can be taken together with findings from various other techniques such as fMRI, MEG and TMS, in order to locate the neural source of the interaction effect. Based upon previous evidence these interaction effects are likely to be generated from within the motor system where common activity for action and language has already been verified.

Behavioural Interactions between Action and Language

Previous studies have found evidence for behavioural interactions between action and perception when they share certain features (see Chapter 1 for a more detailed review). Importantly, perception can affect action planning/performance (Castiello, et al., 2002; Edwards, et al., 2003; Scorolli, Borghi, & Glenberg, 2009; M. Tucker & Ellis, 2004) and action planning/performance can affect perception (M. Brass, Bekkering, & Prinz, 2001; Craighero, et al., 2002; Craighero, et al., 1999; Craighero, Fadiga, Umiltà, & Rizzolatti, 1996; Hamilton, et al., 2004; Muesseler & Hommel, 1997; Wohlschläger, 1998, 2001; Zwickel, et al., 2007). More specifically interaction effects occur between action performance and action language comprehension when they share particular features such as direction (Glenberg & Kaschak, 2002; Taylor, et al., 2008; Taylor & Zwaan, 2008; Zwaan & Taylor, 2006), distance (Gentilucci & Gangitano, 1998; Gentilucci, et al., 2000), size (Gentilucci, et al., 2000; Glover & Dixon, 2002; Glover, et al., 2004), weight, (Scorolli, et al., 2009) and hand shape (Bub, et al., 2008; Klatzky, Pellegrino, McCloskey, & Doherty, 1989; Masson, Bub, & Newton-Taylor, 2008; Masson, Bub, & Warren, 2008). Furthermore, these interaction effects have even been found to occur very early in processing within 200ms (Boulenger, et al., 2006). This is evidence to suggest that action language is rapidly recruiting the same feature specific information that is also required for action performance.

Critically little attention has been focussed on interactions between action and language/perception tasks when they share physical effort information. This information is vital in order to establish whether the motor system plays a functional role in the comprehension of physical effort information conveyed via action sentences as is suggested by the fMRI data described in chapter 2. In one experiment, Hamilton, Wolpert and Frith (2004) investigated interactions between

action and perception when particular objects shared specific weight information. Weight is a feature that is strongly linked to physical effort as the heavier an object is the more physical effort is required from muscles when interacting with it. Participants were asked to lift a light box, a heavy box, or no box, and shortly after, while still performing the action, they observed videos of differently weighted boxes being lifted. The subsequent task was to judge the weight of the boxes in the videos. Compared to the no-lift trials participants were found to judge the same boxes as being lighter when they were concurrently lifting a heavy box and heavier when they were concurrently lifting a light box. As the performance of a weight specific action interfered with the perceived box weight this provides evidence that at some level there is functional overlap between the two tasks for shared weight information.

In a follow up study, using a very similar task, Hamilton and colleagues (2006) used fMRI to identify the brain locus of this bias effect. On an individual subject level a regression analysis was performed to find voxels where the magnitude of the psychophysical bias (as seen in the behavioural experiment) covaried with the magnitude of the BOLD response. Significant correlations arose in a network of motor and visual areas that have been implicated in processing action stimuli including the IFG, central sulcus, intraparietal sulcus and the extrastriate body area. As activity in the motor system correlates with the magnitude of the bias in weight judgement, this suggests that the motor system houses weight specific action representations that are recruited during the perception of object weight.

Evidence of shared representations for weight features has also been found between action performance and action *language* (Scorolli, et al., 2009). Participants heard an action sentence that described either lifting a light or a heavy object onto a table (e.g., “move the *pillow/tool chest* from the ground to the table”). Shortly after, they bimanually lifted either a light box (3kg) or a heavy box (12kg) onto a pedestal and answered a comprehension question related to the sentence. Action kinematics were measured to assess whether weight specific language influences the way in which the action was performed. It was found that the time taken for the hands to reach peak velocity when lifting a light box was longer after hearing a light object versus a heavy object sentence (20ms). The opposite result was found for the heavy box lifting condition where peak velocity of the hand was reached much more quickly for the light sentences than the heavy sentence (60ms). Therefore, when the

to-be-lifted box weight and the weight of the object in the sentence were compatible, the latency of the peak velocity was delayed compared to when the weights in the two tasks were dissimilar. These interference results suggest that action language recruits effort-specific action representations that are also required for the performance of an effort-specific action and therefore supports the functional role of the motor system in processing detailed action language.

Current Study

Despite demonstrating that there may be a functional role for motor representations in language comprehension, these described experiments had several shortcomings. Firstly, the results reported by Hamilton and colleagues (2004; 2006) were inconsistent. In contrast to the interference effect found in the first study (Hamilton, et al., 2004) where participants overestimated object weight when lifting a light box and underestimated object weight when lifting a heavy box, the bias in the follow up study (Hamilton, et al., 2006) varied from interference to facilitation across participants. The replicability of these results is therefore questionable and makes it difficult to make solid conclusions about the mechanisms that underlie these effects across different individuals in different experimental environments.

The results reported by Scrolli and colleagues (2009) were also weak as despite the statistical significance of the interaction between the weight of the box that was lifted and the weight of the object in the sentence, it was mainly driven by a difference between light and heavy sentences in the heavy box lifting condition. Less of a difference was seen between light and heavy sentences in the light box lifting condition as would be predicted. In addition, very few items were used in each sentence condition (6 heavy and 6 light object sentences) and across conditions the items were not adequately controlled for a number of factors that are known to affect reaction time such as lexical frequency and sound file length (e.g., Monsell, 1991). The results may also have been confused by the failure to control for the types of action the objects in each condition afforded. For example, it may have been that there was greater congruency and therefore different responses in the heavy object condition than the light object condition because the objects in the heavy object condition better afforded a bimanual action (which matches the action being performed) than a unimanual action and vice versa for the light object condition. Another uncontrolled factor was action experience. It has been shown

that the more experience we have of performing an action, the more the motor system is engaged when performing or perceiving that action (e.g., Beilock, et al., 2008; Buccino, Lui, et al., 2004; Calvo-Merino, et al., 2005). As we are interested in the shared representations for action and language it could be predicted that differential effects would be observed for those actions that are better experienced. Therefore, if the objects in each condition are *not* matched for experience then this may cause kinematic differences across the conditions. The current studies therefore tightly controlled these factors by extensively norming a large array of different objects on factors such as experience, typical lift type, lexical frequency and word length to rule out possible effects of these factors.

As only few studies have identified weight-specific language induced motor activity, and as it was felt that these previous experiments have several shortcomings, the current experiments aimed to further investigate these effort-specific language effects. Two different experimental designs that in the past have successfully identified interactions between action and language/perception were selected for use in the current investigation. The experimental design chosen for experiment 1 has previously been used to demonstrate effects between action and perception for weight features, but has not been used to show interactions between action and language. On the other hand, the design chosen for experiment 2 has previously been used to demonstrate effects between action and language but not for shared weight features. It was thought that the exploration of these two designs would give the best chance of capturing any interactions between action and language for weight.

4.2 Experiment 1

The design was based upon that of Hamilton and colleagues (2004) and therefore aimed to find the same behavioural bias effects for shared action features but between action and language as opposed to action and perception. Participants were asked to either lift a light or a heavy tube (LightLift or HeavyLift), or to grasp one of the tubes (as a control where no weight would be experienced) while listening to everyday object names that described either light or heavy items (LightObj or HeavyObj). While still performing the action, participants rated the weight of the object described in the language. The light and heavy object words were chosen so to be of a similar mean weight to the light and heavy tubes (as determined by extensive

pre-test questionnaires) in order to maximise the similarity/dissimilarity between the objects and the to-be-lifted tubes and to encourage large weight-specific effects.

The bias results found by Hamilton and colleagues (Hamilton, et al., 2004) were interpreted as interference and were explained using the MOSAIC model (Modular Selection and Identification for Control) (Wolpert & Kawato, 1998). This model assumes that the brain is made up of many modules (similar to “TEC’s feature codes: Hommel, et al., 2002) that represent different types of features. For example, it would predict that in the motor system we store weight-specific kinematic plans that are recruited in action performance and also in action perception/language, i.e., a representation specific to every possible weight that is likely to be encountered. When observing the actions of another individual a pattern of predictive activity is present across all weight specific modules with the most accurate module (i.e., the one closest to the true weight of the object) being the most strongly activated giving rise to the perception of the object’s weight. Once a specific weight module is used for a specific task such as lifting an object of a certain weight, it is then rendered temporarily unavailable for use by other tasks such as a weight judgement task. As a result the full set of modules cannot be used to predict the weight of a similarly weighted object, and the system relies upon the remaining less accurate weight modules to perform the task. For example, when a heavy box is lifted any subsequent prediction of observed box weight can only be made using the remaining less accurate “lighter” modules causing all boxes in the videos to be judged as lighter than they truly are and vice versa when lifting a light box.

If both action language comprehension and action performance recruit a common array of weight representations, then it is expected that performing an action on a light/heavy object will result in a interference driven bias in the weight perception of linguistically presented objects. It is therefore predicted that compared to a control condition (grasping only), when lifting a light tube weight judgements will be overestimated, and when lifting a heavy tube weight judgements will be underestimated irrespective of the weight of the object word. Therefore, the first dependent measure is the weight rating that is assigned to each object stimulus. This interaction between action and language may also manifest itself in the speed at which a weight judgement is made, whereby a weight match between action performance and action language may lead to interference that manifests itself in

slower reaction times compared to when there is no match. Therefore, the second dependent measure is the time (ms) it takes for the weight rating to be given. Light and heavy object word conditions were included in order to assess the possibility of these reaction time interaction effects. These findings would suggest that the motor system is necessary for understanding weight-related language and rule out the possibility that action language is understood using amodal mechanisms.

4.2.1 Method

Participants

54 York University students took part in the experiment (43 female, mean age 21.2, age range 18-50). They were recruited via the York University Psychology Electronic Experiment Booking System and were rewarded with £2 or ½ hour course credit. To ensure that all object words were familiar, only native English speaking participants were recruited. Only right handed individuals were included and the extent to their handedness was tested using an adapted version of the Edinburgh Handedness Inventory (Oldfield, 1971). This questionnaire confirmed that participants were right handed (average score 91.7, where anything above 40 is an indication of right handedness). Evidence suggests that the prevalence of having atypical language lateralisation is higher in left than right-handed individuals (e.g., Pujol, Deus, Losilla, & Capdevila, 1999). As it is unknown how factors like hemispheric language dominance affect the interactions between action and language, only right-handed participants were recruited in this study. Participants had corrected or corrected to normal vision and provided informed consent.

Stimuli

Stimuli were created from a series of pre-test questionnaires where 143 everyday objects were rated for different semantic properties (see descriptions of questionnaires below?). All items in the questionnaire were everyday highly familiar objects that afford a whole hand grasp. From these questionnaires, 18 items were chosen for inclusion in a light object (LightObj) and a heavy object condition (HeavyObj) (see Figure 1). The stimuli in each group differed in their perceived weight but were matched on several other factors such as experience, length (ms, no.

characters), and log frequency (see Figure 1), t-tests indicated that the two conditions were not significantly different for these variables ($p > .05$).

	Light condition	Heavy condition
Stimuli	Soft sponge	Iron
	Ping pong ball	Unfilled suitcase
	White envelope	Wok
	Pair of dice	Hardback book
	Ruler	Leather coat
	Box of matches	Paperweight
	Yellow duster	Bag of sugar
	Twig	Carton of milk
	Wooden spoon	Phone book
	Bag of crisps	Wine bottle
	Lightbulb	Bag of flour
	Toilet roll	Spade
	Chocolate bar	Bottle of lemonade
	Frisbee	Champagne bottle
	Paintbrush	Hammer
	Ripe banana	Filled kettle
	Box of tissues	Full jug
Apple	Brick	
Mean weight in grams (sd)	90.37 (52.00)	594.81 (155.30)
Mean experience rating (sd)	4.16 (1.34)	4.81 (1.43)
Size (sd)	2.06 (0.56)	4.02 (0.87)
Mean stimulus length in ms (sd)	949 (215)	938 (251)
Mean no. characters	10.56 (4.51)	10.67 (3.34)
Mean log freq 1st position (sd)	4.15 (0.53)	3.99 (0.81)
Mean log freq 2nd position (sd)	3.51 (0.84)	3.77 (0.78)

Figure 1. Experiment 1: Stimulus details. Mean values (and standard deviation) for weight rating, experience rating, size, stimulus length (ms), number of words, character length and the log frequency at the first and the second position for each condition.

Weight questionnaire. The purpose of the weight questionnaire was to obtain accurate measures of the perceived weight of different objects. 15 independent participants (10 female, mean age 20, range 18-21) matched the weight of each object to the weight of one of nine visibly identical cardboard tubes (length 300mm, diameter 63mm) that ranged in weight from 100-1400g (100g, 200g, 300g, 400g, 600g, 800g, 1000g, 1200g, 1400g). These reference tubes were numbered from 1-9 with the lightest being tube 1 and the heaviest being tube 9. During the questionnaire the participants were free to handle the tubes as much as was required for them to make an accurate weight judgement. This tube task was used to get accurate weight judgements without participants having to have explicit knowledge about different units of weight. Participants were asked to imagine picking up the object with their dominant hand and to indicate: “Which tube best matches the weight of the object?”. They made a response from 1-9 on a keyboard and also had the option of saying that the object was “heavier than tube 9” or “lighter than tube 1”. The rating values were then converted into grams.

The ratings obtained in each questionnaire were used to choose the experimental items for the two weight conditions (see Figure 1). Any objects that were rated as being heavier than tube 9 by more than half the participants were instantly excluded as the precise weight of these objects could not be determined. 18 objects were selected for each weight condition, the average rating for the light condition was around 100g and the average weight rating for the heavy condition was around 600g. T-tests demonstrated that weight ratings of objects in the light condition were rated as being significantly lighter than the objects in the heavy condition, $t(34) = -20.27, p < .001$.

Experience questionnaire. The same participants who carried out the weight questionnaire also carried out the experience questionnaire and rated how often they physically pick up each of the questionnaire objects. For each object they were asked the question: “How often do you physically pick up this object?” and gave one of seven answers: “More than once a day”, “Once a day”, “More than once a week”, “Once a week”, “Once a month”, “A few times a year”, or “Never”. It is known that experience of interacting with different objects can influence the strength of the motor representation for that action (Calvo-Merino, et al., 2005; Cross, et al., 2006; Haslinger, et al., 2005; Kiefer, et al., 2007). Any behavioural interaction between

the action task and the language task may depend somewhat upon participants having a motor representation associated with each of the objects that has been generated via experience. Therefore, it is important that all objects chosen for the study are objects that participants are likely to have physical experience with. For the same reason it is important that experience is matched between the two conditions as otherwise this may cause a greater interaction in one condition compared to the other.

The ratings obtained in each questionnaire were used to choose the experimental items for the two conditions. Any items that were rated as never being picked up by more than half of the participants were instantly excluded, and only objects that most individuals were likely to have been picked up at least once a year were further considered. A Mann-Whitney test showed that the differences in experience ratings were not different across the two conditions ($U=203.5, p>.05$)

Hand questionnaire. The purpose of the hand questionnaire was to identify how people usually pick up different objects. 16 right-handed participants (11 female, mean age 25.6, age range 19-54) rated whether they would use one hand only (dominant right), both hands only or *either* one or both hands to pick up each object. As hand-specific motor representations have previously been observed (see chapter 3), it may be that different objects are associated either with unilateral dominant hand actions or bilateral actions based on their properties. As in the current experiment participants are expected to perform tube lifting with their dominant right hand only, the object stimuli were included only if they too were rated as affording a unilateral dominant hand action in order to maximise the chances of the same specific representation being recruited in the action and language task. Items that were rated as affording a bilateral hand lift only were instantly excluded from the further consideration.

Size questionnaire. The same participants who carried out the hand questionnaire also carried out the size questionnaire and rated how big each of the questionnaire objects were on a scale of 1-7 (where 1 is very small and 7 is very big). The purpose of this questionnaire was to match the items in the weight conditions for size to ensure that it did not influence weight judgements. Unfortunately the conditions could not be matched for size ($t(34) = -8.06, p < .001$)

due to its strong correlation with weight. Any implications of this confound on the results will be discussed later.

Further stimulus matching. Stimuli across the two conditions were also matched on a number of other variables. Firstly, there was no significant difference in the length of the stimulus sound files ($t(34) = 0.14, p > .05$), therefore differences in reaction time could not be accounted for by the time taken for the sentence to unfold. The stimuli were made up of either one or two words therefore, to keep the two conditions as similar as possible, the average number of characters was kept the same for the light and heavy conditions ($t(34) = -.084, p > .05$). The log frequency of the words in both the first position and the second position was matched for the two conditions (Cobuild Corpus: 20 million words). Here any single word object names were classed as being at the second position. At the first position (for example “unfilled” in “unfilled suitcase”) there was no difference between the log frequency of words in the light condition and the heavy condition, ($t(22) = 0.59, p > .05$). Similarly at the second position (for example “suitcase” in “unfilled suitcase”), there was no difference between the log frequency of words in the light condition and the heavy condition, ($t(34) = -0.94, p > .05$). These linguistic factors therefore could not account for any differences between the two conditions.

Procedure

Participants were seated directly in front of a computer monitor (Screen type: Sharp, Screen size: 17”, screen resolution: 1280 x 1024) on which the experiment was presented using E-Prime (Version 1.0, Psychology Software Tools). See Figure 2 for a complete diagram of the apparatus layout. Before the start of the experiment participants were instructed to lift each of the 10 numbered tubes that were positioned on their right and to try to remember the weight of each one (with “Tube 1” being the lightest and “Tube 10” being the heaviest). After this point all tubes were removed except for tubes weighing 100g and 600g which were placed in front of the starting position. The numbers from these tubes were removed and replaced with colours (light tube: blue, heavy tube: green) so their weight could not be referred to by participants when rating the target object words. Colours were chosen as alternatives to letters or numbers as it was thought their serial scale could interfere with the rating task. The right/left position of the light and heavy tubes was

counterbalanced across participants to counteract any kinematic differences associated with lifting tubes that are positioned differently relative to the body.

Participants began each experimental trial by placing their right hand on the starting position. Before each trial they received a “ready” cue and were asked to press the spacebar with their left hand to continue. A written action command was then presented on the screen for 5 seconds (font style: Arial Bold, font size: 20). The action command instructed participants to either lift or grasp the blue tube or the green tube with their right hand. In the lifting trials participants were required to lift the tube approximately 5cm and in the grasping trials they were required to perform a whole hand grasp of the tube with no lifting. After the 5 s instruction period, the screen went blank and while still performing the action an object word was heard over headphones (Beyerdynamic DT 770). See Figure 3 for a diagram of this procedure. The sound files were recorded by a native speaker of English with what was judged to be a neutral accent. All files were two channel with a sample rate of 44,100kHz and a volume of 2.16dB (5.4dB at 40% volume).

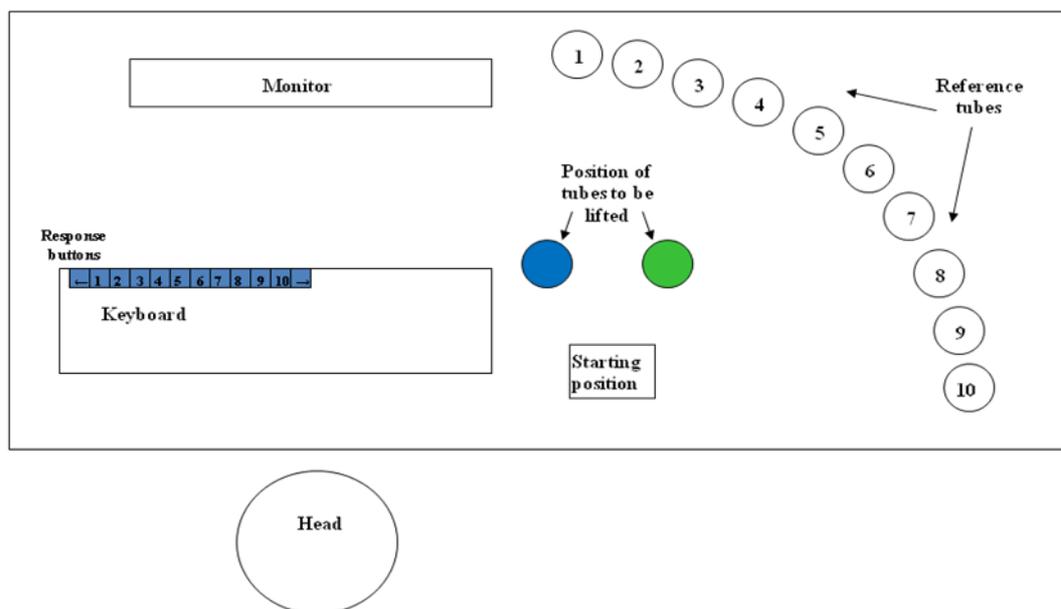


Figure 2. Experiment 1: Apparatus.

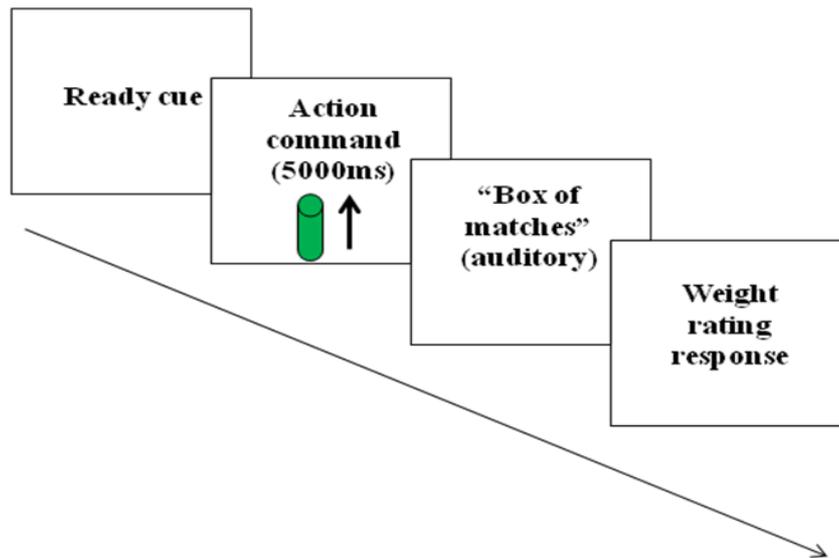


Figure 3. Experiment 1: Procedure. Arrow indicates the passage of time.

Using their left hand, participants were instructed to rate the weight of the object as quickly and as accurately as possible after hearing the object name using the numbered keys on the keyboard (1-10) referring back to the 10 weighted tubes that were presented at the beginning of the experiment. Participants could also rate the objects as being lighter than tube 1 or heavier than tube 10. Importantly participants continued to perform the action with their right hand until they had made their weight judgement (with their left hand) to maximise any influence the object weight would have on the weight judgement. They were then told to return their hand to the starting position. This end cue was on the screen for 4 seconds before the next ready cue appeared. Before the start of the experiment, participants were given 9 practice trials for each tube weight firstly to ensure that they were performing the actions correctly and secondly to give them the chance to experience the weight of the tubes so they knew what to expect.

Design

The experiment has a 2 (object weight: heavy, light) x 3 (action type: grasp, light lift, heavy lift) repeated measures design. There were 36 trials in the experiment made up of 6 light tube grasps, 6 heavy tube grasps, 12 light tube lifts and 12 heavy tube lifts. So that each participant heard each of the 36 object names only once, three lists were created so that each object would be paired with a different action command in each list (either grasp, lift light or lift heavy). For example

“paperweight” was paired with a grasp in List A, a light lift in List B and a heavy lift in List C. Participants would then be randomly assigned to one of these lists. The stimuli paired with their predefined action command were presented in a random order within each run to eliminate any effects that may be due to order of presentation.

4.2.2 Results

6 participants were excluded from the analysis; 5 participants failed to follow task instructions for example by not performing the actions correctly or for prematurely releasing their grasp/lift of the boxes before performing the weight judgement and 1 participant was removed due to experimenter error.

Weight Ratings

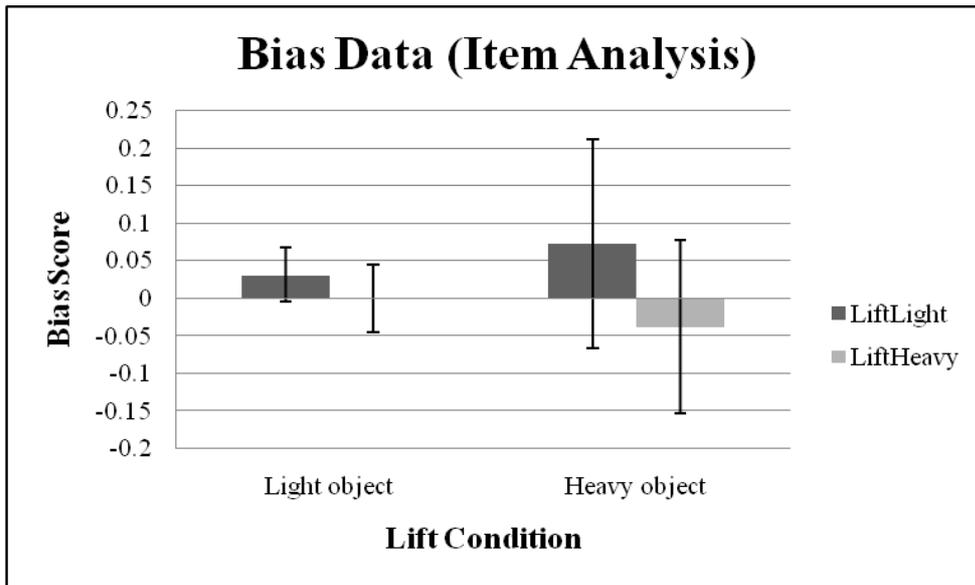
The weight judgement bias was calculated to identify whether there was an under/overestimation of the weight of the objects depending on the weight of the tube that was lifted. For each individual object word (HeavyObj or LightObj), a bias score was created by subtracting the weight rating given when a tube was simply grasped from when a light tube (LightLift) or heavy tube (HeavyLift) were lifted. Therefore, positive bias scores should indicate an overestimation and negative bias scores should indicate an underestimation. It was predicted that when lifting a heavy tube, weight ratings would be underestimated and when lifting a light tube, weight ratings would be overestimated compared to when the tube was simply grasped (control condition). As participants saw items only once and did not experience the same items in both lifting and grasping conditions the average rating across participants for each item when in the grasping condition was used in the subtraction.

When entering the bias scores into an independent ANOVA with item as a random factor no significant main effect of action condition ($F(1, 68) = .21, p > .05$), no significant main effect of object condition ($F(1, 68) = 0, p > .05$), and no interaction between the two factors ($F(1, 68) = .066, p > .05$) was found. Similarly, with subjects as a random factor, a repeated measures ANOVA revealed that there was no effect of action condition ($F(1, 47) = 1.26, p > .05$), no effect of object condition ($F(1, 47) = 0, p > .05$), and no interaction between the two factors ($F(1, 47) = .282, p > .05$). Therefore, the bias scores were no different between the

LightLift and HeavyLift action condition for either light or heavy object stimuli. Therefore, contrary to the predictions, when compared to the grasping condition (where no bias was predicted), the ratings given to the items did not differ depending on whether a light or a heavy box was being lifted (see Figure 4a and 4b for condition means).

One potential concern with these analyses was that a bias may have occurred in the grasping control condition meaning that these ratings may not represent a true baseline rating of object weight. Even though grasping does not entail lifting the light and heavy tubes, the objects being grasped are still of a known weight. This weight-related semantic knowledge may have been activated to a high enough degree to interfere with perceptual weight judgement and bias their responses. Consequently this may have led to less detectable differences between the ratings in the grasping and lifting conditions. This may be expected in light of the small bias effect in the passive condition in study by Hamilton and colleagues (Hamilton, et al., 2004) where simply having an object of a certain weight placed on the hand without any actual action performance caused a slight bias in weight judgements. Therefore, the same analysis was conducted but this time the control ratings were taken from weight pre-test questionnaires where no actions were performed (albeit with different participants). As the same null results were found, this indicates that weight ratings are not affected by the simultaneous performance of a weight specific action.

a).



b)

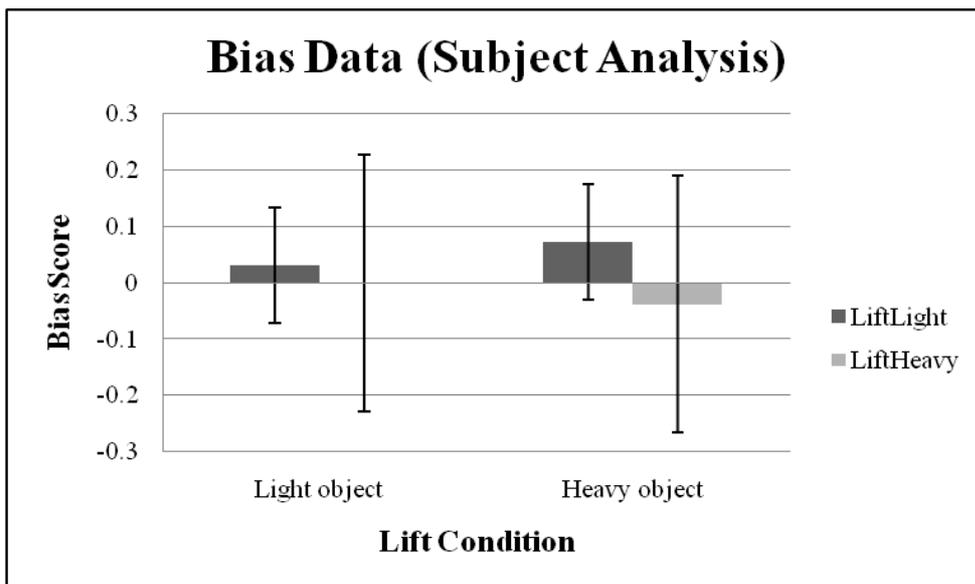


Figure 4. Experiment 1: Mean bias scores. Comparison of the item ratings from each of the lifting conditions and the average item ratings from the grasp condition (bars represent standard errors) with item (a) and subject (b) as a random factor.

Reaction Time Data

The time taken to perform each weight rating was recorded. Although the length of the sound files did not differ on average across the LightObj and HeavyObj condition, to further reduce noise in the response times the length of each sound file was subtracted from the overall response time (as measured from the onset of the sound file). Trials were labelled as outliers and removed if they were ± 2.5 standard deviations from a subject's condition mean (separately for the grasp, light and heavy lift conditions) resulting in the removal of 0.46% of the data. To account for the positive skew that is often seen in reaction time data, all reaction times were log transformed and statistical analyses were conducted on these altered values (however all graphs report reaction time data in ms). The average time to make a weight rating judgement was 2227s.

An independent ANOVA with item as a random factor found a main effect of action type ($F(2, 102) = 3.74, p < .05$). Post hoc tests (with Bonferroni correction applied) showed that judgement times were significantly longer in the grasp condition than in the HeavyLift condition ($p < .05$), however there were no significant differences between the LightLift and HeavyLift conditions or between the LightLift and Grasp conditions. There was also a main effect of object type ($F(1, 102) = 72.48, p < .001$) where reaction times were significantly longer when making a weight judgement in the HeavyObj condition than the LightObj condition. No significant interactions were present between the action and object factors ($F(2, 108) = .002, p < .05$) indicating that judgement times for object weight were unaffected by the weight of the tube that was being lifted. See Figure 5a for a graph of the results.

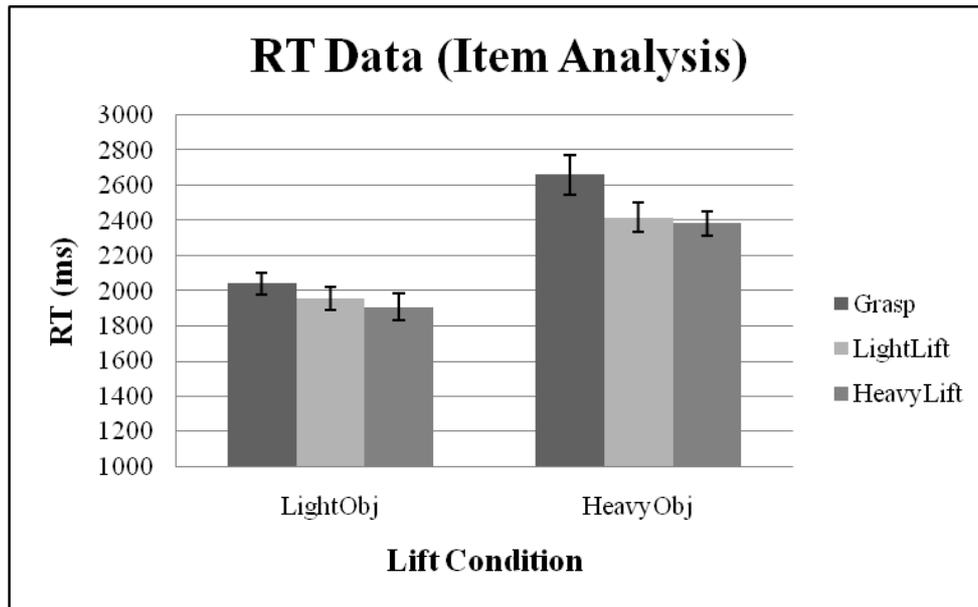
In a repeated measures ANOVA with subject as a random factor a significant main effect of action was found ($F(1.69, 79.46) = 8.64, p < .005$). Maunchley's test indicated that the assumption of sphericity had been violated for the main effect of action ($\chi^2(2) = 9.30, p < .05$). Therefore, in the analysis the degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity ($\epsilon = .85$). Post hoc tests (with Bonferroni correction applied) show that reaction times in the grasp condition were significantly longer than in the LightLift condition ($p < .05$) and in the HeavyLift condition ($p < .005$). However, there were no differences between reaction times in the LightLift and the HeavyLift condition. In everyday life, it is

very rare that we grasp objects without simultaneously lifting them; therefore it is possible that the grasping trials may have been less natural than the lifting trials, causing participants to be distracted from the weight judgment task and to respond more slowly.

There was also a significant main effect of object condition ($F(1, 47) = 95.4, p < .001$). This is due to reaction times being significantly longer in the HeavyObj than in the LightObj condition. This may have been due to the variation of objects included in each condition as the weight ratings given to the light objects (SD: 1.20) in the pretest questionnaire were much less variable than the weight ratings given to heavy objects (SD: 2.35). The heavy object condition therefore contained items that were spread over a larger weight range than the items in the light object condition. This may have made the weight of “heavy” objects less predictable than the weight of light objects resulting in a harder judgement decision and longer reaction times.

Importantly, no significant interaction was found between the action and the object condition ($F(2, 94) = 1.48, p > .05$) indicating that the reaction times for weight judgements were unaffected by the weight of the tube that was being lifted. Figure 5b for a graph of the results.

a).



b).

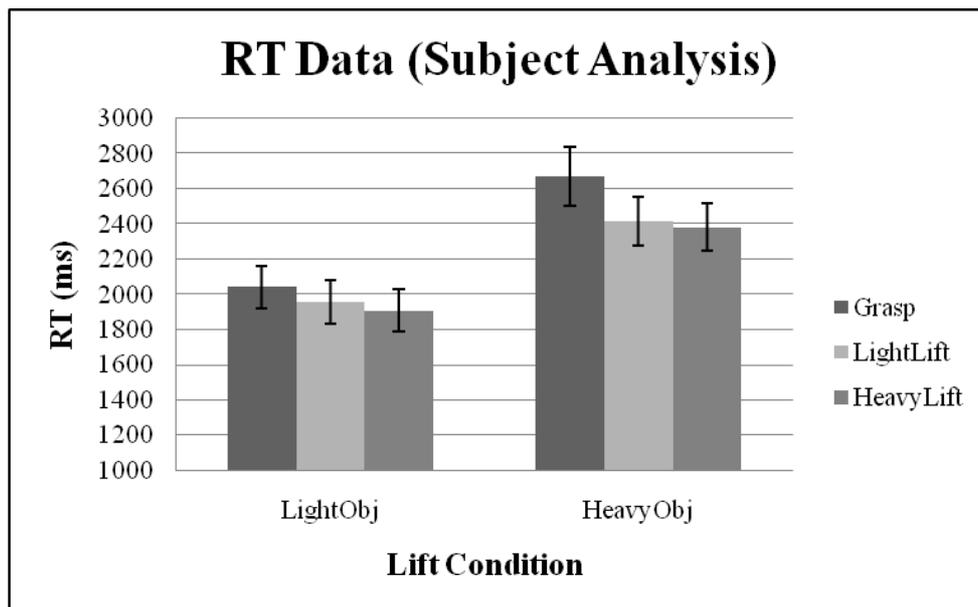


Figure 5. Experiment 1: Mean response times: With item (a) and subject (b) as a random factor (bars represent standard error).

4.2.3 Discussion

The current experiment aimed to replicate effects found by Hamilton and colleagues (2004) whereby performing a weight-specific action interfered with subsequent perceptual weight judgements. However, rather than conveying weight information via videos, weight information was conveyed via language in the form of object words. Participants were instructed to lift either light or heavy tubes while rating the weight of objects that were themselves light or heavy. Both the weight rating and the time taken to make the weight judgement were collected for light and heavy object words and were compared across the heavy lifting, light lifting and control grasping conditions. The data was then analysed to assess whether the weight of the lifted tube influenced weight judgements in any way.

Hamilton and colleagues (2004) found that irrespective of the weight of the object, participants overestimated the weight of objects when concurrently lifting a light object and underestimated the weight of objects when concurrently lifting a heavy object. The same over/underestimations were predicted in the current experiment for the heavy and light tube lifting conditions. However, no bias in weight ratings (compared to grasping) was found for the lifting conditions and consequently no difference in the bias between the light and heavy lifting conditions was found. Therefore, neither the action type (grasping vs. lifting) nor the tube weight (LightLift vs. HeavyLift) had any influence on weight ratings.

Secondly, it was predicted that any influence of the tube weight on weight ratings may manifest itself in the time it takes to judge the weight rather than in accuracy. Longer reaction times may reflect more difficult decisions which themselves may be caused by interference of the lifted tube weight. Despite finding main effects for the object and action conditions, the lack of statistical interaction between the weight of the tube and the weight of the object demonstrates that the time to make a judgement for a particular object was the same irrespective of whether a heavy or light tube was concurrently being lifted. Therefore, in contrast to the study by Hamilton and colleagues (2004) the weight of the lifted object had no influence upon the perceived weight of the objects as presented via action language. This suggests that when object information is presented via language, the weight of an object that is concurrently lifted has no effect upon weight judgements.

There are several methodological reasons why action performance may not influence the weight ratings of these language stimuli. Firstly, it could be argued that the single word stimuli did not provide enough action context in comparison to the action videos used in the original study (Hamilton, et al., 2004). This may have resulted in less activation of weight specific information and therefore less interaction with the action performance task. However, the explicit nature of the weight rating task meant that participants were already actively encouraged to access object-specific weight

Secondly, the null result may have been due to the nature of the representation that was recruited in this task. The representation of the weight of an object can also involve visual information as well as action information for example size is a good indicator of weight. Therefore, it may be that the weight judgements of the linguistically presented stimuli may be performed using the visual system (a non-action system) rather than the action system alone. As was mentioned above, the size of the object stimuli could not be controlled in that the heavy objects were always rated as being larger than the light objects. Weight judgements may therefore have primarily relied upon visual representations i.e., on hearing the object word the size information contained in visual imagery may have been recruited. This is unlike the original study (Hamilton, et al., 2004) where the boxes were of a uniform size, meaning that the weight judgement would rely much more upon the motor system where information about the action kinematics for differently weighted objects is stored. Therefore, weight-specific action representations may have been recruited to a higher degree in the original study than in the current study, leading to stronger action-perception interactions. However, certain stimuli were included in the current experiment that did not fit this pattern for example “paperweight”, an object that is small but also heavy and “frisbee”, an object that is large but relatively light. The time taken to judge the weight of these anomalous objects (e.g., “paperweight” average RT = 2412.65ms) was very similar to the time taken to judge the other objects (average 2228.41ms, SD 328.51ms) suggesting that a visual strategy based upon size information was not utilised as there was no time penalty.

The null result may also have been due to the timing of events in the design. Results from the planning experiment described in chapter 3 and several other behavioural studies (Bub, et al., 2008; Glover & Dixon, 2002; Glover, et al., 2004)

have suggested that action language recruits action representations that are also recruited during action *planning*. Furthermore, the premotor and parietal cortex, regions implicated in action planning processes, are often found to be active during action language comprehension (e.g., Hauk, et al., 2004; Tettamanti, et al., 2005). This is compatible with findings from the study by Hamilton and colleagues (2004) where the onset of the video and the onset of the box lift coincided temporally in the task design, therefore the interaction could well have occurred during the time at which the action was planned. In contrast, in the present study participants were given the action command 5.5 s before they were required to perform the action (in order to simplify the design and allow the collection of reaction time data), therefore by the time the stimulus word was heard, the planning stage of the action had already occurred. Many experiments have used designs where the action cue and the language are *not* presented simultaneously (e.g., Glenberg & Kaschak, 2002; Masson, Bub, & Newton-Taylor, 2008; Zwaan & Taylor, 2006), however they still occur close enough in time for the action planning to overlap with the language – this is especially so in studies where the language meaning determines what action must be planned and performed as the semantic information must be kept in mind while the action is chosen and planned. Therefore when there is a long delay between the language and the action cue as in the current experiment, these interaction effects may disappear.

Certain aspects of the task may also have been problematic in the current experiment Firstly, the task is fairly complicated as participants are asked to coordinate tasks using both hands as well as choosing from a possible 12 response options. Furthermore, participants had to retain the memory of the reference tube weights (that they had the opportunity to lift at the beginning of the experiment). It may have been that the weight judgement itself was made very quickly, however, the time taken to locate and press the chosen response button may have masked any subtle differences in reaction time across conditions. In addition any effects in the bias may have been eradicated by participants forgetting the weight of the objects at the beginning of the experiment. The weight ratings may therefore have become much more inaccurate as the experiment progressed, adding noise to any existing small bias effects. Furthermore, as participants rated each object word only once, for each item there was no within subject comparison for the LightLift, HeavyLift and

grasp conditions which may have compromised the experimental power. The cross participant variability in responses may therefore have introduced more noise and may have hidden any interaction effects.

In conclusion, it was found that unlike previous experiments that have identified weight-specific interactions between action and language/perception, in the current experiment the weight experienced in action performance did not interfere with either the time taken to make a weight rating or with the weight value that was assigned to the objects. This null result therefore, supports the proposition that we understand action meaning via amodal systems and that the activation of the motor system is not required for action language understanding. However, it may be that the current design is not be as suitable for assessing the interaction between action and language as it is for assessing the interaction between action and perception, therefore a more suitable design that has already been found to be sensitive to shared properties between action language and performance may be required. Experiment 2 aims to address this point by employing a different experimental design that has previously revealed interactions between action and language. This experimental design also overlaps the time at which the action language was presented with the time at which the action planning occurs to assess whether the lack of overlap in the current design led to the null results.

Experiment 2

Experimental Design

The experiment uses a simpler experimental design that was used by Bub and colleagues (2008) to investigate the effects of grip-specific action language on the performance of a congruent/incongruent grip action. As this design was successful in eliciting reliable automatic interaction effects between action and *language* for an action feature it was adapted for use in the present study to investigate the effect that weight-specific action language has on the performance of weight congruent/incongruent actions.

Isolating Action Planning

A methodological problem suffered by experiment 1 concerned the relative timing of the action cue and the language onset. The presentation of language stimuli did not overlap with the action planning phase of the action that was performed, therefore, if this is the crucial phase where interactions between action and language are likely to exist, this lack of temporal overlap may have contributed to the null effect that was found. The current experiment therefore aimed to present the language and the action cue simultaneously and to separately assess any effects of action language on action planning and action execution separately. Two dependent measures were recorded: the time it takes to process the sentence meaning and plan the movement towards the tube (planning time), and the time taken to lift the tube after the initiation of the movement (lift time). In this stroop-like design, participants are presented with both the action language and the action cue (text colour relating to either the heavy or light tube) simultaneously, therefore, they must plan the action that they are to perform while they are processing and memorising the sentence meaning. This means that the semantic information conveyed by the sentence can directly interact with the planning and early stages of the action where interactions are expected to occur. Any effects at the lifting stage of the action would provide evidence that language semantics not only influence early planning stages but also the post-planning online control stages of action execution.

Automatic Effects

In contrast to experiment 1, the current experimental design included a more implicit task. Rather than being asked to explicitly rate the weight of the object in the language, participants were simply asked to read the sentence and lift the appropriate tube according to the text colour. This design therefore assesses the automatic nature of access to the weight representations of the object stimuli. If, as embodied cognition would predict, we automatically activate the action properties of the object words we read, then participants should activate the weight features even in an implicit task where they are not required to make an explicit weight judgement. Any resulting behavioural interactions will therefore indicate that we automatically access the weight features of object words even when we are not required to. The results of the effort experiment (Chapter 2) support automatic effects as the activity

of the motor system was modulated by the implied effort content of the sentence when simple non-effort related comprehension questions were answered. Furthermore, several behavioural experiments have shown action-language interactions for tasks that are unrelated to the feature that is being manipulated (e.g., Bub, et al., 2008; Glenberg & Kaschak, 2002; Taylor & Zwaan, 2008).

Rather than using a completely implicit passive reading task, it was decided to include occasional comprehension questions (that did not relate to the object's weight), firstly so that we could measure participant's attention, and secondly because some degree of processing is thought to be required in order to elicit interaction effects as shown by Bub and colleagues (2008). They found no effect of congruency when presenting coloured words in a passive reading task, however did find effects after the addition of a lexical decision response. They concluded that the words alone "fail to provide adequate context for gesture representations to be evoked", therefore in the current experiment the comprehension questions were added to provide this "adequate context". Although not completely implicit as participants are still required to perform a task (sentence comprehension), this experimental design would give some indication as to the contribution that the implicit/explicit nature of the task makes to embodied effects.

Sentential Context

Single words have been shown to elicit motor activation in several previous studies (Boronat, et al., 2005; Hauk, et al., 2004; Lewis, 2006; J. A. Phillips, Humphreys, Noppeney, & Price, 2002) and to interact with the performance of actions when the action and the object share certain features (Bub, et al., 2008; Gentilucci & Gangitano, 1998; Gentilucci, et al., 2000; Glover & Dixon, 2002; Glover, et al., 2004) even when embedded within a non-action sentence (such as "John thought about the calculator": Masson, Bub, & Warren, 2008; Myung, Blumstein, & Sedivy, 2006; M. Tucker & Ellis, 2004). This indicates that despite the lack of action context, the action properties of the single word stimuli are still accessed thereby supporting proponents of embodied cognition that have stressed the importance of automatic effects in language comprehension (Boulenger, et al., 2006; Pulvermuller, Shtyrov, et al., 2005).

However, the activation of a word's motor representation is also thought to be modulated by sentential context (Rueschemeyer, Lindemann, van Elk, &

Bekkering, 2009). It is a well established fact that when reading a sentence, we integrate the meaning of all the words in the sentence to come to an interpretation, and that this happens online in an incremental manner (Altmann & Kamide, 1999; Kamide, Altmann, & Haywood, 2003). Furthermore, several studies have shown that action sentences activate the motor system (Desai, et al., 2009; Tettamanti, et al., 2005) and interfere with action performance for shared action features (Klatzky, et al., 1989; Scorolli, et al., 2009; Taylor, et al., 2008; Taylor & Zwaan, 2008; Zwaan & Taylor, 2006). Evidence that the sentential context *does* modulate a word's active semantic features comes from the fMRI effort results (Chapter 2) whereby a stronger BOLD response was found for action compared to non-action sentences in the premotor and parietal cortex for the same objects.

Therefore, unlike in experiment 1 where single object words were presented, in the current experiment the object words were embedded within both action sentences (e.g., "I am picking up the champagne bottle") and non-action sentences (e.g., "I have forgotten the champagne bottle"). Comparing the effects across the action and non-action conditions can provide evidence as to the benefit of the action vs. non-action sentential context in the activation of object-action features such as weight. It was thought that if a word's context influences the degree to which the action relevant properties are accessed then interaction effects should be more readily seen when the object words are given an action context. This would provide evidence that the activation of weight-specific information is modulated by the degree to which attention is directed to the action features of the object. However, if comparable interaction effects are found in both the action and non-action context then this would suggest that the weight features of objects are automatically simulated irrespective of context.

Predictions

If the weight features of object words are automatically activated and if activation of the motor system is required for the comprehension of action language, it is predicted that there will be a reaction time interaction between the weight of the object in the sentence and the weight of the tube to be lifted. This interaction can manifest itself in two ways, firstly as a facilitation effect where reaction times are faster when the weight of the tube and the weight of the object in the sentence are congruent compared to incongruent, or secondly as interference where reaction times

are slower when the weight of the tube and the weight of the object in the sentence are congruent compared to incongruent. Furthermore, if the sentential context within which each object word is embedded influences the properties of the objects that are automatically accessed, it can be predicted that features relating to action such as weight will be less activated when object words are embedded within non-action sentences compared to action sentences. If this is the case then it can be predicted that any interaction effects between action and language for shared features will be greater for the action compared to the non-action context.

Predictions can also be made about when any interaction effects will occur. If it is the early planning and action stages that are influenced by language semantics as has been suggested in the literature, then it can be predicted that effects will be apparent during the planning time. However, if later stages of the action are affected by the sentence meaning, then it can be predicted that the effects will be visible in the lift times. There is also the possibility that language can influence both stages of the action especially as access to the action planning information may be maintained during the online control of the action. The dependent measures in this experiment are therefore the planning time (the time taken to plan and initiate the action by releasing the start key) and the lift time (the time that elapses between the release of the start key and lifting of the tube).

4.3.1 Methods

Participants

34 York University students took part in the experiment (20 female, mean age 26.2, age range 19-58). They were recruited via the York University Psychology Electronic Experiment Booking System (PEEBS) and were rewarded with £4 or 1 hour course credit. To ensure that all object words were familiar, only native English speaking participants were recruited. Only right-handed participants took part and the extent to their handedness was tested using an adapted version of the Edinburgh Handedness Inventory (Oldfield, 1971). This questionnaire confirmed that participants were right handed (average score 90.3, where anything above 40 is an indication of right handedness). Participants had corrected or corrected to normal vision and provided informed consent.

Stimuli

In experiment 1 each object word was only seen once meaning that for each object word there was no within subject comparison across the light and the heavy box lifting condition. Due to the variable effects across subjects, this added noise may have contributed to the lack of observed interaction effects. The design of the current study therefore used a more powerful design where each object word is seen in every box lifting conditions by each subject (18 object words per condition each presented 4 times in different sentence contexts).

Object stimuli were created from the pre-test questionnaires (as described above). From these questionnaires 18 items were chosen for inclusion in a light object and a heavy object condition (see Figure 6 for complete list of items). The average weight rating for the light condition was around 100g (95.93g) and the average weight rating for the heavy condition was around 600g (594.82 g). Any objects that were rated as being heavier than tube 9 in the pre-test questionnaire by more than half the participants were instantly excluded, as the precise weight of these objects could not be determined. T-tests demonstrated that there was a significant difference between the weight ratings for each condition where objects in the light condition were rated as being significantly lighter than the objects in the heavy condition, ($t(34) = -12.79, p < .001$). Furthermore, the object stimuli were included only if they too were rated as affording a unilateral hand action. Items that were rated as affording a bilateral hand lift only were instantly excluded from further consideration. Any items that were rated as never being picked up by more than half of the participants in the experience pre-test questionnaire were instantly excluded, and only objects that most individuals were likely to have been picked up at least once a year were further considered. A Mann-Whitney test showed that the differences in experience ratings were not different across the two conditions ($U=212.5, p > .05$). Again the two conditions could not be matched for their size properties where heavy items were consistently rated as being larger as the light items, ($t(34) = -7.67, p < .001$).

Unlike in experiment 1 individual stimuli across the two heavy and light conditions were paired and closely matched on a number of psycholinguistic variables such as character length and frequency to better control the between item variability and to increase the chances of seeing any weight related effects (see

Figure 6 for pairings). The average difference between the matched pairs for character length is 0.72 characters (SD: 0.67, range: 0-2 characters,). A t-test confirmed that there is no overall significant difference in character length between the light and heavy object conditions ($t(34) = .310, p > .05$). The average difference between the matched pairs for frequency was 0.41 (SD: 0.47, range: 0-1.53) for the first position (e.g. “pair” in “pair of dice”) and 0.61 (SD: 0.47, range: 0.02-1.70) at the second position (e.g. “dice” in “pair of dice”). T-tests confirmed that there was no significant difference in log frequency at either the first ($t(22) = .47, p > .05$) or the second position ($t(34) = -.71, p > .05$). Therefore, the stimuli in each group differed in their perceived weight ($p < .05$) but were matched on several other factors so to ensure that any observed effects can be attributed to the weight manipulation.

	Pair number	Light object	Heavy object
Object stimuli	1	Pair of dice	Bag of flour
	2	Bag of crisps	Bag of sugar
	3	Box of matches	Bottle of coke
	4	Frisbee	Brick
	5	Box of tissues	Carton of milk
	6	Ping pong ball	Champagne bottle
	7	Square envelope	Empty suitcase
	8	Yellow duster	Filled kettle
	9	Ice cream	Full Jug
	10	Banana	Hammer
	11	Chocolate bar	Hardback book
	12	Ruler	Iron
	13	Wooden spoon	Leather coat
	14	Paintbrush	Paperweight
	15	Green Apple	Phone book
	16	Sponge	Spade
	17	Kitchen roll	Wine bottle
	18	Twig	Wok
Mean weight in grams (SD)		95.93 (57.17)	637.65 (143.49)
Mean experience rating (SD)		1.96 (.57)	4.85 (1.33)
Size (SD)		2.11 (.60)	3.99 (.87)
Mean no. characters (SD)		10.56 (3.52)	10.58 (3.99)
Mean log freq 1st position (SD)		4.25 (.41)	4.15 (.59)
Mean log freq 2nd position (SD)		3.86 (.75)	3.80(.75)

Figure 6. Experiment 2: Object stimulus details. List of object stimuli and mean values (and standard deviation) for weight (grams), experience rating, size rating number of characters and log frequency at the first and the second position.

These light and heavy objects were then embedded within action or non-action sentences whereby the verb defines the action/non-action context. The verbs chosen for the action and no-action conditions were paired and these pairs were matched on character length (for the whole verb phrase) and log frequency (see Figure 7). The average difference between the matched pairs for character length is

.78 (SD: 0.83, range: 0-2). A t-test confirmed that there is no significant difference in character length between the action and the no-action verb conditions ($t(16) = .138, p > .05$). The average difference between the matched pairs for frequency was 0.29 (SD: 0.20, range: 0.05-0.69). A t-test confirmed that there was no significant difference in log frequency between the action and no-action verb conditions ($t(16) = .74, p > .05$). Therefore, any experimental differences across the verb conditions cannot be explained by these psycholinguistic variables.

	Pair number	Action Verb Phrase	No-action Verb Phrase
Verb stimuli	1	is moving	can see
	2	is lifting	recognise
	3	is holding	has noticed
	4	is fetching	is admiring
	5	is carrying	is watching
	6	is bringing	is looking at
	7	is removing	is imagining
	8	is relocating	is glaring at
	9	is picking up	has forgotten
Mean no. characters (SD)		11.11 (2.03)	11 (1.32)
Mean log freq (SD)		4.57 (.70)	4.55 (.71)

Figure 7. Experiment 2: Verb stimulus details. List of verb stimuli and mean values (and standard deviation) for number of characters and log frequency.

Design

The experiment has a 2 (object word: light, heavy) X 2 (verb: action, no-action) X 2 (action type: heavy lift, light lift) design. Firstly, as previously described there are two object conditions, light and heavy with 18 items in each (see Figure 6). Each of these items were embedded within action and no-action sentences where the action content was defined by the verb. Action sentences all included verbs

describing physical interactions with the objects whereas the no-action sentences involved perceptual or psychological verbs (see Figure 7). Each sentence was presented twice in the experiment in each of the two lifting conditions (heavy and light lift). The experiment included two dependent measures: the time taken to plan the action and release the start key and the time taken to execute the planned action by lifting the tube.

Apparatus

Stimuli were presented on a computer (Screen type: Sharp, screen size: 17", screen resolution: 1280 x 1024 pixels) using E-Prime (Version 1.0, Psychology Software Tools). A computer keyboard was positioned to the right of the participant and three adjacent keys were marked as the start key (pressed at the beginning of each trial), and a yes and no response key. A response device was positioned in front of the keyboard (Cedrus model RB-520). A light and a heavy tube (100g and 600g) sat above the left and right most keys of the response device and were held in position by a cardboard casing (see Figure 3 for a photograph of the apparatus layout). The way the tubes were positioned meant that the response keys were depressed unless the boxes were lifted upwards. The start key was positioned an equal distance away from the two tubes to ensure that any differences in reaction time would not be influenced by differences in time the hand takes to reach each of the tubes, the device could therefore be used to measure lifting latencies for each tube. The cardboard casing that held the tubes in place consisted of a box (height: 8.5cm, width: 15.5cm, length: 23.5cm) with two holes in the top through which the tubes were placed. Pieces of card lined each of the holes to ensure that the tubes were securely held and that the tubes were upright at all times so as to reliably depress the response buttons. The tubes were the same as those used in the weight questionnaire (described above) but had coloured stickers attached (heavy=green, light=blue). There were two reasons for positioning the keyboard and tubes to the participants' right. Firstly, putting the tubes in front of the screen would have obscured the participants' view of the screen and secondly, it was felt that it was more natural when using the right hand to reach to objects on the right hand side rather than when the tubes were placed in the centre.

The tube weights (100g, 600g) were chosen so as to match the average weight rating of the objects in the light and the heavy condition (from the pretest

questionnaire). The perceived weight of the objects and the actual weight of the tubes were matched in each condition in order to maximise any chance of tapping into weight-specific overlapping representations and finding interaction effects between the action and language.

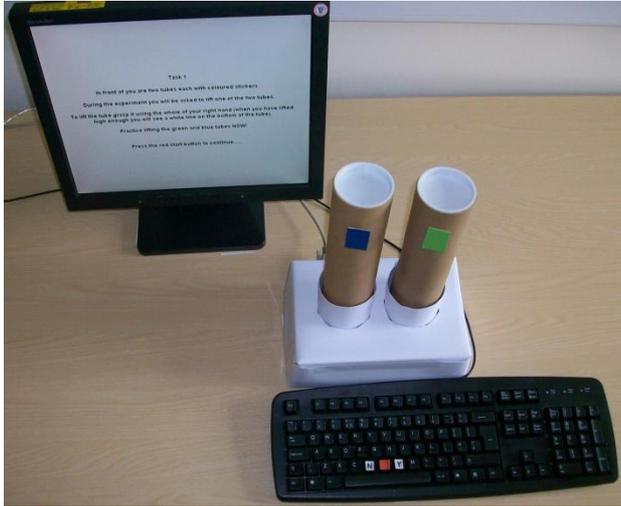


Figure 8. Experiment 2: Apparatus

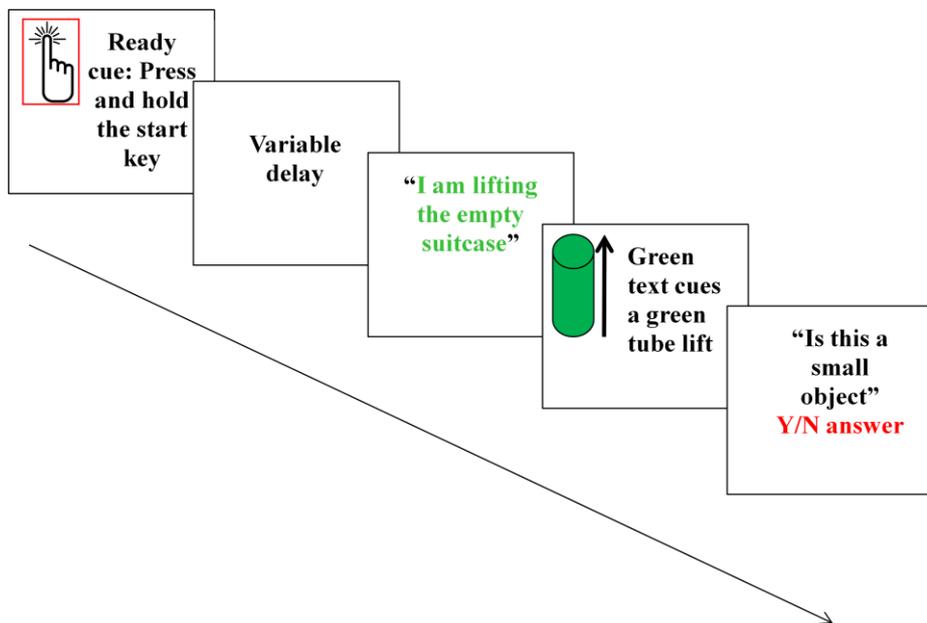


Figure 9. Experiment 2: Procedure. Arrow indicates the passage of time

Procedure

Experiment. At the beginning of each trial participants were told to press and hold the start key with their right middle finger until a coloured action/no-action sentence was presented on the screen for 500ms. The colour of the text informed the participant which tube they were subsequently to lift: green text cued a heavy tube lift and blue text cued a light tube lift. Participants were encouraged to lift the correct tube as quickly as possible after the onset of the stimulus. Once the tube was lifted an instruction then told participants to replace the tube. A random time interval between 500-2000ms was inserted between the start key press and the onset of the stimulus to ensure that participants could not anticipate the onset of the cue. Participants were told to only initiate a movement if they were sure which tube they were going to lift, to ensure that the release time is a true reflection of action planning and it is not cut short by a premature release. Following the tube lift a comprehension question that related to the meaning of the language stimulus was presented; participants were required to respond Y/N by pressing designated keys on the keyboard. The latency of response to questions was not analysed, however the accuracy was calculated to ensure that each participant was paying attention to the sentence meaning. The light and heavy action conditions were randomly ordered, however all participants saw the stimuli in the same predefined order in each of the tasks. See Figure 9 for a timeline of the events.

Repetition of the same action type results in neural response suppression in motor regions for both goal directed (Kroliczak, McAdam, Quinlan, & Culham, 2008) and transitive (de C. Hamilton & Grafton, 2009; Dinstein, Gardner, Jazayeri, & Heeger, 2008) hand actions, therefore to counteract any repetition effects that may manifest themselves in reaction time, in the current experiment it was ensured that each condition followed all other condition types equally often. Despite controlling for the distance between the start key and each of the two tubes, it may be that the difference in the position of the two tubes relative to the hand's start position influences the lifting times, for example if the distance of the tubes from the body plays a role or the physical constraints in moving the hand in slightly different directions to reach the left/right tube. The left/right configuration of the heavy and the light tubes was therefore counterbalanced across participants.

Training. It is essential that participants associate the colour with the weight of the tube (either implicitly or explicitly) as otherwise when planning the tube lift, the weight of the tube will not be considered and therefore will not interact with the language processing. Before taking part in the experiment participants were therefore trained to associate the heavy and the light tube with a specific colour. Rather than presenting coloured text, the cues were simple coloured rectangles. Practice trials (4 for each tube weight) preceded the start of the training so participants were aware of the difference in weight between the two tubes and had prior experience interacting with them. In the training session there were 25 lifting trials for each tube weight, this number of trials per action was chosen as it is similar to the number of training trials used in the study by Bub and colleagues (2008).

4.3.2 Results

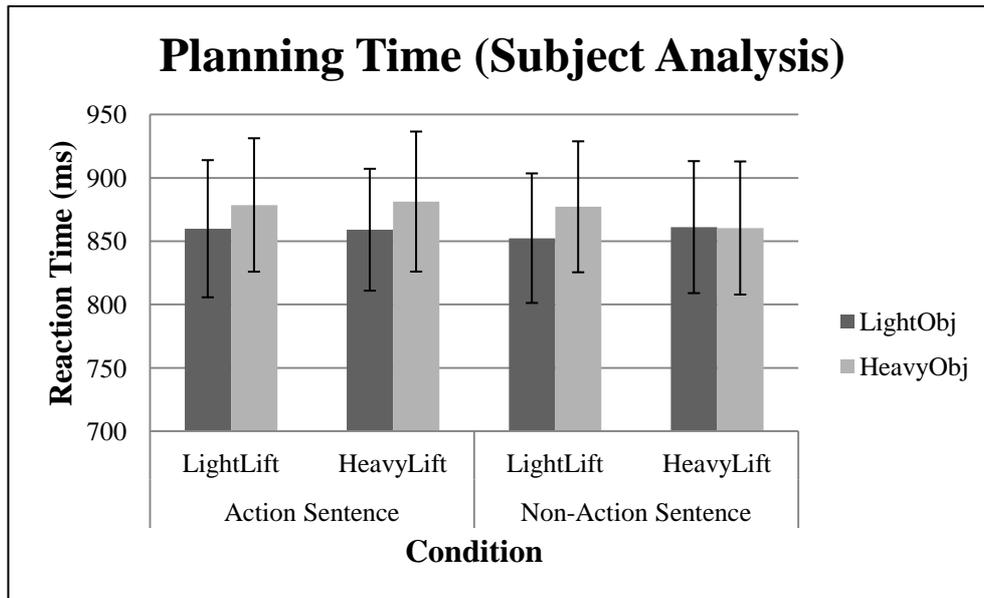
1 participant was removed from the analysis as the instructions were not properly followed. The accuracy of responses in the question trials were also analysed. On average participants were correct on 95.4% of trials. The questions were purposefully difficult to make the participants carefully process the meaning of the sentences, therefore no trials were excluded if wrong answers were given. The high proportion of correct answers demonstrates that participants are attending to the meaning of the sentences.

Trials from the remaining participants were removed if the participant lifted their hand from the start button before the onset of the cue (0.46% of trials), if the wrong tube was lifted (0.78% of trials) or if the apparatus failed to collect a response (0.29% of trials). Trials with outlier data points either for the planning or lift times (more than 3SD from the mean) were also removed from the analysis (2.97% of trials). To account for the positive skew that is often seen in reaction time data, the data were log transformed and statistical analyses were conducted on these values (however all graphs report reaction time data in ms). Repeated measures ANOVAs were performed on the planning and lift times to discover whether there are any differences within the levels of the three different factors (tube weight, object weight, sentence type) and any interactions between them.

Planning Time

In an analysis with subjects as a random factor, a repeated measures ANOVA revealed a marginal main effect of sentence type ($F(1, 32) = 3.37, p = .076$) whereby there were slightly faster responses to non-action than action sentences. However no other significant main effects or interactions were observed ($p < .05$). Furthermore, in an analysis with items as a random factor a repeated measures ANOVA found no significant main effects or interactions ($p < .05$). This indicates that planning times are no different for action vs non-action sentences and that the congruency/incongruency between the weight of the object in the sentence and the weight of the to-be-lifted tube is not affecting planning times. See Figure 10a and b for a graph of these results.

a).



b).

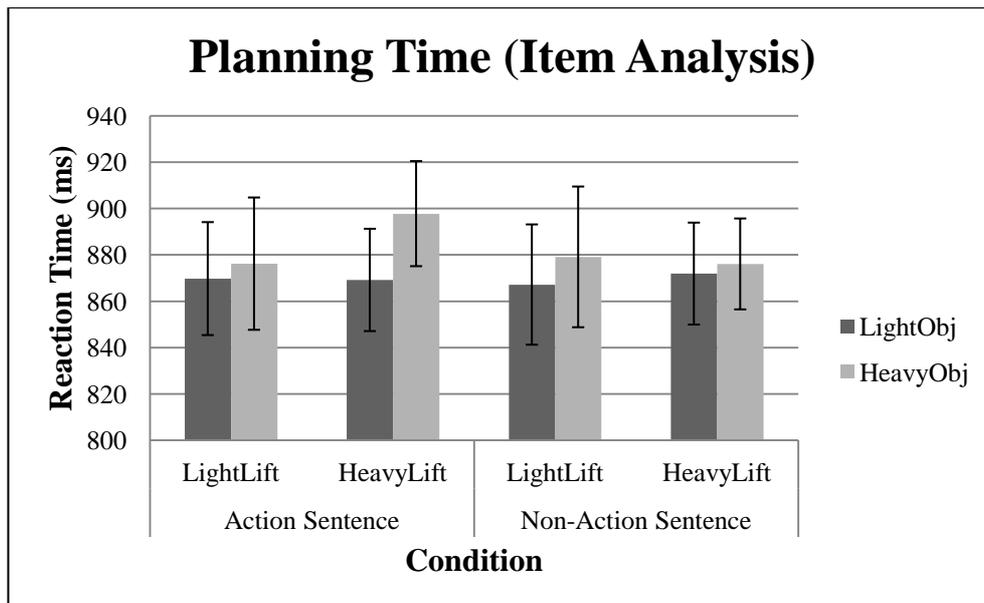


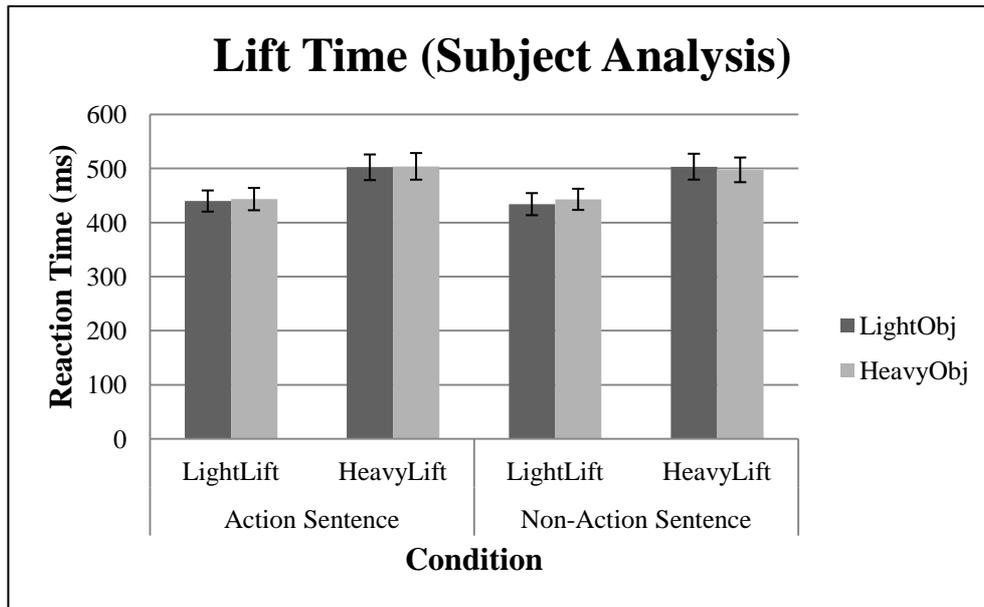
Figure 10. Experiment 2: Mean planning times. With subjects (a) and items (b) as a random factor (bars represent standard error).

Lift Time

In an analysis with subjects as a random factor, a repeated measures ANOVA revealed a significant main effect was found for tube weight ($F(1, 32) = 155.6, p <$

.001). This indicates that it took longer to lift the heavy than the light tube, a result that was expected based on previous studies that have shown that lifting heavy objects requires more time to apply the necessary forces than when lifting light objects (Eastough & Edwards, 2007). No other main effects or interactions were observed ($p < .05$). In an analysis with items as a random factor, again a significant main effect was found for tube weight ($F(1, 17) = 638, p < .001$), however no other main effects or interactions were observed ($p < .05$). This indicates that lift times are no different for action vs. non-action sentences and that the congruency/incongruency between the weight of the object in the sentence and the weight of the to-be-lifted tube is not affecting the time taken to perform the lift. See Figure 11a and b for a graph of these results.

a).



b).

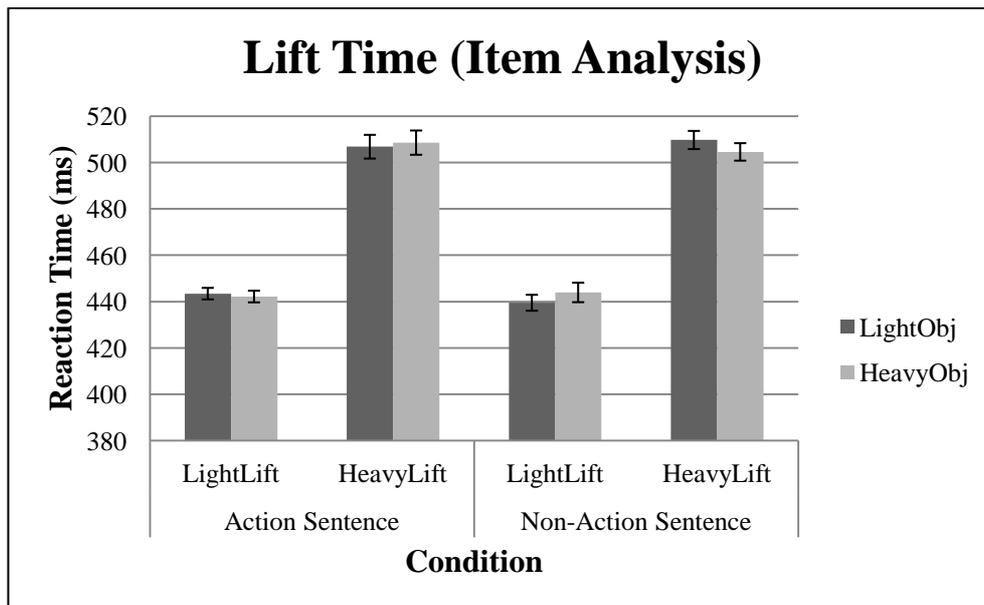


Figure 11. Experiment 2: Mean lift times. With subjects (a) and items (b) as a random factor (bars represent standard error).

4.3.3 Discussion

The aim of the current experiment was to identify whether behavioural interactions between action and language for shared weight features could be revealed when using a design that has previously found successful interaction effects

when action and language tasks share action properties (Bub, et al., 2008). Several predictions were made: If language induced motor system activations (as seen in the experiments described in chapters 2 and 3) are necessary for the comprehension of action language and are weight-specific, then the weight of the object in the language should influence the time taken to plan/perform a weight-compatible vs. a weight-incompatible lift. Furthermore, it was predicted that any effects should be more pronounced in the action compared to the non-action context where action-relevant object properties should be more prominent. And finally, interactions were expected to occur in time taken to plan the action rather than in the time taken to perform the action.

Contrary to the predictions, the speed at which the action was planned or performed was not influenced by the congruency between the weight of the object in the sentence and the weight of the to-be-lifted tube. This indicates that weight-specific motor representations are not recruited by weight congruent action language to a great enough degree to interfere with the planning/performance of a lifting action. Furthermore, no differences in reaction times were observed for the action vs no-action sentences indicating that action language more generally does not recruit the motor system to a different degree than no-action language.

Certain methodological flaws may have contributed to this effect. It may be that action language comprehension does require the activation of motor representations; however the task itself may not have been sensitive enough to detect any interactions that may have been present. An implicit task (where the questions did not refer to the weight of the object) was included in order to assess whether, as embodied proponents have claimed, we automatically access all related features of objects when we encounter them irrespective of task. The results suggest that these automatic effects do not occur, instead it may be that a task is required that explicitly focuses a participant's attention towards the weight properties of the object, a general action context provided by the sentence may therefore not be adequate to activate weight properties to a high enough degree to interfere with action performance.

Comprehension questions were included to encourage participants to process the sentential meaning, as otherwise they could plan the appropriate lift based upon the text colour without reading the language. However, simply because the sentence

is read does not necessarily mean that the meaning has been extracted; it could be that the sentence is kept in mind (via an acoustic pattern) but not fully processed until after the lift when the comprehension question is to be answered. If action-related properties are only processed in a shallow manner until after the lift has taken place, then this may mean that the action planning and language comprehension are not temporally simultaneous, and therefore the object's features (including weight) may not have been processed to a great enough degree to influence the planning time. In several other studies investigating these interaction effects, the action itself *is* the decision (e.g., Bub, et al., 2008; Glenberg & Kaschak, 2002) for example Glenberg and colleagues (2002), asked participants to make sensicality judgements to sentences that implied forwards and backwards motion by making a forward and backwards response. As the decision was the compatible/incompatible response, this ensured that the semantic processing of the sentence coincided with the performance of the action itself. This design flaw must therefore be considered in the design of further experiments to ensure that every effort is made to overlap language processing and action planning.

4.4 General Discussion

The two different experimental designs described above both aimed to uncover behavioural interactions between action language and action performance when the two tasks shared specific weight features. This would provide evidence that the weight-specific language induced motor activations as observed in Chapter 1 are functionally related to the processing of detailed action features via the language we read. So far, no studies have convincingly demonstrated that these action-language interactions exist for compatible vs. incompatible weight features. Therefore, two experimental designs, one that has found action-perception interactions for weight and the other that has found action-language interactions for a non-weight feature were adapted to address the current hypothesis.

Unfortunately, neither design revealed differences in reaction time when there was a weight match vs. mismatch in the action and the language. Each design suffered from different methodological problems that may have contributed to this null effect. The design of experiment 1 was thought to be complex and the lack of within subject comparison may have introduced much noise to the data.

Furthermore, neither design focussed suitably on the temporal overlap between the

action language processing and the action planning. Therefore, due to these timing issues interaction effects may not have been captured and if they were present, the subtle effects may have been overshadowed by noise.

It is possible that language does functionally recruit the motor system during comprehension but that these designs are not appropriate for capturing these effects. The design of experiment 1 has previously been used to demonstrate interaction effects between action perception and action performance for weight, therefore may be suitable for identifying interactions for weight features, but may not be suitable for addressing the way in which action and language interact. It may be that visual action information may be processed in a slightly different way to action language, for example visual information may be more suitable for the direct mapping of actions onto action representations, whereas language may be processed slightly differently as is acquired in a more associative way and requires the transformation from arbitrary symbol to meaning. Similarly, the design of experiment 2 has previously been used to demonstrate interaction effects between action and language, but for compatible vs. incompatible grasp types and not for weight. Therefore, it may be suitable for capturing interaction effects between action and language but not for shared features like weight. For example, grasp information is a more salient action attribute, and it could be argued a more important attribute as when performing an action its success relies upon the execution of a precise grip, whereas the effort used to lift the object can be roughly calculated and adjusted later online. Therefore, more activity may be expected for grasp attributes than weight attributes and therefore bigger effects may be expected. These designs may therefore not be sensitive enough to capture the subtle weight-specific action-language interactions and other designs should be considered.

Rather than completely rejecting the designs, it was decided to further adapt the design used in experiment 2 in order to further explore these effects. This design presented fewer methodological flaws than the design used in experiment 1 and it was thought that its flaws could be more easily rectified. One of the main criticisms of this experiment was that the language processing could have occurred after the action had already been planned. Furthermore, it was thought that the implicit nature of this task (whereby the comprehension questions did not explicitly refer to the object weight) may have contributed to the null effect. Therefore, the experiments

described in Chapter 5 employ an adapted experimental design where the action is itself the answer to the question, thereby forcing participants to plan the action (to a light or heavy tube) while fully processing the meaning of the language.

Furthermore, two different tasks were employed to investigate the effects of an implicit vs. explicit task. These experiments should therefore be better able to detect any existing behavioural interactions for action and language when they share weight features.

Chapter 5

Interactions between Action and Language for Shared Weight Features: Implicit vs. Explicit Interactions Effects

5.1 Introduction

The experiments that have been described so far (Chapter 4) did not provide evidence for behavioural interactions between action performance and action language for shared weight features. To further address the methodological issues that these past experiments suffered, the current set of experiments employ an adapted design that aims to maximise the likelihood of unveiling any weight-specific influence of language on action performance (and vice versa) when they have common weight-specific properties.

Improving Temporal Overlap of Semantic Processing and Action Planning

The design of the current experiment was very similar to the design of the experiment described in Chapter 5; however several improvements were made. In the previous experiments the lift was executed before the comprehension question appeared, meaning that the detailed semantic analysis of the sentence (including accessing information regarding the stimuli weight features) could potentially occur after the lift has been planned and performed. In order to improve the design in the current experiment, it was made certain that the semantic processing of the word and planning of the weight-specific action would temporally coincide as the tube lift itself *was* the answer to the question. This temporal overlap should increase the chances that shared linguistic and planning representations will influence behaviour. Interaction effects have been shown by some to only occur when action processing and action planning occur simultaneously (Borreggine & Kaschak, 2006), therefore, it is important that language and action completely overlap in time in order to see any behavioural effects.

Influence of Task

It was unclear from the previous experiment whether the null results were due to methodological issues (such as the temporal issue described above) or due to

the implicit nature of the task. It may be that contextual cues and attention play a more important role in the activation of semantic memory for a subtle feature like weight, therefore participant attention may need to be drawn to the weight properties of the object stimuli to a greater degree to interfere with action. In the experiments described below, participants were either asked to give explicit weight ratings for the objects (experiment 1), or to perform a more implicit judgement (experiment 2) using the very same experimental design in order to tease apart these two possibilities. As there were two tubes (light and heavy) this meant that there were two possible response choices in each task. For the explicit task participants judged whether the object was lighter or heavier than a comparison weight, and for the implicit task participants judged whether or not the object has a handle. This handle task was designed to divert participant attention away from the weight properties of the objects. Each of the two possible responses in each task were assigned to either the light or the heavy tube, therefore on reading the object word, participants made their judgement by lifting either a weight compatible/incompatible tube.

In light of the lack of interaction effects for sentence stimuli (as described in Chapter 4), and as the task requires participants to pay attention only to the object word itself (for the weight or handle judgement), the stimuli used in the current experiment were single object words. Several previous experiments have found behavioural effects for shared action features such as grip type when presenting single object word stimuli and objects embedded within non-action sentences (Bub, et al., 2008; Masson, Bub, & Newton-Taylor, 2008; Masson, Bub, & Warren, 2008). This suggests that the lack of sentential context in the current experiment will not hamper any attempts to observe any existing interaction effects.

Weight Groups

To increase the experimental power the number stimuli included in the experiment was increased to 63 in total. Furthermore, these object words were split into seven more fine-grained weight categories each spanning 125g bands as determined by a separate group of questionnaire ratings (see Figure 1 for details). As the weights of the objects varied incrementally from light to heavy, this was intended to divert participant attention away from the weight manipulation in the implicit task (i.e., not only *very* heavy or *very* light objects were included). Furthermore, these weight groups were designed to investigate whether there are any

differences in effects across the different weight categories. The object groups were created so that the lightest and heaviest groups were most similar in weight to the light and heavy tubes that were to be lifted. If we have shared weight-specific representations for action performance and action language (as proposed by the MOSAIC model: Hamilton, et al., 2004; Scorolli, et al., 2009), it can be predicted that when the weight of the object and the weight of the tube lifted are most similar/dissimilar the greatest behavioural interference effects will result i.e., for the heaviest and lightest stimulus groups.

Predictions

Again, it was predicted that if we automatically activate weight properties of the objects that we read about, then there should be a difference in reaction times for weight-congruent trials compared to the weight-incongruent trials in both the explicit and implicit task. For example, when the weight of the object described by the word and the weight of the tube that is lifted are congruent, reaction times should be different to when these weight factors are incongruent. However, if we only activate the weight features of objects when we are explicitly asked to pay attention to those features, then it can be expected that any congruency effects will only occur in the explicit task but not in the implicit task (experiment1). It was further predicted that the largest congruency effects would occur for those object stimuli in the heaviest and lightest weight groups (groups 7 and 1) as they are most similar/dissimilar to the heavy and light tubes that are to be lifted. The greater the similarity between the weight of the object and the weight of the lifted tube, the greater the congruency effects are expected to be.

Again the dependent measures are the planning time and the lift time. The planning time is thought to represent the time taken to plan and initiate a weight specific action whereas the lift time is the time taken to execute (reach, grasp and lift) the planned action after releasing the start button. Based on previous evidence it was predicted that any weight-specific interactions between action and language will occur during the planning time rather than the lift time.

5.2 Experiments 1 & 2

5.2.1 Method

Participants

43 participants took part in the explicit experiment (32 female; mean age 20.5; age range 18-45) and 42 participants took part in the implicit experiment (34 female; mean age 19.7; age range 18-27). Participants were recruited via the Psychology Electronic Experiment Booking System at the University of York and were mainly students. Participants were paid £2 or were given 30 minutes course credit for their time. As it was important that all object words were familiar, and as the organisation of semantic knowledge in second language speakers is not clear, only native English speakers were tested. All participants were right-handed and the extent to their handedness was tested using an adapted version of the Edinburgh Handedness Inventory (Oldfield, 1971). This questionnaire confirmed that participants were right handed (average scores 88 (explicit experiment) and 91 (implicit experiment), where anything above 40 is an indication of right handedness). All participants had corrected or corrected to normal vision and filled in a consent form prior to beginning the experiment.

Stimuli

63 highly familiar object words were chosen using the same pre-test questionnaires that were described in Chapter 4 (see Appendix 2 for a list of the stimuli). Based on the mean weight ratings from the pretest questionnaire the 63 items were divided into 7 different weight groups each spanning 125g bands (see Figure 1 for details). A one-way ANOVA confirmed that there was a main effect of object weight ($F(6, 24.70) = 302.0, p < .001$) (Welch's F statistic reported due to a violation of the assumption of homogeneity) and Game-Howell post-hoc tests demonstrated that each of the weight groups differed from all others in perceived weight ($p < .01$) in the expected direction.

For the items that were chosen (with the exception of 4 stimuli), more than half of the participants rated all items as typically being picked up with the dominant hand (or with either the dominant hand or both hands interchangeably) in the hand questionnaire. As the affordances of both the tubes to be lifted and the object stimuli

match (in that they can both be lifted with the dominant hand alone) this will increase the chances of observing a behavioural interaction. A difference between conditions as to how the items are lifted therefore cannot explain any experimental effects. Furthermore, only objects that are experienced at least once a year by the majority of participants were included.

The stimulus groups were created to be equal in other psycholinguistic variables such as character length and log frequency, factors that have previously been shown to affect reaction time (Monsell, 1991). The stimuli consisted of either one or two words (e.g., “leather coat”, “mop”), therefore to match each of the groups on average character length, adjectives were added to some of the object stimuli (e.g., “dirty mop”). A one-way ANOVA confirmed that there was no significant main effect of character length across the groups ($F(6, 24.43) = 0.77, p > .05$) (Welch’s F statistic reported due to a violation of the assumption of homogeneity). As some stimuli consisted of two words the log frequency was calculated for each of the word positions separately with one-word stimuli included at the second position. A one-way ANOVA confirmed that there was no main effect of log frequency at either the first ($F(6, 31) = 0.54, p > .05$) or the second position ($F(6, 56) = 1.14, p > .05$).

One factor that could not be controlled across groups was the perceived size of the objects. A one-way ANOVA confirmed that the size ratings (as taken from the pre-test questionnaire) of the objects in each group were not equal ($F(6, 56) = 6.37, p < .05$). Post hoc tests (with Bonferroni correction) showed that the items in group 1 were rated as being significantly smaller than the items in group 4 ($p < .01$), group 5 ($p < .05$), group 6 ($p < .01$) and group 7 ($p < .001$), and that the items in group 2 were rated as being significantly smaller than the items in group 4 ($p < .05$) and group 7 ($p < .01$). These differences between the lighter and the heavier groups are due to the inherent nature of heavier objects being larger.

Weight Group	Weight range (g)	Mean Weight Rating (g) (SD)	Mean Length (characters) (SD)	Mean Experience Rating (SD)	Mean Size rating (SD)	Mean log frequency (1st position) (SD)	Mean log frequency (2nd position) (SD)
1	0-125	68.89 (28.67)	9.78 (3.53)	4.73 (1.18)	2.45 (1.49)	4.29 (0.29)	3.21 (0.88)
2	126-250	191.11 (49.55)	10.33 (3.32)	4.50 (1.76)	2.76 (0.80)	4.15 (0.85)	3.32 (0.79)
3	251-375	325.1 (38.12)	10.00 (2.45)	4.73 (1.25)	3.54 (0.92)	4.03 (0.34)	4.07 (1.14)
4	376-500	428.15 (32.45)	9.11 (4.04)	5.49 (0.88)	4.33 (0.84)	3.86 (0.52)	3.31 (1.45)
5	501-625	557.04 (43.60)	11.56 (1.74)	4.99 (1.69)	4.01 (1.08)	3.85 (0.65)	3.98 (0.91)
6	626-750	688.89 (49.89)	10.56 (5.10)	5.68 (0.85)	4.17 (0.57)	4.19 (0.30)	3.71 (0.84)
7	751+	862.22 (74.53)	9.89 (4.65)	5.11 (1.28)	4.52 (0.67)	4.20 (0.69)	3.73 (0.30)

Figure 1. Experiment 1 & 2: Stimulus details. Means (and standard deviation) for weight rating (g), length (characters), experience rating, size rating, and log frequency (first and second position) for each of the seven weight groups.

Design

The experiment has a 2 (congruency: congruent, incongruent) X 7 (weight group: 0-125g, 126-250g, 251-375g, 376-500, 501-625g, 626-750g, 750g+) design. Each weight group contained 9 stimuli all of which were seen twice during the experiment, once in the weight-congruent condition and once in the weight-incongruent condition. This was done to increase power in comparing across stimulus categories, since participants can vary in their speed of response. Thus, comparisons within participants, rather than between groups, may be more likely to reveal differences.

Apparatus

The apparatus was the same as described in Chapter 4, all except for the weight of the tubes, whereby in this experiment the heavy tube weight was increased to 860g (from 600g). The lightest tube was kept at 100g so to be heavy enough to reliably depress the response button. These weights were also chosen to be most similar to the average weight ratings of the heaviest (862.22g) and lightest (69.89g) object groups. A third tube labelled “comparison tube” was also included for purposes of the task and was positioned on the table to the right of the response box. This tube was 440g making its weight similar to the mean weight rating of all the stimulus objects (446g) and most similar to the weight rating of the objects included in the middle weighted object group (428g).

Procedure

Explicit experiment. The participants’ task was to read object words and judge whether the objects were lighter or heavier than the comparison tube. For example on seeing the name “dirty mop” participants would have to make a comparison between the weight of a typical mop and the comparison tube and then make their response by lifting one of the coloured tubes (either the heavy or the light tube). Participants were allowed to remind themselves of the comparison tube weight at any between-trial time during the experiment. There were two sections in the experiment, a congruent and an incongruent section. To make their response in the congruent section participants were told to lift the blue (light) tube for a “lighter than” response and to lift the green (heavy) tube for a “heavier than” response. In

the incongruent section participants were told to lift the green (heavy) tube if the object was lighter than the comparison tube and the blue (light) tube if the object was heavier than the comparison tube. So, when switching between the two congruency conditions the colour-response pairing was reversed, i.e. if the green heavy tube was paired with the “heavier” response in the first section, it was paired with the “lighter” response in the second section (see Figure 2). The degree of congruency was therefore driven by the similarity in the stimulus weight rating (either light or heavy) and the weight of the tube that was being lifted (either light or heavy).

As well as there being compatibility/incompatibility between the weight of the object and the weight of the tube which may lead to different response times there was also the possibility that response times would be affected by the compatibility between the response label itself (i.e., “heavier than”, “lighter than”) and the weight of the tube (i.e. heavy, light). In other words, if participants are using the tube weight to remember what response label is associated with that particular tube, when the light tube is paired with the “lighter than” response and the heavy tube is paired with the “heavier than” response, participants may naturally be faster than when the heavy tube is paired with the “lighter than” response and the light tube is paired with the “heavier than” response irrespective of the weight properties of the object stimulus. Colours were therefore assigned to the light and heavy tubes and participants were encouraged in the instructions to associate the response labels to the tube colours rather than to the weight of the tube. Furthermore, 16 trials of training were given before the beginning of both the first and the second section to train participants in the new labels and to reduce any need to rely upon strategies to remember the tube-response association.

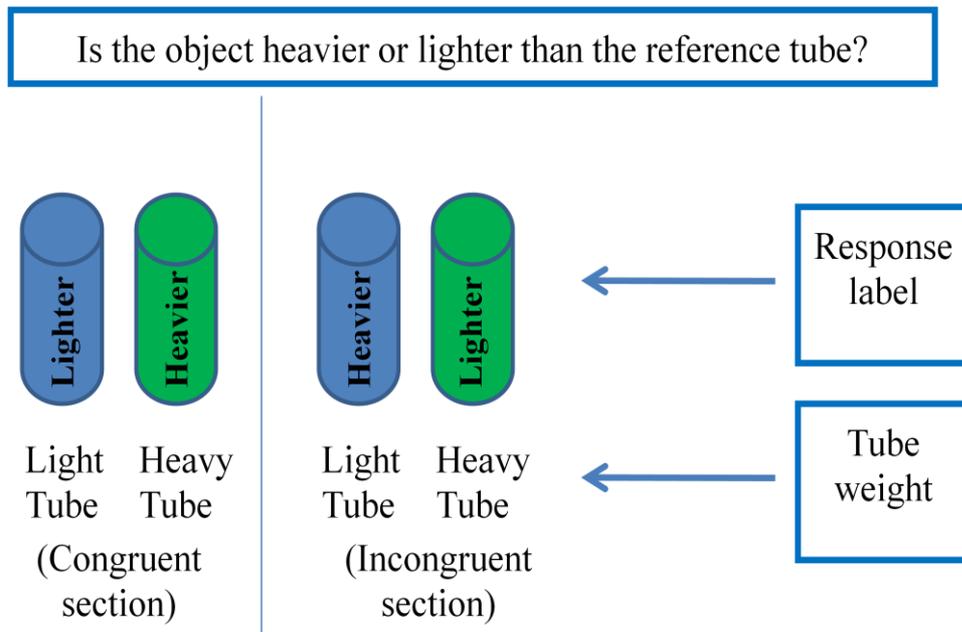


Figure 2. Experiment 1: Design. In the congruent section, if the object is thought to be lighter than the reference tube, then the blue (light) tube was lifted and if the object is thought to be heavier than the reference tube then the green (heavy) tube was lifted. In the incongruent section, if the object is thought to be lighter than the reference tube, then the green (heavy) tube was lifted and if the object is thought to be heavier than the reference tube then the blue (light) tube was lifted.

Implicit experiment. The participants' task was to read object words and judge whether the objects did or did not have a handle and to respond "yes" or "no" by lifting either the heavy or the light tube. Again there were two sections and each section adopted a different colour-response association i.e. in one section the blue (light) tube would correspond with a "yes" answer and the green (heavy) tube with a "no" answer and in the other section the blue (light) tube would correspond with a "no" answer and the green (heavy) tube would correspond with a "yes" answer (see Figure 3). The experiment was made up of both congruent trials (where the weight of the tube and the weight of the object matched) and incongruent trials (where the weight of the tube and the weight of the object mismatched) as opposed to there being separate congruent and incongruent sessions as in the explicit experiment. Again 16 trials of training were given at the start of each section to provide

familiarity with the procedure and to help them to associate the response labels with the appropriate tube colours so the task switch did not affect reaction times.

As the implicit task did not require individual light/heavy explicit weight ratings, a post-experiment questionnaire was implemented in order to assess whether the trials were weight congruent (where the weight of the object and the weight of the tube matched) or incongruent (where the weight of the object and the weight of the tube mismatched) from the perspective of each individual. To ensure that participant attention was not directed towards the manipulation the questionnaire was administered after the experiment.

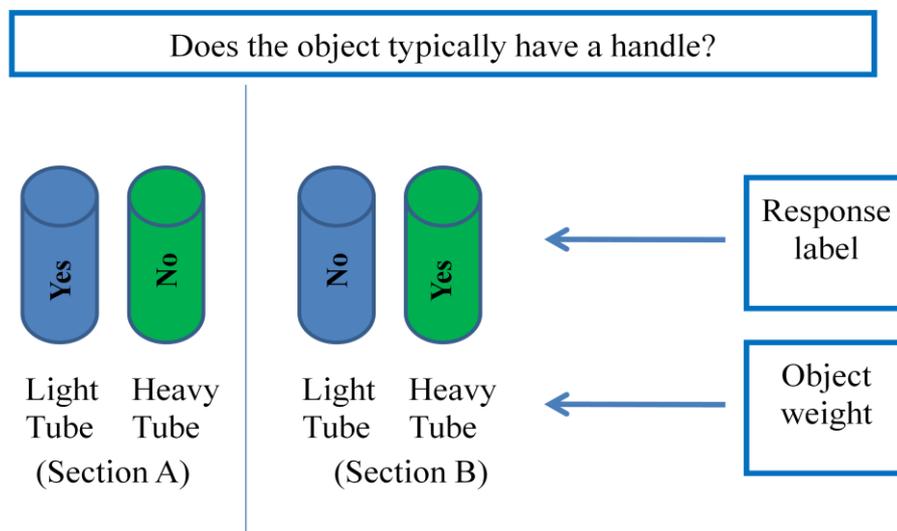


Figure 3. Experiment 2: Design. In section A, if the object is thought to have a handle, then the blue (light) tube was lifted and if the object is not thought to have a handle then the green (heavy) tube was lifted. In the incongruent section, if the object is thought to have a handle, then the green (heavy) tube was lifted and if the object is not thought to have a handle then the blue (light) tube was lifted.

Order of events. In both experiments each trial began with a command “press and hold the start button until you are ready to lift”. A blank screen was then presented for a variable interval (between 500-2000ms), its purpose being to make the word onset less predictable and to increase participant attention. An object word appeared on the screen and participants then made their judgement depending on the task requirements. A response was made by releasing the start button (at which point

the object word disappeared from the screen) and by lifting up the appropriate tube. The time taken to plan which tube they are going to lift and to initiate their action by releasing the start button is defined as the planning time. The time taken to lift the tube relative to the time at which they released the start button is defined as the lift time. See Figure 4 for a visual depiction of the timeline of events within a trial. Each tube had a line around 2 inches from the bottom and participants were told to lift the tube until they saw this line. In the practice session the experimenter also made sure that the grasp applied during the lift was a whole hand grasp around the middle of the tube. These measures ensured that the mechanics of the lifting action was controlled across the subjects. Participants then replaced the tube and continued onto the next trial.

The order in which participants experienced each of the two sections was counterbalanced across participants to account for any effects of order and practice that may occur. This is especially important as the same objects are presented twice, once in each of the sessions. The order of stimulus presentation within each condition was randomised for each individual (using the e-prime randomisation function) to prevent order effects. As participants had to physically move their hands to the right/left of the start point in order to pick up each tube and as these physical factors may have had an impact on reaction times (i.e. it may be easier to reach for a tube on one side than the other) the position (i.e. right, left of the starting position) of the tubes was also counterbalanced across subjects.

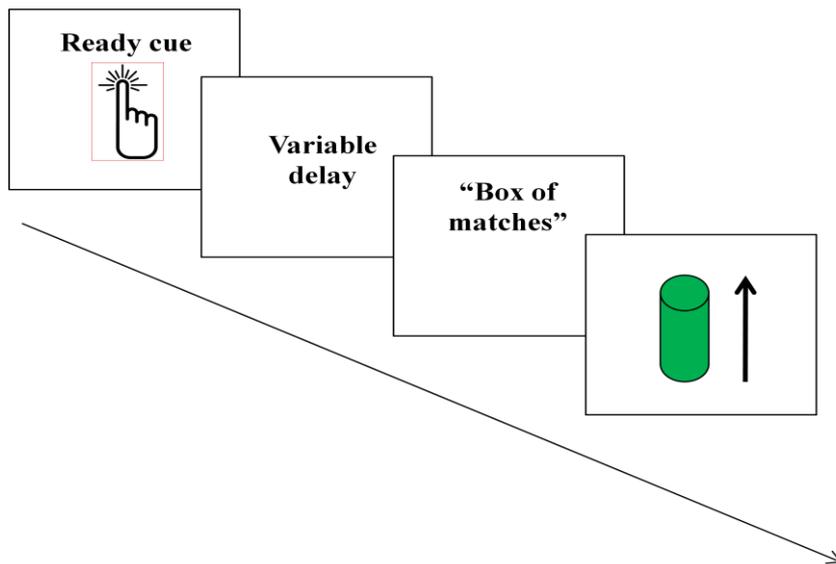


Figure 4. Experiment 1 & 2: Procedure. The arrow indicates the passage of time. In this example the participant depresses the start button when they are ready for the trial to begin. After a variable delay they are presented with the stimulus “box of matches” and respond depending on the task requirements by lifting the green tube.

5.2.2 Results: Experiment 1 (Explicit Task)

4 participants were removed from further analysis as they did not follow instructions correctly. On average 14.5% of the data was removed due to participants switching their response across the two trials (i.e., stated that the same object e.g., “vase” was “lighter” in the first section and “heavier” in the second section). If the response assignment changed across the two sections, this meant that for items where a judgement switch occurred, the same weight tube was lifted in both sections resulting in a lack of both incongruent and congruent trials for that item. As we are interested in comparing congruent versus incongruent trials, these trials were therefore removed. As expected most of these removed items came from the stimulus groups that were close in weight to the comparison tube (groups 3, 4 and 5). The heavier/lighter decision may have been harder for the objects that are close in weight to the comparison tube (e.g., can of coke) compared to objects that are further from the comparison tube weight (e.g., box of matches, hammer) therefore when they made their weight judgement for the second time they were more prone to

switch their answer on these trials. See Figure 5 for the average removal of these items for each weight group.

Weight Group (g)	% Items Removed in Experiment 1	% Items Removed in Experiment 2
0-125	0.53	0.90
126-250	1.34	0.64
251-375	3.54	0.73
376-500	2.97	1.42
501-625	2.40	0.91
626-750	2.16	0.91
751+	1.55	0.99

Figure 5. Experiment 1 & 2: Item removal. % of all experimental items removed due to an answer switch for each weight group.

Separate data analyses were then performed on the liftoff and movement times for the main body of data. Any outlying data points more than 3 standard deviations (SDs) away from the subject's overall mean reaction time were removed from further analysis (calculated separately for heavy and light tube trials for lift times based on the expectation that they would each have different distributions due to the mechanics of lifting differently weighted objects). Often outliers are removed using standard truncation methods across all subjects (Ulrich & Miller, 1994), however due to the large variability in the range of responses in the task across subjects (see Figure 6) it was felt that outliers should be removed on a participant by participant basis to avoid removing any participant-specific valid trials. An upper and lower cutoff of 3SDs from the mean was chosen so as to remove as little data as possible while still eliminating extreme values. 2.32% of the planning time data and 2.63 % of the lift time data was removed.

Measurement	Condition	Experiment 1	Experiment 2
		Reaction Time Range (ms)	Reaction Time Range (ms)
Planning	Congruent	504 - 1976	378 - 1817
Planning	Incongruent	551 - 2319	406 - 1813
Lift	Congruent	262 - 1099	886 - 2381
Lift	Incongruent	361 - 962	902 - 2455

Figure 6. Experiment 1 & 2: Reaction time range. Smallest and largest participant reaction times for each condition.

The weight groups were created using the pretest questionnaire ratings from an independent sample of participants whereby 50% of the stimuli were rated as lighter than the comparison weight and 50% were heavier. To ensure that participants in the current study made similar ratings, the proportion of “lighter” and “heavier” ratings were assessed. Excluding the more ambiguous items in the middle weight group it was found that 50.63% of the remaining items were classed as being lighter than the comparison tube and 49.37% of the items were classed as being heavier than the comparison tube. The distribution of weight ratings in the current experiment was therefore very similar to the distribution of the weight ratings in the pretest questionnaire, therefore suggesting that the weight ratings of objects are relatively consistent across different populations of participants in different task conditions. Furthermore, as the numbers of light and heavy object stimuli were equal, participants should not have been able to anticipate the weight of the upcoming item.

The reaction times were log transformed to account for the skew that naturally occurs in the distribution of reaction time data, and the statistical analysis was then performed on these transformed data points (however the graphs show the reaction time in ms). Two different analyses were performed on the data. Firstly, in order to be able to generalise the results to the population more generally, subjects were treated as a random factor and item as a fixed factor. Secondly, to be able to generalise the results to other items that were not selected for use in this study, items were treated as a random factor and subjects as a fixed factor.

Planning Time

Subject as a random factor. It was firstly predicted that there would be a significant effect of congruency whereby reaction times would be different in the congruent compared to the incongruent condition. This prediction was supported as in a repeated measures ANOVA a main effect of congruency was found where planning times were faster on congruent than incongruent trials ($F(1, 35) = 34.32, p < .001$).

There was also a main effect of weight group ($F(4.47, 156.57) = 21.31, p < .001$; degrees of freedom corrected (Greenhouse-Geisser) due to a violation of sphericity) demonstrating that there were differences in reaction time across the 7 weight groups. Post-hoc tests (with Bonferroni correction $p < .05$) showed that reaction times in weight group 1 were significantly faster than reaction times in all other weight groups, reaction times in weight group 2 were significantly faster than reaction times in groups 3, 4, and 5, and reaction times in weight groups 6 and 7 were significantly faster than reaction times in weight group 4. The longer planning times observed for the middle weighted groups (3, 4 and 5) compared to the more extreme weighted groups (1, 2, 6 and 7) reflect the difficulty of the decision as middle weighted groups are more similar to the comparison tube than the more extreme weight groups.

It was further predicted that the size of the interaction effect would be greater for the more extreme weight groups where there was the bigger similarity/dissimilarity between the weight of the stimulus and the weight of the tube. This prediction was not supported as no interactions were found between congruency and weight group demonstrating that the congruency effect was consistent across all weight groups ($p > .05$). See Figure 7a for a graph summarising this data.

The position of the blue tube (right vs. left) and the order that the sections were presented to the participant (either congruent first or incongruent first) were also included in the ANOVA as between subject factors. No main effects or interactions were found for tube position or order ($p > .05$). However, an interaction was found between order and congruency ($F(1, 35) = 18.70, p < .001$) caused by a smaller congruency effect when participants took part in the congruent section first

(order 1) than when they took part in the incongruent section first (order 2) (see Appendix 3 for further exploration of explanation of this interaction effect).

Item as a random factor. When including items as a random factor in a mixed ANOVA with congruency as a repeated factor, and weight group as a between item factor the same main experimental effects were observed for both congruency ($F(1, 56) = 161.27, p < .001$) and weight group ($F(6, 56) = 7.0, p < .001$) and no interaction was found between congruency and weight group ($p > .05$). See Figure 7b for a graph summarising this data. These findings demonstrate that the results can be generalised not only across other subjects that were not included in the present experiment but also across other heavy or light stimuli.

Lift Time

Subject as a random factor. It was predicted that the same congruency effects would not be found for the lift times and this was supported in the statistical analysis where no main effect of congruency was obtained ($p > .05$). A main effect of group was found ($F(4.56, 159.46) = 9.47, p < .001$; degrees of freedom corrected (Greenhouse-Geisser) due to a violation of sphericity) and post-hoc tests (with Bonferroni correction) showed that reaction times in weight group 1 were significantly faster than reaction times in weight groups 3, 4, 5, 6 and 7, reaction times in group 2 were significantly faster than reaction times in groups 3, 4, and 5, and reaction times in group 7 were significantly faster than reaction times in group 4. See Figure 8a for a graph summarising this data.

As it was not expected that any congruency effects would occur in the lift data, any interactions between congruency and weight group were not expected, however an interaction of this type was observed ($F(2.35, 82.2) = 13.84, p < .001$; degrees of freedom corrected (Greenhouse-Geisser) due to a violation of sphericity) showing that there were differences in the congruency effect across the weight groups. On closer inspection it appeared that there was a large congruency effect (faster reaction times to congruent than incongruent trials) for groups 1, 2 and 3, whereas for the heavier groups this congruency effect was not as apparent, and if anything was reversed. This pattern of data was confirmed by planned contrasts: for the items in weight group 1 ($t(38) = -4.54, p < .001$), weight group 2 ($t(38) = -4.68, p < .001$), and weight group 3 ($t(38) = -2.00, p = .54$), reaction times were faster for

the congruent compared to the incongruent condition, whereas for the items in weight groups 4, 5, 6 and 7 the pattern switched where numerically (but not statistically) reaction times were faster for the incongruent than the congruent condition.

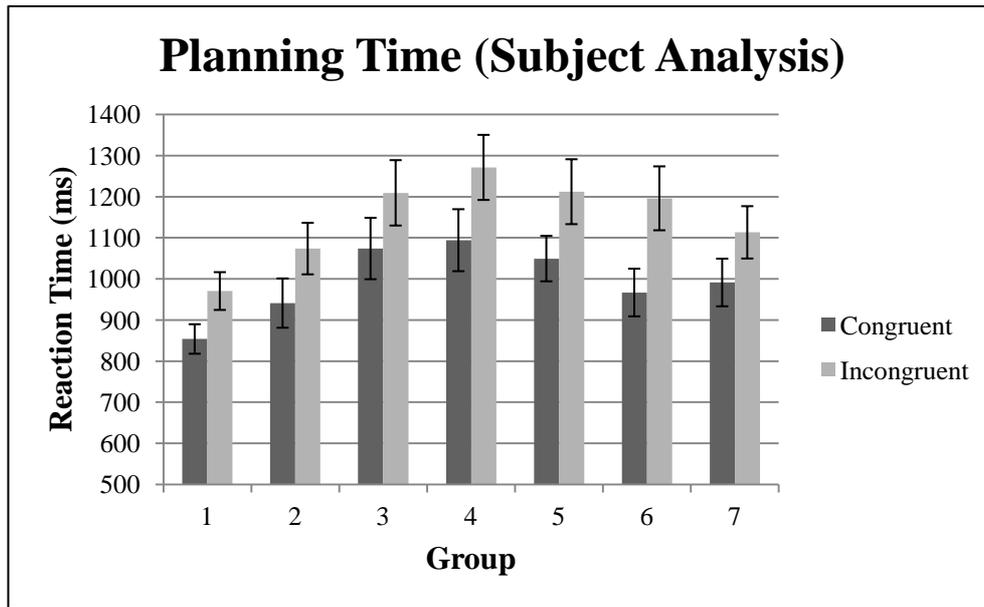
To understand these results we must split the light and heavy groups and treat them separately. The objects in the light groups (1, 2 and 3) are most likely to be rated as being “lighter” than the comparison tube, therefore in these cases the light tube is likely to be lifted on congruent trials and the heavy tube is likely to be lifted on incongruent trials. As the light tube may well be easier to lift than the heavier tube as is lighter and requires less control of force (Eastough & Edwards, 2007), this can explain why for the light object groups the congruent trials are faster than the incongruent trials. If this is the case, the opposite should be expected of the heavier groups (5, 6 and 7) where the objects are likely to be rated as “heavier” than the comparison tube. Here the heavy tube is likely to be lifted on the congruent trials and the light tube is likely to be lifted on the incongruent trials. Therefore, if it takes longer to lift a heavy vs. a light tube you would expect faster reaction times on the incongruent trials compared to the congruent trials. This pattern is seen in the data where the congruency effect (faster for congruent than incongruent trials) switches to an incongruency effect (faster for incongruent than congruent trials) as you go from weight group 1 to weight group 7 thereby supporting this explanation for the interaction. However, it is interesting to note that the congruency effect for the light groups is much larger than the incongruency effect for the heavier groups which suggests that the semantic properties of the objects may well be interacting with the lift times to some degree i.e., the differences between congruent and incongruent trials may therefore be due to a combination of the mechanics of lifting a light vs a heavy tube *and* the stimulus-tube weight congruency.

No main effects were found for the left/right position of the tubes or for section order ($p > .05$). A three way interaction between group, congruency and left/right tube position was found ($F(2.35, 82.2) = 3.56, p < .05$) and was due to bigger congruency effects for the lighter weight groups than the heavier weight groups when the blue tube was on the right compared to when it was on the left. As yet there are no explanations for why this should be. An interaction was also found between order and congruency ($F(1, 35) = 11.06, p < .01$) caused by a smaller

difference between the congruent and incongruent conditions in order 1 (congruent section first) than in order 2 (incongruent section first) (see Appendix 3 for further exploration of this result).

Item as a random factor. When including items as a random factor in a mixed ANOVA with congruency as a repeated factor, and weight group as a between item factor similar experimental effects were observed as when subjects were included as a random factor. A significant main effect of congruency was not found but a main effect was found for the weight group ($F(6, 56) = 10.46, p < .001$) and a significant interaction was observed ($F(6, 56) = 18.22, p < .001$) with post hoc tests (with Bonferroni correction) showing a similar pattern of differences across each of the groups (see Figure 8b for a graph of this data).

a).



b).

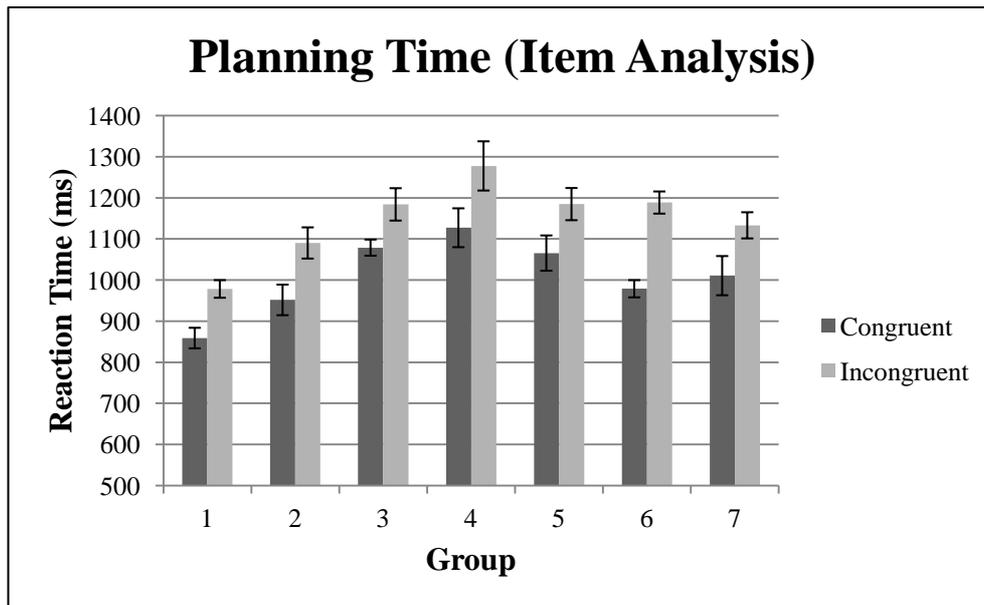
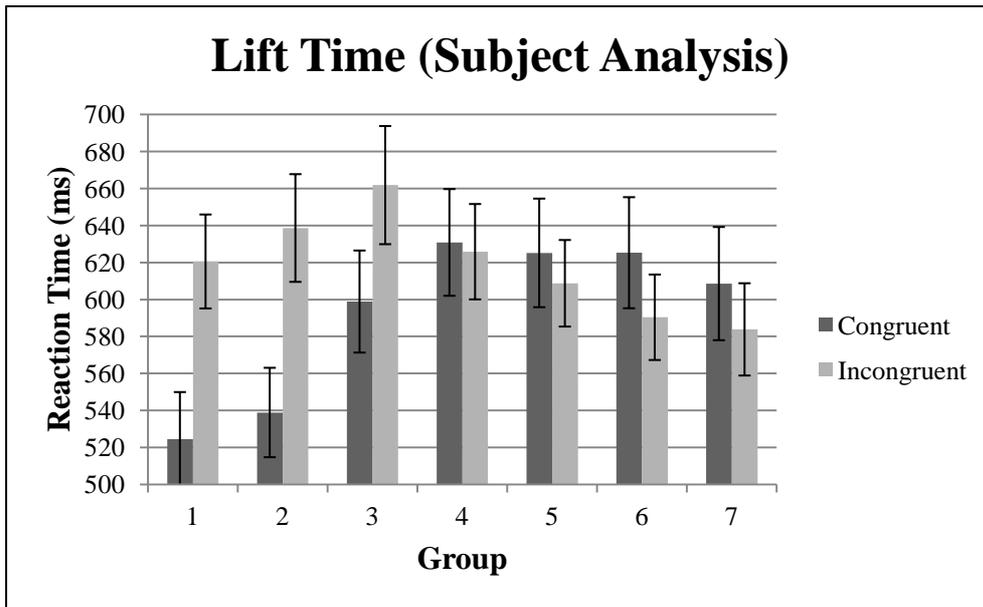


Figure 7. Experiment 1: Mean planning times. With subjects (a) and items (b) as a random factor (bars represent standard error).

a).



b).

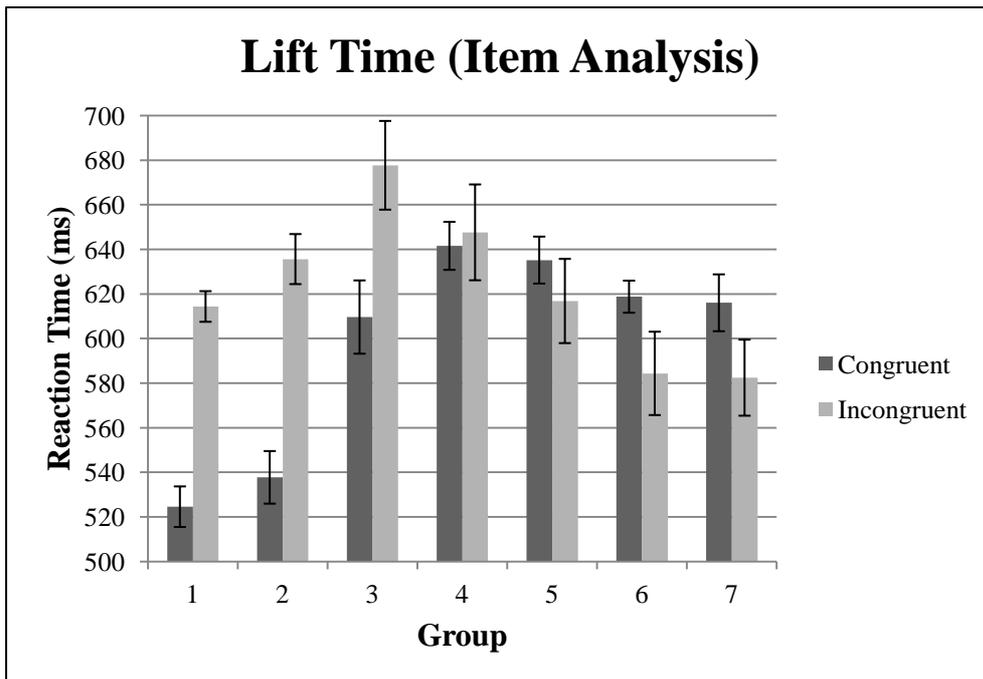


Figure 8. Experiment 1: Mean lift times. With subjects (a) and items (b) as a random factor (bars represent standard error).

5.2.3 Results: Experiment 2 (Implicit Task)

5 participants were removed from further analysis as did not follow the task instructions. To ensure that the task was implicit, participants were asked whether they understood the purpose of the experiment post-experiment. Only 5 out of the 42 participants mentioned the words “weight”, “heavier” or “lighter” in their answer demonstrating that on the whole participants were not aware that the experiment was related to object weight.

On average 6.48% of trials were removed because participants answered differently in each section (i.e., if they thought the same object had a handle in one section but not in the other). This is much lower than the number of trials removed in the explicit experiment (14.5%) due to the more easy categorical nature of the task compared to that in the explicit experiment. As can be seen in Figure 5 the distribution of trials that were removed were distributed across all 7 groups compared to the previous experiment where the largest removals came from the middle groups where the object was closest in weight to the comparison tube.

The implicit data was treated in the same way as the explicit data whereby trials with reaction times further than 3SDs away from the overall participants mean (split by tube weight for the lift time data) were removed from the analysis. As can be seen in Figure 6 there is a large amount of between subject variability in the range of reaction times thereby justifying this subject specific method of outlier removal. On average 2.23% of the planning trials and 2.46% of the lift trials were classed as outliers and removed from the analysis. The number of outlying data points is very similar to those in the explicit experiment.

On average roughly half the objects were thought to have a handle (43.32%) and half not to have a handle (56.67%) therefore participants would not have been able to anticipate the handle status of upcoming stimuli. To remove the positive skew that is inherent to reaction time data the planning time and lift time data were log transformed and again analyses were performed with both subjects and items as a random factor.

Planning Time

Subject as a random factor. It was predicted that if we automatically activate the weight properties of the objects we read about then there should be a difference

in reaction times for weight-congruent trials compared to the weight-incongruent trials even in an explicit task. This prediction was not supported as in a repeated measure ANOVA no main effect of congruency was found ($p > .05$). There was however a main effect of group ($F(6, 198) = 5.90, p < .001$) with post hoc tests (with Bonferroni correction) confirming that reaction times for items in groups 2 and 3 were faster than reaction times for group 4 and 5 items and reaction times for items in group 6 were faster than reaction times for items in group 5. It is not clear why these differences were present. No interactions were seen between the size of the congruency effect and the weight group indicating that the congruency effect was equal across all weight groups ($p > .05$). See Figure 9 for a graph of these results.

Both the blue tube position (right or left) and the order in which participants were given the congruent and incongruent sections were added into the analysis as between subject factors and it was found that no main effects or interactions with other factors were present ($p > .05$).

Item as a random factor. A mixed ANOVA was performed with congruency as a repeated factor and weight group as a between item factor. No main effects or interactions were observed between any of the factors ($p > .05$).

Lift Time

Subject as a random factor. It was predicted that no significant congruency effects would be found for the lift times and this prediction was supported as in a repeated measures ANOVA no main effect of congruency was found ($p > .05$). A significant main effect of group was found ($F(4.55, 150.21) = 3.45, p < .01$, degrees of freedom corrected (Greenhouse-Geisser) due to a violation of sphericity) and post-hoc tests (with Bonferroni correction) showed that lift times were significantly slower in groups 3 and 4 compared to group 5 and significantly slower in group 4 than group 3. There was a close to significant interaction between congruency and group ($F(3.76, 124) = 2.24, p = .072$, degrees of freedom corrected (Greenhouse-Geisser) due to a violation of sphericity). This result indicates that the differences in lift time for the congruent and incongruent conditions was not equal across the different weight groups. Planned contrasts indicate that for items in weight group 1 reaction times are significantly faster in the congruent compared to the incongruent condition ($t(36) = -2.35, p < .05$) and for weight group 7 reaction times are faster in the incongruent compared to the congruent condition ($t(36) = 2.57, p < .05$). These

differences in the congruency effect therefore result in the group-congruency interaction. See Figure 10a for a graph summarising this data. No main effects or interactions were found for tube position and order when they were added into the analysis.

Item as a random factor. In a mixed ANOVA with congruency as a repeated factor, and weight group as a between item factor, it was found that there was no main effect of congruency or weight group ($p > .05$). A significant interaction was found between congruency and weight group ($F(6, 56) = 3.64, p < .01$) with the same pattern of results as seen in the subjects analysis. See Figure 10b for a graph of this data.

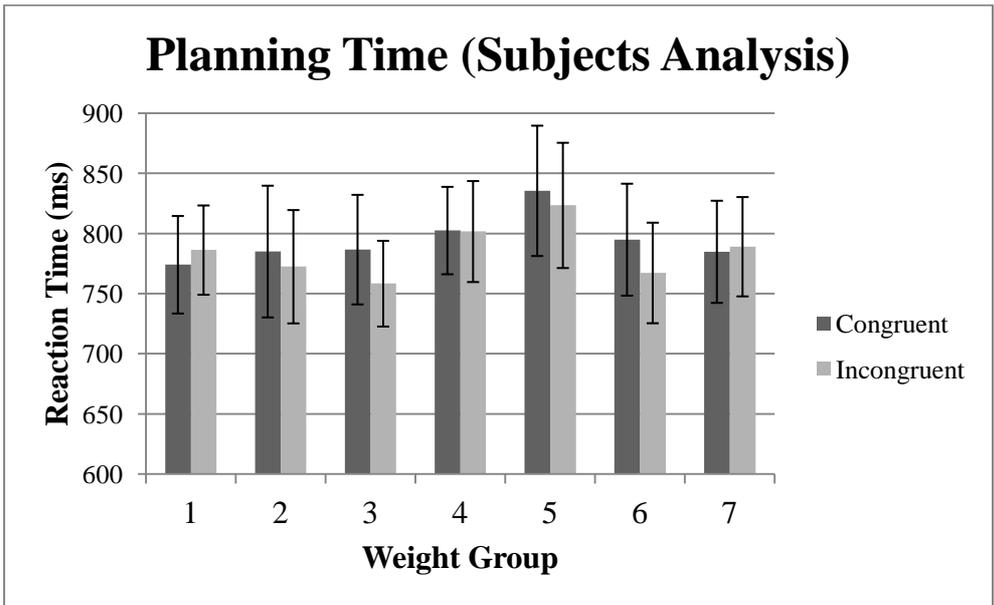
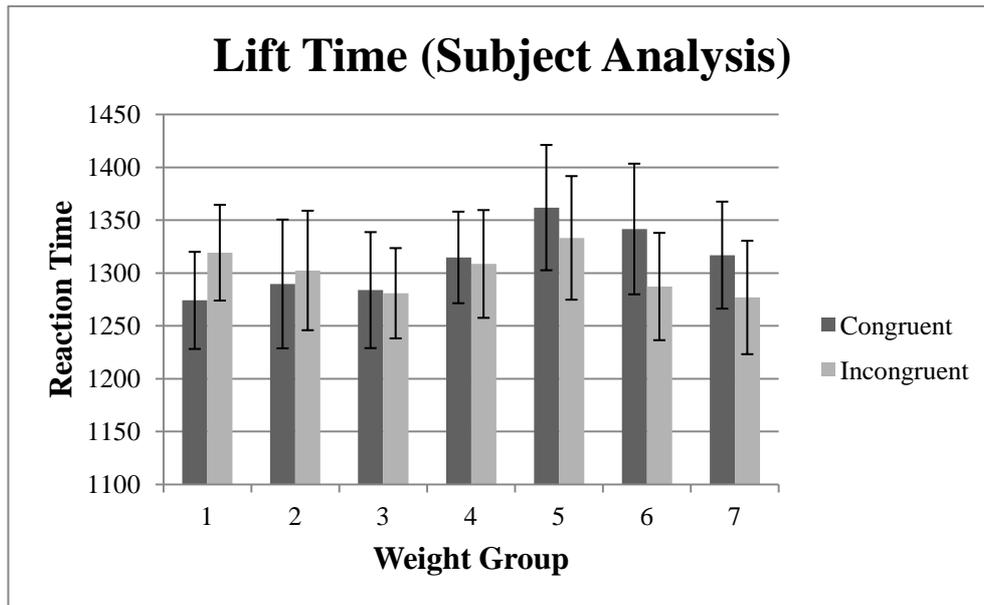


Figure 9. Experiment 2: Mean planning times. With subjects as a random factor (bars represent standard error).

a).



b).

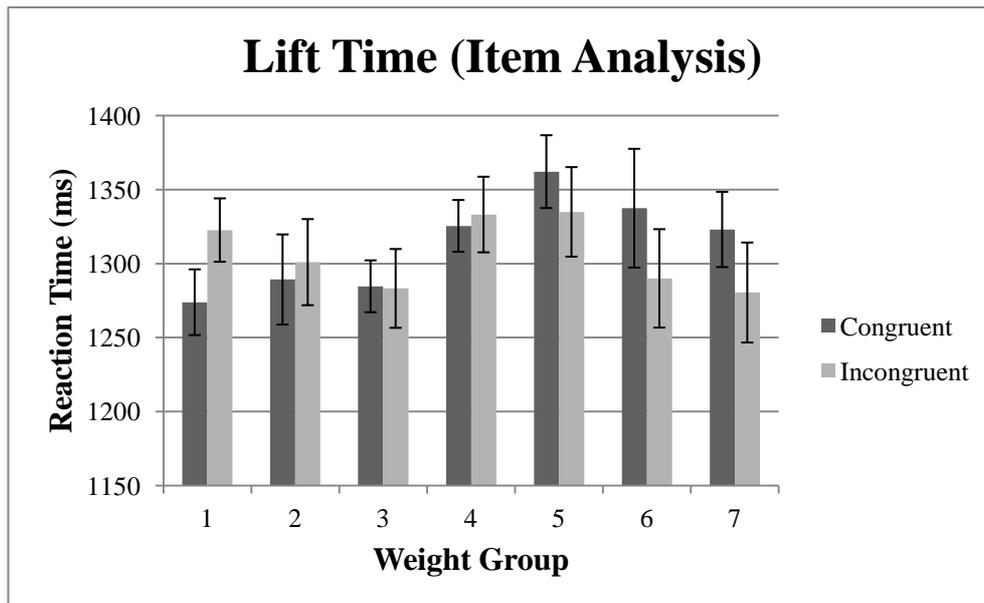


Figure 10. Experiment 2: Mean lift times. With subjects (a) and items (b) as a random factor (bars represent standard error).

5.2.3 Discussion

Explicit Task

A robust congruency effect was observed in the planning time whereby participants responded more quickly when the weight of the rated object and the lifted tube were congruent compared to incongruent. This suggests that when judging the weight of an object word we activate a weight specific representation, the same representation that is required for planning a weight congruent action. The results therefore support the prediction that we have shared weight specific representations for both action and language when performing an explicit weight rating task. However, the degree to which the object and the tube were similar did not seem to matter as no interaction was present between congruency and weight group, instead the congruency effect was equal across all weight groups rather than being larger for those weight groups (1 and 7) that were best matched/mismatched to the light/heavy tube weights as was predicted. It is not clear whether the congruency effect is driven by facilitation compared to baseline (when there is a weight match) or interference compared to baseline (when there is a weight mismatch) or a combination of the two. Without the inclusion of an extra baseline condition for example where participants read words that contain no weight association these possibilities cannot easily be teased apart.

The same congruency effect also occurred for lift times but was less robust as only appeared when items and not subjects are included as random factor. Therefore the congruency effect for lift times is specific to the items used in this particular experiment and does not generalise to other participant populations. This difference across the two different lift times analyses is likely to be due to increased noise and reduced power when subjects are used as a random factor, as the reaction times varied considerably across participants and fewer subjects than items were used. Rather than directly affecting the lifting action, it may well be that the weight of the object stimulus is affecting lift times via the planning mechanism which is kept partially active when carrying out the planned movement for an accurate outcome.

Implicit Task

In contrast to the explicit task, the implicit task revealed no main effects of congruency either for the planning or the lift time. Even though participants are performing a judgement task, as they are not required to explicitly access the object's weight properties the congruency between the weight of the object stimulus and the weight of the to-be-lifted tube does not affect the time taken to plan and perform a weight specific action. These results suggest that the task has an important influence on the way in which we access semantic representations such as weight, in that we only access semantic properties of objects to a great enough degree to interfere with action performance when we actively attend to that particular feature of the object. However, despite this, we may still automatically activate all semantic features of an object as has been previously suggested (L. Barsalou, 1999, 2008; Gallese & Lakoff, 2005; Glenberg, 1997; Jeannerod, 2001), but not to a high enough degree to alter the way in which we perform a congruent action. This was observed in the fMRI experiments described in Chapter 2 and 3, whereby the language induced activity was very slight when compared to the activity induced by action performance suggesting that a higher recruitment of the motor system via language may have been necessary to interfere with the action performance.

Is it a True Congruency Effect?

In the explicit experiment the congruency/incongruency was generated by the similarity in weight between the *stimulus object* and the tube weight. However, the design introduced a potential confound, as although participants were encouraged to associate the colour of the tube with the response (i.e. blue for "heavier", green for "lighter") a second congruency/incongruency was present between the *response label* (heavier vs. lighter) and the *tube weight* (heavy vs. light). In the congruent section, as a strategy for remembering the tube-answer pairings, participants may have associated the tube weight with the response i.e. they may have remembered that lifting the heavy tube constituted a "heavier" answer and lifting the light tube constituted a "lighter" answer. This strategy may have been easier and responses may have been faster than when pairing the responses with the arbitrary tube colours. The same would not be true of the incongruent section where lifting the

heavy tube constituted a “lighter” answer and lifting the light tube constituted a “heavier” answer. As in this scenario there was no congruency between the weight response and the tube weight it may have been more useful to use the colour-response association than the tube weight-response association.

If participants use such a strategy whether consciously or unconsciously, then faster responses would have been expected in the congruent section than the incongruent section irrespective of the weight of the stimulus object. The apparent congruency effect may simply have been caused (or partially caused) by the strategy that the participants were using in the task. Therefore, to rule out this possibility a further experiment was conducted which preserved the congruency/incongruency between the stimulus object weight and the weight of the lifted tube, but removed any confounding compatibility between the response label and the tube weight.

5.3 Experiment 3

A simple change was made to the design of the explicit experiment, instead of having the choice to lift a heavy OR a light tube on a given section, both tubes that participants were presented with were of the same weight. If participants were given the light tubes in the first section then they were given the heavy tubes in the second section, and vice versa when participants were given the heavy tubes in the first section. The tubes were labelled blue or green and each colour was associated with a “lighter” or “heavier” response (see Figure 11 for a comparison between the explicit experiment and experiment 3). Again participants were asked to judge whether the objects were light or heavier than the reference tube and to lift the correctly coloured tube in response. This alteration meant that there was still congruency/incongruency between the weight of the stimulus object and the weight of the to-be-lifted tube, however any additional compatibility between the tube weight and the response label is no longer present as participants always lift a tube of the *same* weight within each section. This means that participants cannot use the weight of the tubes to learn the associated response labels, and instead they must pay attention only to the colour of the tubes thereby reducing the need for any strategy. Furthermore, there is no task switch in this experiment, as unlike in the previous experiments where the colour-response pairing was changed in between sections participants now had the same colour-response pairings throughout.

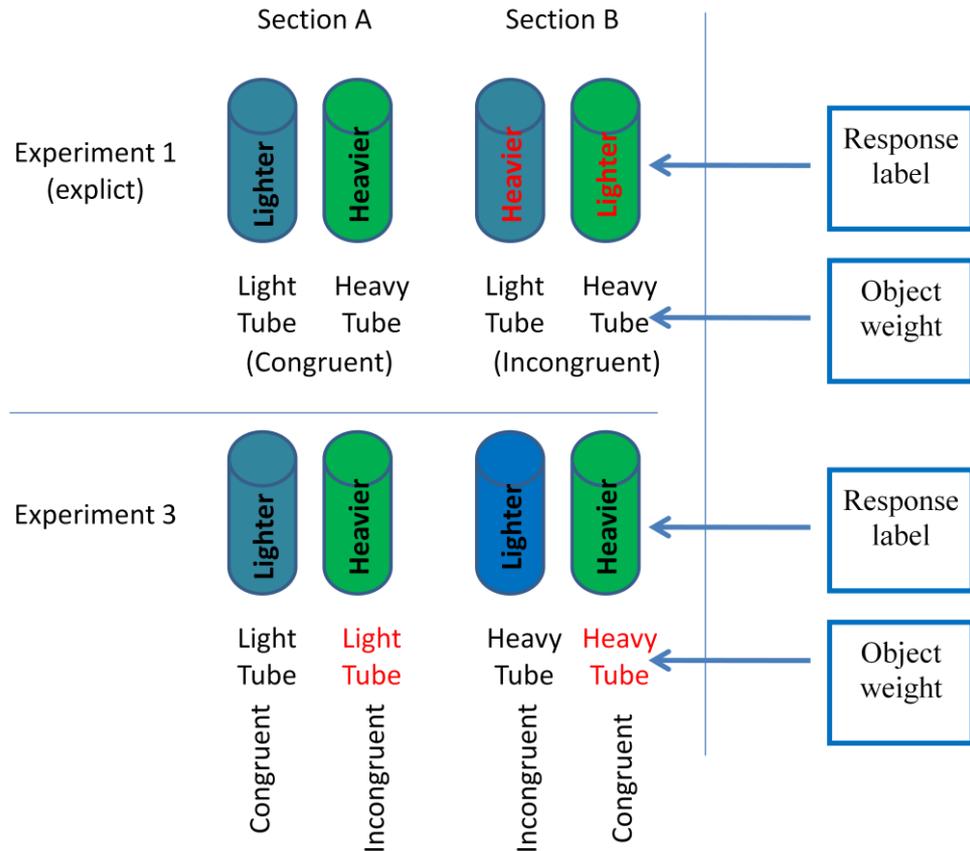


Figure 11. Illustration of the tube colour and tube response-label assignment in experiment 1 (explicit experiment) and experiment 3. The red text highlights indicates what aspect of the experiment was switched in order to reverse the congruency/incongruency.

5.3.1 Method

29 native English speakers took part in experiment 3 (20 female; mean age 19.86, age range 18-29). Participants were recruited for both via the Psychology Electronic Experiment Booking system at the University of York and were mainly students. Participants were paid £2 or were given 30 minutes course credit for their time. All participants were right-handed and the extent to their handedness was tested using an adapted version of the Edinburgh Handedness Inventory (Oldfield, 1971). This questionnaire confirmed that participants were right handed (average scores 86, where anything above 40 is an indication of right handedness). All

participants had corrected or corrected to normal vision and filled in a consent form prior to beginning the experiment.

The stimuli, apparatus, design and procedure were the same as was used in the explicit experiment, therefore participants were asked to make explicit judgements as to whether the object stimuli were heavier or lighter than a comparison tube. A small change was made to the design in that the two tubes options in each section were of the same weight (either either both light, or heavy). The order in which participants received the light tube and heavy tube sections was counterbalanced across participants. Therefore, participants still received congruent and incongruent trials where the weight of the stimulus object and the weight of the to-be-lifted tube matched or mismatched respectively.

5.3.2 Results: Experiment 3

3 participants were removed from further analysis as did not follow task instructions. On average 15.93% of the data was removed due to an answer change across the different sections (a similar value to the explicit experiment). All trials more than 3SDs from the overall participant mean (split by tube weight for the movement data) were removed from the analysis. On average 2.16% of the planning trials and 2.14% of the lift trials were found to be outliers and were removed. To remove the positive skew that is inherent to reaction time data the liftoff and movement data were log transformed and analyses were performed with both subjects and items as a random factor (graphs are shown in ms).

Planning Time

Subject as a random factor. In a repeated measures ANOVA, no main effect of congruency was found ($p > .05$). A main effect of weight group was found ($F(6, 54.25) = 11.63, p < .001$; degrees of freedom corrected (Greenhouse-Geisser) due to a violation of sphericity). Post hoc tests (with Bonferroni correction) demonstrated that planning times for weight group 1 were significantly faster than planning times in weight groups 3,4,5,6 & 7 and planning times in weight groups 2 were significantly faster than planning times in weight group 5. No interactions were found between group and congruency demonstrating that the lack of congruency effect was true for all weight groups (see Figure 12).

Item as a random factor. A mixed ANOVA was performed with congruency as a repeated factor and weight group as a between item factor. No main effects or interactions were observed between any of the factors ($p > .05$).

Lift Time

Subject as a random factor. In a repeated measures ANOVA no main effect of congruency was found ($p > .05$). A main effect of weight group was found ($F(6, 57.7) = 4.52, p < .001$; degrees of freedom corrected (Greenhouse-Geisser) due to a violation of sphericity). Post hoc tests (with Bonferroni correction) demonstrated that lift times for weight group 1 were significantly faster than lift times in weight groups 4 & 5 and lift times in weight groups 7 were significantly faster than lift times in weight group 5. No interactions were found between group and congruency demonstrating that the lack of congruency effect was true for all weight groups (see Figure 13a). The size of the benefit for lifting a light vs. a heavy tube was investigated for light and heavy rated objects. The benefit for lifting a light vs. a heavy tube was no different for light than heavy rated objects ($p < .05$).

Item as a random factor. A mixed ANOVA was performed with congruency as a repeated factor and weight group as a between item factor. It was found that there was no main effect of congruency ($p > .05$) but there was a main effect of weight group ($F(6, 56) = 4.22, p < .01$) and a significant interaction between congruency and weight group ($F(6, 56) = 3.15, p < .05$). Paired t-tests confirmed that there were faster responses in the compatible compared to incompatible condition but only in weight groups 1 and 2 ($p < .05$). However little is read into this result considering that the same results were not found for the heavier stimuli (see Figure 13b). Again, the benefit of lifting a light vs. a heavy tube was no different for light than heavy rated objects ($p < .05$).

Summary. It was found that when the compatibility between the weight of the tube and its associated response label were removed, the remaining congruency/incongruency between the weight of the stimulus object and the weight of the to-be-lifted tube did not affect reaction times as was predicted. This suggests that the compatibility effect that was observed in the explicit experiment may not have been true compatibility effects and may have been affected by this extra confound.

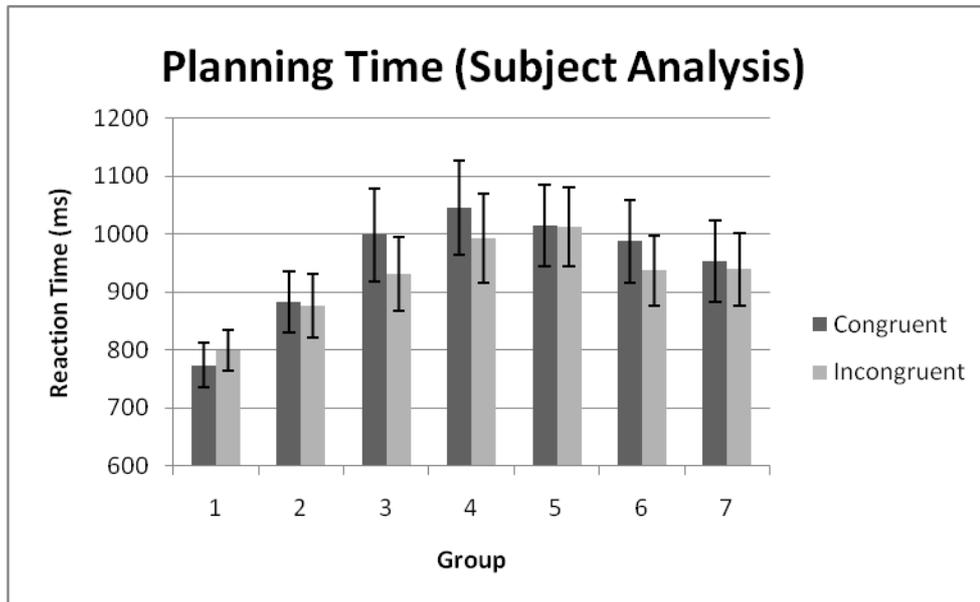
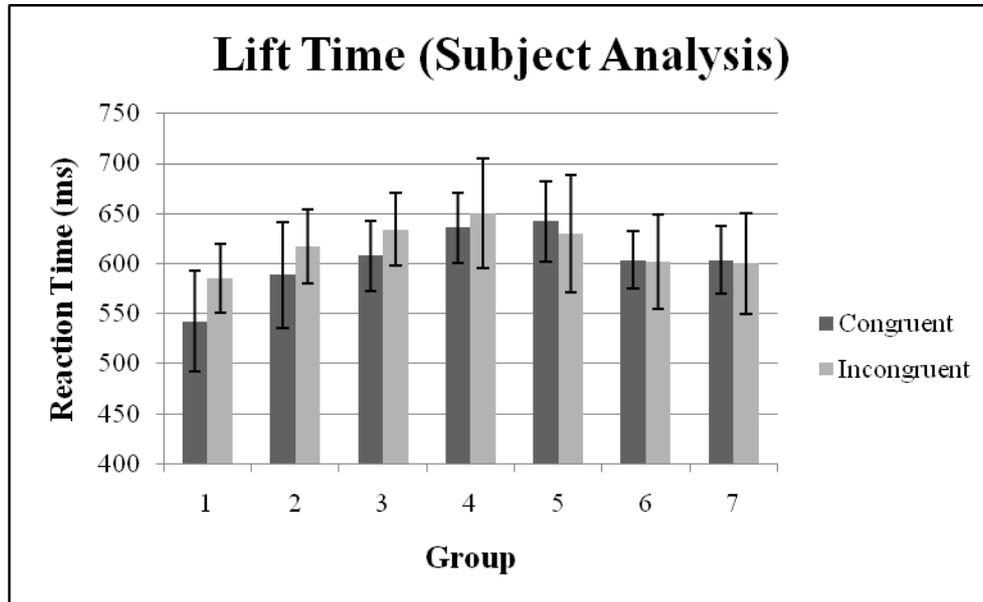


Figure 12. Experiment 3: Mean planning times. With subjects (a) as a random factor (bars represent standard error).

a).



b).

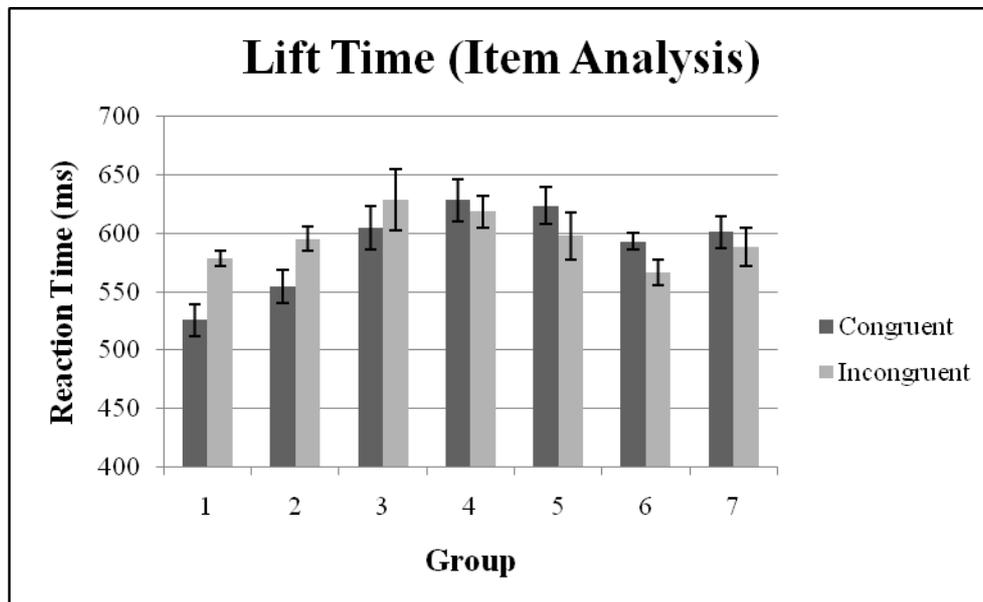


Figure 13. Experiment 3: Mean lift times. With subjects (a) and items (b) as a random factor (bars represent standard error).

5.4 General Discussion

The primary aim of this series of experiments was to identify whether when reading object words we activate the weight properties of those objects to a great enough degree to interfere with action performance. Trials were either congruent or incongruent whereby the weight of the object stimulus and the weight of the to-be-lifted tube either matched or mismatched. It was firstly predicted that there would be differences in the reaction time on these trials if both the action and language task share weight representations. The degree of similarity between the weight of the tube and the weight of the object stimuli also varied: the light tube was most similar to the pre-test ratings of those objects in group 1 and less so as the weight groups increased, similarly the heavy tube was most similar to the pre-test ratings of those objects in group 7 and less so as the weight groups decreased. It was thought that if we represent weight in a modular way (as proposed by the MOSAIC model: Hamilton, et al., 2004; Scorolli, et al., 2009) then there would be greater congruency/incongruency effects for groups 1 and 7 due to the similarity/dissimilarity between the stimulus object and tube weight.

Furthermore, the context in which the congruency/incongruency was embedded was manipulated to assess whether the size of any effects were enhanced by the degree to which attention was drawn towards the weight features of the object words. Therefore, participants performed a task that either explicitly required the activation of the object's weight features or was more implicit and did not require access to the object's weight information. It was predicted that if we automatically activate specific weight representations when reading language that effects would be seen in both the explicit and implicit task. However, if it is necessary for attention to be consciously diverted towards the weight information in order for an interaction to take place, then congruency effects were only expected in the explicit and not the implicit task. These congruency effects were expected to affect the time taken to plan the tube lift rather than the time taken to physically lift the tube.

Interestingly in the explicit task (experiment 1) a congruency effect was observed whereby reaction times were faster in the congruent compared to incongruent condition supporting the main prediction, however, the second prediction was not

supported as the same sized congruency effect was found across all weight groups and was no larger/smaller for weight groups 1 and 7. The same congruency effect was not observed in the implicit task suggesting that the weight of the object stimulus *does* alter the time it takes to plan and perform a weight congruent action, but only when the weight of the stimulus object was consciously processed. This opposes the suggestion by several researchers that we automatically activate the weight of the objects that we read about to a great enough extent to interfere with action performance (Boulenger, et al., 2006; Pulvermuller, Shtyrov, et al., 2005), for weight at least as in the implicit context this was not the case. It may be that weight is a more subtle action feature and is itself not salient enough to interfere with action performance as are other features such as grip type (Masson, Bub, & Newton-Taylor, 2008; Masson, Bub, & Warren, 2008) and movement direction (Glenberg & Kaschak, 2002; Taylor, et al., 2008; Taylor & Zwaan, 2008; Zwaan & Taylor, 2006).

However, it was possible that despite several control measures, an additional confounding factor may have influenced the positive results in the explicit task, as not only was there a congruency/incongruency between the stimulus object weight and the tube weight, but there was also a congruency/incongruency between the tube weight and its associated response label. It was thought that participants may have strategically used this confounding compatibility to remember the tube–answer pairings and therefore have been faster in the congruent than the incongruent condition regardless of the weight of the stimulus object. Furthermore, as the same sized congruency effects were observed across all weight groups, this suggests that a more general non-weight specific compatibility effect was the cause.

A further experiment was therefore carried out to remove this confounding factor and retest the initial hypotheses. Instead of being presented with one light and one heavy tube choice on each trial participants were given same weight (light or heavy) pairs of tubes. Across the experiment the same congruent and incongruent trials were presented where the stimulus object weight and tube weight either match/mismatched respectively, but this design enabled the removal of the extra confound to assess its contribution to the existing congruency effect. It was found that once the confound was removed the compatibility effect disappeared suggesting that this confound played a

significant role in producing the congruent effect in the initial experiment. This indicates that even in an explicit task that required the activation of the object weight features, participants did not activate motoric weight representations to a great enough degree to interfere with action performance. Thus, the results from the first experiment represent a compatibility effect between the weight of the object and the response label (lighter or heavier) rather than between the weight of the object and the weight of the tube to be lifted.

There is a possibility that the effects found in the initial experiment are a combination of the targeted compatibility effect and the confounding label compatibility effect, and that this experiment was not powerful enough to reveal any effects generated solely by the targeted compatibility effect. Perhaps with the addition of more participants (nearly double the number was recruited in the initial experiment) an effect would have been more apparent, however no hints of an effect were seen with the number reported here. It is also possible that the other changes to the task may have resulted in a lack of effects in this final experiment, for example participants were presented with the same weight tubes as opposed to one light and one heavy tube. It may be that the physical contrast between the light and heavy tube was necessary in the initial experiment to generate compatibility effects.

Weight is a very subtle object feature as we less frequently talk about objects in terms of their weight, instead we are more likely to talk about the more salient visual features of an object or the function than the object plays (which is not necessarily physical). Therefore, it may be much more difficult to find behavioural interactions between action and language for a feature like weight, as we may be less likely to automatically access the stored weight features of an object. This is clear from the literature where numerous successful interaction effects have been identified in the visuo-spatial domain but less so for weight. Furthermore, weight may become much more of an important and salient feature when in context, for example, when viewing an object picture, or better still a video of a physical interaction with an object (Hamilton, et al., 2004). Therefore, it may be interesting to identify whether effects using this experimental design can be obtained for a different stimulus domain. However, it is

worth noting that the explicit nature of the task used in the third experiment clearly puts the object words in a weight-relevant context and still no effects were observed.

Another alternative theory is that participants are using visual rather than motoric features of the objects in order to access weight information for example they may visualise the size of the object in order to estimate an object's weight. If this is the case then these purely visual representations would not be expected to interfere with motoric representations that are themselves used in action performance, and therefore interactions would not occur. Furthermore, the size of the objects could not be controlled across the heavy and light groups so it is possible that participants can use this information to inform their decisions.

A final consideration is that measurable congruency effects may be present, however they may not have manifested themselves in the time taken to plan or perform an action. Many kinematic differences exist between light and heavy object lifts for example more force and a stronger grip is used to lift a heavy than a light object. Therefore, the weight of a linguistically presented stimulus object may interact with these specific kinematic aspects of action performance. This is especially shown in the study conducted by Scorolli and colleagues (Scorolli, et al., 2009) where participants were faster to reach their peak velocity when the weight of the object in the sentence and the weight of the lifted box were congruent compared to incongruent. Therefore, it may be important in any future work to consider fine grained kinematic factors as well as reaction times.

In conclusion, it is clear from the fMRI data that motoric areas responsible for the performance of hand actions are activated to a weight specific degree when reading action sentences. However, any behavioural consequences of this neural organisation cannot be revealed using the methodologies described so far. It may be that these fMRI activations for action language are below a certain threshold needed to interfere with action performance or that action language is really being processed in some other format elsewhere, and doesn't engage crucial weight representations that are housed in motor regions. However, many other methodologies are still available to further explore the effect that weight specific action language has on action performance and future work may well reveal these shared weight specific action representations.

Chapter 6

Discussion

Action language dominates much of our human communication and allows us to flexibly communicate detailed motoric information. Importantly, the experiments included in this thesis attempt to further our understanding of the mechanisms that underlie our ability to seamlessly comprehend action events that are described to us via action language, using a combination of fMRI and behavioural methods. The work is divided into several hypotheses, each of which aims to evaluate the outstanding questions relating to the representations that action language recruits during comprehension. In Chapters 2 and 3 it was firstly hypothesized that action language recruits very detailed representations (i.e., beyond the level of the body part) that are grounded within the motor system, and furthermore that these representations are specific, in that the same activity will be elicited by the language as if the action itself were performed (in terms of the regions that are activated and the amplitude of the activity). Secondly in Chapter 3, the nature of these shared representations was investigated to explore the role of the regions that are involved in action language comprehension: Do we understand language by re-enacting the full pattern of neural activity that would be required for its performance, or is the activated representation to an extent removed from our experience of performing actions and instead more cognitive in nature? Finally in Chapters 4 and 5 behavioural methods were employed to test the hypothesis that language induced activations are functionally related to action language comprehension, as opposed to being unrelated to accessing the word meaning. The resulting experimental findings provide novel insights as to the information we recruit when attempting to understand the action language we encounter, and can help us to better understand how we are so able to easily interpret the action information that we are provided with via language.

6.1 The Nature of the Representations that Action Language Engages?

6.1.1 Specificity of Representations

Previous research has demonstrated that action language recruits body-part specific regions of the motor system (Boulenger, et al., 2008; Hauk, et al., 2004; Tettamanti, et al., 2005). However, it was felt that in order to test the limits of the specificity of the representations that language recruits, it must be shown that other more subtle action features are activated when reading action language. Therefore, the experiments described in Chapters 2 and 3 aimed to identify whether when reading action language the same pattern of activity is found as if the action itself were to be performed for features other than body part. As described in Chapter 2 it was found that when reading action language that implies different degrees of physical effort, activity in the motor system was modulated in an effort specific manner whereby more effort produced greater activity in the same way as it would if the actions themselves were performed. Furthermore, as described in Chapter 3 the same experience based hand specific pattern of activity is elicited in the motor system both when performing a hand specific action and when reading about an action that requires that same hand. This evidence suggests that when we read about actions we do not simply activate a generic body part specific representation; instead language recruits much more detailed action features thereby supporting the embodied framework.

A further finding was that the effort specific neural modulation (as described in Chapter 2) occurred when the effort information could only be ascertained by the semantic combination of words across the sentence. This demonstrates that these effects are not simply driven by the verb (e.g., “pull”) and its strong association with an action as could be the case in countless other experiments, instead these activations are driven by the combination of all words across a sentence and therefore truly reflect language processing. Therefore, when reading action language, there is an interaction between each word’s “cell assembly” that allows the reader/listener to extract the action relevant properties of each word, integrate this information and therefore interpret the meaning of the sentence as a whole. In addition to the motor system, the pars triangularis was also found to be sensitive to the effort content of the sentence and its activity was

correlated with that of sensorimotor regions. As this area was not activated by action performance, this region appears to play a specific role in language processes – in this case in the integration of detailed action information across a sentence. It is proposed that semantic information from sensorimotor areas feeds forward into the pars triangularis in order for combinatorial processes to occur and for detailed action language understanding to take place.

6.1.2 A Common Abstract Representational System

It is clear from previous fMRI experiments (e.g., Hauk, et al., 2004) that when action and language tasks share a specific action feature the two patterns of activity do not completely overlap. The results from the current fMRI experiments support these findings, as even when the action that was described was the same as the action performed the overlap was minimal (see chapter 3, Figure 1), with action language activity extending much further anteriorly than the action performance activity. The extent to which action language recruits motor representations is therefore unclear – what does the overlapping activity represent? When breaking down the action performance task into its different action components, it was found that action language recruits those regions that are responsible for the planning of actions (secondary motor regions) and not areas responsible for the execution of the planned action (primary motor regions). This suggests that during the comprehension of action language we do not fully re-enact or “simulate” the described action using all the same neural resources as are required for the performance of the action, instead we partially re-enact the action using only certain components of the action system.

This finding opposes any strong Hebbian accounts of embodied cognition where a word’s meaning becomes established during experience through the concurrent firing of neurons responsible for action/perception and neurons involved in processing the visual/auditory/phonological attributes of the action word (Pulvermuller, 1999). An account such as this would predict that on encountering an action word, all the same neurons would be re-activated as if the action itself were to be performed irrespective of any other factors such as task or context. This prediction was not supported in the

described experiment, where only a subset of more anterior action areas related to action planning were re-engaged during action language processing.

The observed results are more compatible with other alternative models of embodied cognition that despite still grounding language meaning within modality specific regions, propose language recruits only more abstract representations that are somewhat separated from those neural mechanisms that are exclusively involved in action/perception itself (L. Barsalou, 1999; L. W. Barsalou, Kyle Simmons, Barbey, & Wilson, 2003; Martin & Chao, 2001). One such model is the Perceptual Symbols System (L. Barsalou, 1999; L. W. Barsalou, et al., 2003) where action meaning is represented as perceptual symbols within association cortices away from primary motor/perceptual regions. As in the current studies more anterior action planning areas were commonly activated by action and language, whereas more posterior primary motor regions were exclusively activated by action performance, this provides support for the existence of these more symbolic representations. It is possible that within a modality-specific system, as you move anteriorly from primary motor/perceptual regions the type of representation changes becoming more cognitive and abstract whereby our experiences of objects and actions become more generalized. In the motor domain it has been proposed that the more rostral the activation in the dorsal premotor cortex, the more cognitive the role that the areas plays and the less associated with our experience of performing actions it becomes (Boussaoud, 2001; Johnson, et al., 1996; Picard & Strick, 2001; S. Simon, et al., 2002). As more rostral/anterior regions were recruited in the current experiments, this suggests that action language recruits representations that are abstract and cognitive in nature.

Results compatible with this type of grounded account are also found more broadly in other modalities. For example, in the motion literature V5/MT a region responsible for the perception of motion is insensitive to motion language, however an area just anterior to it in the posterior middle temporal gyrus is activated both by motion perception and by motion language (Gennari, MacDonald, Postle, & Seidenberg, 2007; Kable, Lease-Spellmeyer, & Chatterjee, 2002). As similar activation patterns to those found in the present studies can be found in other domains, this suggests that this

representational structure can be thought of as a general rule of conceptual organization that can be applied across all modalities.

But why does language recruit more anterior regions of the motor system that are involved in the more cognitive planning aspects of action processes? One contributing factor may reflect the nature of language processing more generally. Language differs from visual perception as when viewing an object or an action taking place, all the relevant information is present. However, when reading/hearing action language less detail is available, for example, for a sentence like “the man is lifting the box” we have a rough understanding of the event taking place, however we do not know other factors that may be relevant for the action meaning, such as whether the man is big and strong as opposed to small and weak, or using one/both hands, furthermore, we do not know how big the box is and how heavy it is and how far off the ground the box is being lifted. These are all factors that would be apparent if we were to observe the action taking place, however understanding action language relies upon these more generic representations and that is why we may recruit more flexible cognitive representations that are more anteriorly represented.

In addition, information from the action modality is itself fairly complex to represent as often several variables need to be taken into consideration for the formation of an accurate representation. For example, the representation of an object’s weight depends on several factors including the size of the object, whether it is hollow or solid and the material it is made from. Furthermore, the effort required to lift the object depends of a further number of factors such as the position/orientation of the object, whether the object has handles, and the strength of the actor. As these action attributes are fairly complex and as the physical effort required must be calculated from the combination of multiple factors, their representation may rely on more abstract and cognitive rostrally located planning representations that are found to be active in the current experiments.

The results of the initial experiments therefore suggest that, as well as activating those regions that are involved in language processing more generally, action language activates a representational system for action meaning that is housed within the motor system itself. However, the representation that language elicits is abstract in nature and is removed from the original neural state that existed when the action itself was initially

executed. More specifically, language recruits the more cognitive aspects of the motor system, those that are involved in the planning aspects of the action process.

6.2 Engaging the Classic Mirror Neuron System

Traditionally, one of the key areas thought to be involved in the representation of action information is the ventral premotor cortex/ *pars opercularis* (Broca's area BA44). Much work has found evidence for "mirror neurons" at the physiological level within the monkey cortex (e.g., Gallese, et al., 1996) and several human imaging studies have found it to be engaged during both action perception and action performance (Buccino, Lui, et al., 2004; Buccino, Vogt, et al., 2004a; Calvo-Merino, et al., 2005; Cross, et al., 2006; Cross, et al., 2009; Filimon, et al., 2007; Gazzola & Keysers, 2009; Grezes & Decety, 2001; Iacoboni, et al., 1999; Nishitani & Hari, 2000, 2002; Postle, et al., 2008). However, it is less clear what involvement this area has in action language processing. Several experiments have found that this region is sensitive to action language (as opposed to non-action language) more generally in a body-part independent manner (Aziz-Zadeh, et al., 2006; Hauk, et al., 2004; Tettamanti, et al., 2005), however, this region does not appear to be active in the same way during action language comprehension *and* action performance for actions other than those related to the mouth (Hauk, et al., 2004). Instead common overlap for the two tasks for hand and leg actions seems to engage the dorsal premotor cortex according to a body-part somatotopic mapping. The current fMRI experiments found the same engagement of the dorsal premotor cortex, as despite being activated by language more generally, the ventral premotor region was no more sensitive to action language than non-action language. It has been suggested that the ventral premotor cortex may be active in previous experiments due to uncontrolled factors such as verbalisation of stimuli or due to the inclusion of a non-language baseline (this area is also considered to be vital for the phonological representation of linguistic information) (De Zubicaray, et al., 2010; Hashimoto & Sakai, 2002). As the current experiments employed strict control over linguistic variables, this may explain the lack of action language sensitivity in this area.

Alternatively, it may be that different types of action information activate Broca's area (BA44) to differing degrees, resulting in a lack of effects in this area in the current

experiments. Two different action circuits have been postulated in the literature; the dorsolateral circuit that includes the ventral premotor cortex and the dorsomedial circuit that includes the dorsal premotor cortex (see chapter 1). It is thought that the dorsolateral circuit is involved in the direct one-to-one mapping of the sensory properties of a perceived action onto an action plan, for example, it would play a role in mapping an observed grip onto one's own grip motor plan (Fogassi, et al., 1998; Fogassi & Luppino, 2005; Gallese, et al., 1996; Gallese, et al., 2002; Murata, et al., 2000; Rizzolatti, et al., 1996; Rizzolatti, et al., 2001; Rizzolatti & Luppino, 2001; Sakata, et al., 1995; Taira, et al., 1990). The dorsomedial circuit on the other hand is thought to represent associations between arbitrary action cues and their associated action plans where there is no one-to-one mapping involved, for example, it would play a role in learning to associate colour with an action (Cisek & Kalaska, 2004; Johnson, et al., 1996).

For a number of reasons the stimuli used in the current experiments can be considered relatively arbitrary and reliant upon learned associations with action plans, therefore it may be that this causes the dorsomedial circuit (and consequently the dorsal premotor cortex) to be activated rather than the dorsolateral circuit and the ventral premotor cortex. Firstly, the actions were presented via language which is itself dependent on our ability to map the words that we read/hear onto meaningful action information. Language can therefore be thought of as an arbitrary cue, as words themselves are symbols whose meaning bears no relation to the semantic information they represent. For example, in the case of the hand-specific stimuli in the experiment described in chapter 3, the words "left" and "right" only gain meaning by becoming associated with movement of the left versus the right hand. The activation of the dorsal premotor cortex may therefore have been due to participants consulting these stored language-action neural associations during the language tasks in the current experiments.

Additionally, it may be that there is something special about the type of action features that are manipulated which can explain the dorsal position of the activation. Unlike, other attributes such as size, shape or graspability, an object's weight information that is necessary for planning a specific action cannot be accurately

calculated from the visual appearance of an object, as there is no consistent visual-to-motor mapping between an object's weight and its visual appearance (small objects can be very heavy and large objects can be very light) therefore we must therefore learn to associate an object with its weight through experience (Chouinard, et al., 2005). If learned associations between arbitrary stimuli (such as an object's visual features or associated word label) and motoric features such as weight are thought to be represented in the dorsal premotor cortex, this may explain the responsivity of this area in the current experiments and the lack of activity in the ventral premotor cortex.

From the fMRI experiments it can be concluded that as well as activating an anterior abstract representation, weight specific action language specifically activates a dorsomedial mirror system as opposed to a dorsolateral mirror system. This can explain why the dorsal premotor cortex was active in the current experiment as opposed to more classic ventral areas.

6.2 What is the Significance of Language Induced Motor Activations?

Despite observing motoric activity during action language comprehension that is specific to the action performed, this does not mean that our understanding of the action meaning is dependent upon the motor system. Instead comprehension may recruit an amodal system housed in non-modality specific regions such as the temporal lobe (Lambon Ralph, et al., 2009). Therefore these motoric activations may simply reflect post-comprehension processes such as imagery or be the meaningless bi-product of associations between words and motor plans (Mahon & Caramazza, 2008). To aid our understanding of the purpose of these motoric activations, the experiments described in Chapters 4 and 5 focussed on understanding the effort-specific effect in more detail via behavioural methods. If the activity observed in the experiments described in chapters 1 and 2 are meaningful and reflect access to action semantics by recruiting shared representations, then it was predicted that action language and action performance tasks should behaviourally interact with one another when weight information is congruent versus incongruent.

Two experimental designs were used, both of which were based on those used in previous studies. The first was originally utilised by Hamilton and colleagues (2004)

who found that the weight of a lifted box was able to bias weight ratings made on objects presented via action videos. The second experimental design was previously used by Bub and colleagues (2008) to reveal interaction effects between action performance and action *language* but for a non-weight action attribute. Using these designs (with alterations in some cases) the current experiments aimed to replicate these results and unveil any existing interaction effects for compatible versus incompatible weight within a linguistic context. Once any confounding factors had been accounted for, it seemed that no effects of action on language and vice versa could be found even when an explicit weight rating task was used where participant attention was focussed on weight itself.

These null findings have serious implications for our understanding of how we represent weight information and comprehend weight-specific action language. As behavioural interactions could not be found, this suggests that motoric activations as seen in the fMRI experiment are not required for the understanding of action language. Instead, action language may be understood using an amodal mechanism whereby we can understand the meaning of weight information independently of the action system. However, taking into account many other experiments that have found interaction effects for shared action features other than weight (see Chapter 1 for a review), it seems likely that we do functionally recruit these regions for at least some action attributes. An alternative argument is that these null results are specifically due to the weight manipulation – perhaps weight is represented in a very different way to these other action features leading to the lack of observable effects.

It is clear that we plan the effort required before the action itself is performed as our pre-grasp kinematics are altered by the mass of the object to be lifted (Eastough & Edwards, 2007). However, it could be argued that during action performance it is *less* important to pre-plan the effort required for the movement before its initiation than other features such as grip type. Physical effort can be re-adjusted online based upon muscular feedback during the movement, whereas grip type is very specific and without being precisely executed could have disastrous consequences as to the action's outcome. If effort information does not need to be as extensively planned before the movement, and if much of the planning is calculated online during the action, then this may explain

why action language does not interfere with action during this planning stage to as great a degree as other action features. However, if this was the case we would expect to see interactions between action and language later, during the action execution stage which was not the case - therefore, an alternative explanation may be required.

During action language comprehension, weight could be considered a less salient action feature. Objects such as a “radio” are likely to have a multi-modal representation involving visual features, auditory features, as well as action features such as how the object is grasped, how it is manipulated and how heavy it is. Weight therefore plays a small part in this large semantic network and may not have a role in an object’s representation at all for those objects that are rarely lifted (e.g., a vase or a painting) or those that we do interact with but in a non-volumetric functional way e.g., we press buttons on a radio but rarely pick the radio up. If this is the case, when reading action language (or objects alone as in the experiments described in chapter 5), weight may not interfere with action performance, as it is not activated to a high enough degree, thereby causing a lack of behavioural interaction effects. However, it is important to note that in order to counteract these effects, the current behavioural experiments took these factors into account to some degree. For example, the object stimuli that were included were those that are likely to be lifted on a regular basis (based on pre-test weight rating questionnaires) and therefore have salient volumetric properties. Weight should therefore have been an integral part of their semantic network and therefore should have been easily activated in this task. Furthermore, participants were required to actively access the object weight, therefore, associated weight feature should have been highly activated and maximally able to interact with the action performance task. As the experiments to some degree accounted for these confounding factors a different cause for the null result must be sought – perhaps the experiment was flawed due to the choice of dependent measure?

It may be that language *does* functionally recruit motor planning areas, but that any behavioural interactions for weight do not manifest themselves in reaction time differences. A more sensitive method of measurement may therefore be necessary that goes beyond the capabilities of the behavioural designs presented in the previous chapters. Interactions between action language and action performance were found by

Scorolli and colleagues (2009) for the time taken for the hand to reach peak velocity during an object lift suggesting that more detailed kinematic measures may be more sensitive for measuring interactions related to weight. In addition Eastough & Edwards (2007) found that certain pre-contact kinematic factors such as peak grasp aperture were affected by the mass of the to-be-lifted object. Subtle kinematic effects such as these would not have been picked up using overall reaction time measures, therefore it would therefore be interesting to assess whether action language relating to weight could induce similar consequences for grasp during planning. Furthermore, repetitive TMS may be a useful measure as to the functionality of the motor system during the comprehension of weight information. Asking participants to rate object weight after rendering the dorsal premotor cortex temporarily inactive would give an indication as to whether this area is essential for the comprehension of weight information. Without using more fine grained measures or TMS, it is not yet clear whether language induced premotor activations are necessary for the comprehension of action language. The results from the current experiments alone suggest little influence of weight features in language on action performance.

The study by Hamilton and colleagues and Scorolli and colleagues explained their findings using the MOSAIC model, which assumes there are discreet modules devoted to individual weight categories. In light of the positive findings by these previous experiments, the behavioural experiments described in chapters 4 and 5 were also designed to exploit this modular organisation. However, it is difficult to reconcile this modular view with the fMRI data where there is a general increase in the amplitude of the activity across motor areas as the effort in the sentence increases. How the weight-specific modules in the MOSAIC model are implemented in a neural system and whether the brain in fact processes effort in a modular fashion is therefore unclear. It is unlikely that what we see in the fMRI experiment is a reflection of a modular system, because a modular system would not necessarily predict a greater amplitude of activation for higher effort actions, instead the pattern of activity would be distributed across a group of neurons that are responsible for weight-specific action representation with a consistent net output for processing of all weights. So is it the case that the behavioural experiments were not designed to capture activity produced by a continuous

magnitude system? Predictions based on this type of system could still be posited, for example that the greater the effort content of the sentence/weight of the object stimulus the greater the recruitment of neurons in the motor system and the bigger the interference effects. This pattern of activation was not seen, suggesting that the experiments did not capture interactions effects that could be generated from either a continuous or modular system type. More high level, abstract modular representations of physical effort cannot be ruled out, for example, a system that is able to more broadly categorise an object as heavy vs light or an action as effortful vs non-effortful. However, the fMRI experiment was not designed to capture this type of effect and the behavioural experiment did not reveal any interactions of this kind.

6.3 The Relationship between Action and Language

One of the main aims of this work was to further our understanding of the relationship between action and language and to assess whether we really do require activation of the motor system for the comprehension of action language. However, the findings described in the fMRI experiments and the behavioural experiments seem to conflict with one another somewhat. On the one hand when reading action language we activate very specific regions of our parietal and premotor cortex that are not only involved in performing that same action, but are activated to the same degree depending on the effort required or our hand-specific experience. In addition these activations occur even in an implicit task where participants did not need to explicitly attend to the weight information in order to perform the task. On the other hand, there is no evidence that these motoric activations are functionally involved in the comprehension of weight specific action language, insofar as reaction times are unchanged when action and language tasks include compatible versus incompatible weight features. So what can be concluded from the experiments described? Can we reconcile these findings and still consider these motoric activations to be meaningful or should they be regarded as being unrelated to the process of comprehension?

6.3.1 Sub-threshold Activation

A consistent finding across the two fMRI experiments was that the degree to which the motor system was activated was of a far lesser amplitude for action language than action performance. Motor representations may therefore be recruited to different degrees depending on whether the task is comprehension or action performance, whereby comprehension only requires slight activation of the motor system but action performance requires more intense activation. This raises the possibility that action language may be essential for the comprehension of action language but that it is not capable of successfully interfering with action performance, as it cannot vastly influence the relatively larger amplitude of action performance activity. In other words, language comprehension may activate the motor system to a level that is sub-threshold for action performance thereby resulting in a lack of observable effect of language on action and null results in the current behavioural work. As this issue itself was beyond the scope of this thesis, additional work would be required to further explore this issue.

6.3.2 How “Shared” are Motoric Representations for Action and Language Tasks?

On the one hand it may be that we do have shared representations between action and language for weight features as proposed in those theories employing Hebbian principles. If this was the case then the fMRI activity seen in the motor system may well reflect access to meaning during language comprehension. In this scenario it could be argued that the reason behavioural interactions were not uncovered was due to the use of an inappropriate dependent measure. Alternatively, the functional overlap between action and language may be minimal and not shared as such, in that the regions responsible for action language comprehension are somewhat removed from those that are involved in action execution. This is supported by the fMRI data whereby the overlap between action and language was minimal, with action language activity extending much further anteriorly than that of action execution. If the overlap between the two tasks is minimal, then interference for shared weight would not be predicted. It is important to note that despite a lack of spatial overlap with action performance, these

language activations can still be considered as modality-specific as opposed to amodal, as they are still housed within the action system. It may be that the motor system *is* required for the processing of action language but that the action representations are distinct from those areas involved in the actual performance of an action. If this scenario is correct, then despite not strictly following the embodied framework, action language can still be considered to be loosely embodied as still involves the action system itself. Furthermore, this pattern of results is also congruous with findings from other modalities such as motion (Gennari, et al., 2007; Kable, et al., 2002; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995) whereby more anterior activations are found for motion perception as opposed to motion language comprehension. It would therefore be interesting to extend the current investigation into other modalities to identify whether the same rules can be applied to different modality-specific representational systems.

6.4 Future Directions

There are several future directions that this research could take, and the most important workstreams are outlined below. It is firstly important to further probe the significance of the imaging data, by exploring other weight-sensitive dependent measures. As well as the speed at which the movements are performed, kinematic measures such as grip position or the strength of the grip could also be investigated as these may reveal differences across the conditions that are specific to interacting with light/heavy objects. Other techniques could also be employed such as TMS to help interpret these results. Recording of motor evoked potentials (MEPs) in combination with single pulse stimulation of the premotor cortex during the presentation of weight-specific language stimuli may well provide a more pure and sensitive measure than reaction times alone. Furthermore, the behavioural consequences of repetitive TMS on the premotor/parietal cortex could be examined to more clearly identify whether these regions are required for the comprehension of weight information. The specific contributions of each of the secondary motor areas could also be investigated using this method.

As the majority of the work followed on from the effort experiment (described in chapter 2), it would be interesting to further investigate the role of the secondary motor areas in the comprehension of hand specific language, in order to follow on from the work described in chapter 3. Firstly, unlike in the effort experiment described in chapter 2, the task used in the experiment described in chapter 3 was explicit in nature, in that participants were expected to actively focus on the hand information in the sentence. Plus the stimuli in the experiment (chapter 3) were very simple in that the sentences described simple button presses. It would be interesting to explore whether the same effects would be generated from an implicit task which uses more complex stimuli. For example, participants could read about object-directed actions that are typically associated with the dominant hand such as writing, shaking hands etc compared to less unilateral actions such as drinking in a passive task.

It was also unclear from this work (chapter 3) whether the results were truly dependent on the experience of the right handed participants. Therefore, additional work could involve testing left handed individuals to identify whether an opposite or more bilateral pattern of results is obtained. Alternatively, object stimuli could be manipulated to assess whether the strength of activity varies with the degree of interaction experience e.g. more activation for “shelves” vs. “mug”.

It would also be worthwhile to investigate how the weight-specific language data compares to data from other stimulus types. The embodied literature has consistently found that although similar areas are engaged for different types of stimuli, stronger activation is generated from visual/auditory compared to language stimuli. It would therefore be important to ascertain whether similar areas are engaged with weight-specific visual stimuli (pictures/videos) to firstly identify whether similar regions are found to be active, and secondly whether behavioural results across conditions are more readily achieved with this more salient stimulus type.

6.5 Conclusions

There are many demonstrations of embodied effects in the literature; however, rather than simply demonstrating their existence, it is essential to further investigate the

mechanisms that underlie embodied cognition in order to understand the nature of what is grounded in the action system and what its role is in action language processing. The experiments described provide novel findings in that language comprehension recruits highly detailed action representations within the dorsomedial motor system that are specifically involved in abstract action planning processes, and that these effects reflect the content of action sentences as a whole as opposed to being driven by single action words. However, it is still unclear as to whether these activations are necessary for action language processing and whether a distinction can be made between those representations that are required for action and language processes. Further work is therefore needed to firm up these conclusions by assessing the sensitivity of more fine grained kinematic measures and to more widely explore the role of language processing regions outside of that which is shared with action performance. On the whole, the reported work contributes to the embodied semantics literature, in further clarifying the nature of the representations that are activated, and by supporting those theories that postulate the representations that language activates are those that are more symbolic and abstract in character. There are clear parallels between the representational systems housed in the motor system and those in other systems (e.g., motion) suggesting that conceptual principles of a representational system fed by low level sensory information can be applied across all domains within the brain.

Appendices

Appendix 1: List of Stimuli Included in the Experiment Described in Chapter 2

Item	<i>No Effort</i>	<i>Low Effort</i>	<i>High effort</i>
1	The artist is curious about the big drawing	The artist is fetching the big drawing	The artist is fetching the big sculpture
2	The athlete noticed the frisbee	The athlete is throwing the frisbee	The athlete is throwing the javelin
3	The boxer loves his white gym bag	The boxer is carrying his white gym bag	The boxer is carrying his large punch bag
4	The builder needs the empty bucket from the apprentice	The builder is giving the empty bucket to the apprentice	The builder is giving the full bucket to the apprentice
5	The businessman is pleased with the big umbrella	The businessman is carrying the big umbrella	The businessman is carrying the big suitcase
6	The butcher is admiring the carcass on the hook	The butcher is hanging the pheasant from the hook	The butcher is hanging the carcass from the hook
7	The chef hates the saucepan	The chef is lifting the saucepan	The chef is lifting the fridge
8	The child could smell the sock	The child is flinging the sock	The child is flinging the brick
9	The child is fond of the ball	The child is tossing the ball	The child is tossing the rock
10	The cleaner is happy with the duvet	The cleaner is shaking the duster	The cleaner is shaking the duvet
11	The clown remembers the monkey	The clown is pulling the monkey	The clown is pulling the elephant
12	The delivery man has forgotten the piano	The delivery man is pushing the chair	The delivery man is pushing the piano
13	The delivery man is curious about the empty crate	The delivery man is fetching the empty crate	The delivery man is fetching the loaded crate
14	The electrician needs his ladder	The electrician is moving the mirror	The electrician is moving his ladder
15	The farmer is thinking about the bag of groceries in the truck	The farmer is putting the bag of groceries on the truck	The farmer is putting the bag of potatoes on the truck
16	The farmer is worried about the horse	The farmer is pushing the door	The farmer is pushing the horse
17	The farmer is looking at the bucket on the truck	The farmer is putting the bucket on the truck	The farmer is putting the barrel on the truck
18	The farmer is watching the milk in the barrel	The farmer is pouring milk from the bucket	The farmer is pouring milk from the barrel
19	The fireman is happy with his job	The fireman is carrying the baby	The fireman is carrying the man
20	The fisherman is sleeping in the boat	The fisherman is dragging the fish	The fisherman is dragging the boat
21	The fisherman is waiting for the shark	The fisherman is pulling the trout	The fisherman is pulling the shark
22	The gardener hates the spade	The gardener is throwing the stick	The gardener is throwing the spade
23	The gardener is happy with the bench	The gardener is pulling the gate	The gardener is pulling the bench
24	The gardener is observing the wheelbarrow full of leaves	The gardener is pushing the wheelbarrow full of leaves	The gardener is pushing the wheelbarrow full of stones
25	The gardener is pleased with the tree	The gardener is dragging the branches	The gardener is dragging the tree

26	The gymnast is enjoying the new ribbon	The gymnast is moving the new ribbon	The gymnast is moving the big mat
27	The handyman has forgotten the document	The handyman is tearing the document	The handyman is tearing the curtain
28	The housewife is admiring the thick quilt	The housewife is hanging the thin vest to dry	The housewife is hanging the thick quilt to dry
29	The hunter remembers the dead deer	The hunter is picking up the dead rabbit	The hunter is picking up the dead deer
30	The lady is peering at the full pitcher	The lady is fetching the small souvenir	The lady is fetching the full pitcher
31	The lumberjack is looking at the log on the truck	The lumberjack is putting the small saw on The truck	The lumberjack is putting the large log on the truck
32	The maid is watching the new trolley	The maid is pushing the new trolley	The maid is pushing the new wardrobe
33	The man hates the truck	The man is pushing the desk	The man is pushing the truck
34	The mechanic is peering at the jacket	The mechanic is flinging the jacket	The mechanic is flinging the tyre
35	The miner is watching the wagon	The miner is pulling the rope	The miner is pulling the wagon
36	The mountaineer is sleeping by his pack	The mountaineer is dragging his stick	The mountaineer is dragging his pack
37	The mover is curious about the TV	The mover is clutching the CD	The mover is clutching the TV
38	The museum guide worships the tall statue	The museum guide is relocating the small trophy	The museum guide is relocating the tall statue
39	The musician is inspired by the flute	The musician is handing over the flute	The musician is handing over the cello
40	The nurse admires the patient	The nurse is lifting the plant	The nurse is lifting the patient
41	The nurse is observing the large bed	The nurse is dragging the small chair	The nurse is dragging the large bed
42	The plumber dislikes his brown plunger	The plumber is swinging his brown plunger	The plumber is swinging his heavy toolbox
43	The postman has forgotten the bulging packages	The postman is piling the flimsy envelopes	The postman is piling the bulging packages
44	The receptionist has seen the notebook	The receptionist is taking the notebook away	The receptionist is taking the monitor away
45	The rider noticed his helmet	The rider is lifting the helmet	The rider is lifting the motorcycle
46	The servant is pleased with the pillow	The servant is carrying the pillow	The servant is carrying the monitor
47	The shopkeeper is satisfied with the small sweets	The shopkeeper is stacking small sweets	The shopkeeper is stacking big tins
48	The shopkeeper likes the computer on the shelf	The shopkeeper is putting the footballs on the shelf	The shopkeeper is putting the computer on the shelf
49	The soldier is worried about the grenade	The soldier is rolling the grenade	The soldier is rolling the cannon
50	The teacher detests exams	The teacher is stacking the exams	The teacher is stacking the chairs
51	The teacher is pleased with the filing cabinet	The teacher is picking up the golden package	The teacher is picking up the filing cabinet
52	The teenager is focusing on the hoop	The teenager is rolling the hoop	The teenager is rolling the tyre
53	The teenager is glancing at the rugby ball	The teenager is rolling the rugby ball	The teenager is rolling the bowling ball
54	The vet is praising the cat	The vet is holding down the cat	The vet is holding down the sheep
55	The woodcutter is ignoring the log	The woodcutter is carrying the saw	The woodcutter is carrying the log
56	The worker noticed the sand in the bucket	The worker is pouring cereal into the bowl	The worker is pouring sand into the bucket
57	The workman needs a wooden bucket	The workman is picking up an empty bucket	The workman is picking up a beer barrel

Appendix 2: List of Stimuli Included in the Experiment Described in Chapter 4

Weight Group	Object Word	Weight Group	Object Word
0-125g	Envelope Wooden Spoon Pair of dice Ruler Box of matches Yellow duster Twig Lightbulb Shuttlecock	501-625	Leather coat Briefcase Paperweight Carton of milk Picnic basket Cricket bat Phonebook Bag of sugar Hardback book
126-250g	Toilet roll Frisbee Paintbrush Box of tissues Cushion Potato Small torch Screwdriver Badminton racket	626-750g	Wine bottle Rock Bag of flour Spade Bottle of lemonade Champagne bottle Bathroom scales Hammer Hack saw
251-375g	Empty jug Coke can Chopping Board Umbrella Frying pan Hairdryer Tennis racket Tea pot Cricket ball	751+	Drill Filled kettle Terracotta pot Washing powder Sack of rice Full jug Bag of potatoes Brick Log
376-500g	Pineapple Gym bag Garden trowel Iron Rusty saw Dirty mop Empty suitcase Colourful vase Wok		

Appendix 3: Discussion of the Order x Congruency Interaction (Chapter 5, Experiment 1 (with Subjects as a Random Factor))

In the explicit experiment participants could experience one of two different orders: order 1 where they receive the congruent section first and order 2 where they receive the incongruent section first. It was found that in both the planning and lift phase of the response, the size of the congruency effect differed depending on whether participants received order 1 or order 2 (see Figure App 3a, App 3b) for a graph summarising these effects). It is thought that this interaction effect may have been due to a combination of congruency and ease of rating. As participants are rating each of the objects for the second time in section B they may therefore be quicker than in section A irrespective of congruency. When combined with a congruency effect whereby participants are faster for the congruent than the incongruent condition, this may result in an interaction between congruency and order. For instance in order 1, participants are no faster in section A (congruent) than in section B (incongruent). Despite the incongruency in section B which may cause reaction times to slow, this effect may be cancelled out as participants are rating the objects for the second time which may result in faster reaction times. In contrast, in order 2 participants are much slower in section A (incongruent) than in section B (congruent), as participants are not only making their weight judgements for the first time in section A but they are also experiencing the incongruency between the weight of the object and the weight of the tube. This effect is not solely being driven by the stimulus repetition effect as otherwise you would expect a similar pattern of results in both order one and order two where participants were always faster in the second compared to the first section and this was not the case in order 1, therefore congruency is also playing a role. Furthermore, the congruency effect is still present when including all participants irrespective of the section order. This effect is seen not only in the planning phase but also in the lift phase demonstrating that even during the execution of the action itself, the action plan itself may still be active and therefore able to influence the time taken to perform the lift.

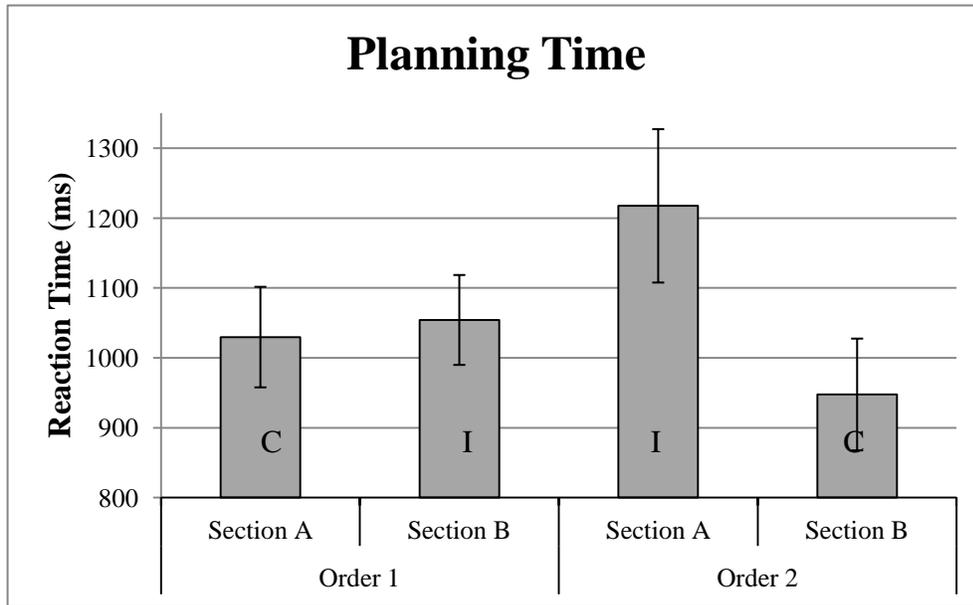


Figure App 3a. Graph depicting reaction times data for planning times demonstrating the interaction between congruency and order. The letters indicate whether that section was congruent (C) or incongruent (I) (subjects as random factor).

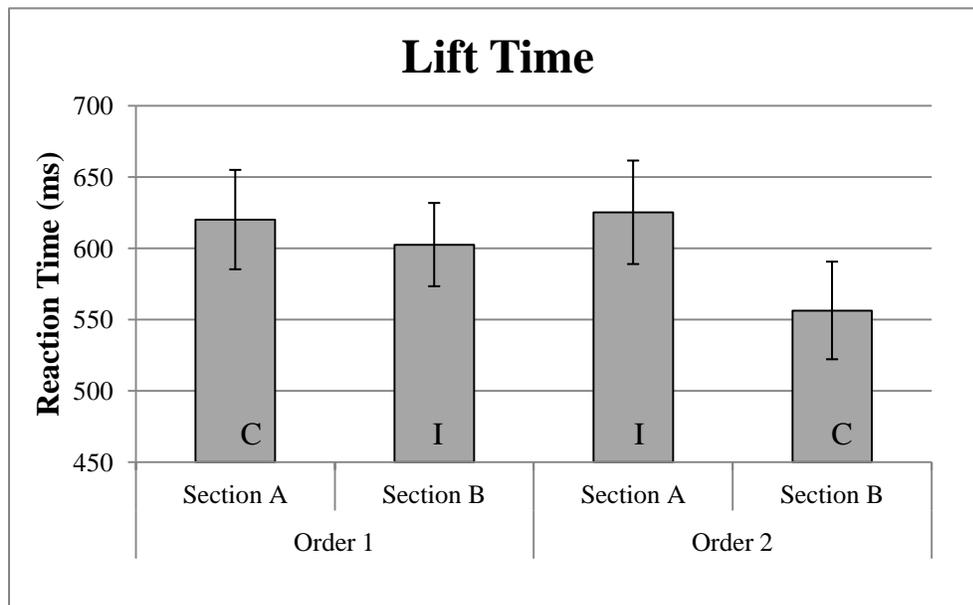


Figure App 3b. Reaction time data for lifts time demonstrating the interaction between congruency and order. The letters indicate whether that section was congruency (C) or incongruent (I) (subjects as random factor).

References

- Aglioti, S., & Pazzaglia, M. (2010). Representing actions through their sound. *Experimental Brain Research*, 1-11.
- Alaerts, K., Senot, P., Swinnen, S., Craighero, L., Wenderoth, N., & Fadiga, L. (2010). Force requirements of observed object lifting are encoded by the observer's motor system: A tms study. *European Journal of Neuroscience*, 31(6), 1144-1153.
- Alaerts, K., Swinnen, S., & Wenderoth, N. (2009). Is the human primary motor cortex activated by muscular or direction-dependent features of observed movements? *Cortex*, 45(10), 1148-1155.
- Alaerts, K., Swinnen, S., & Wenderoth, N. (2010). Observing how others lift light or heavy objects: Which visual cues mediate the encoding of muscular force in the primary motor cortex? *Neuropsychologia*.
- Altmann, G. T. M., & Kamide, Y. (1999). Incremental interpretation at verbs: Restricting the domain of subsequent reference. *Cognition*, 73(3), 247-264.
- Ameli, M., Dafotakis, M., Fink, G., & Nowak, D. (2008). Predictive force programming in the grip-lift task: The role of memory links between arbitrary cues and object weight. *Neuropsychologia*, 46(9), 2383-2388.
- Aziz-Zadeh, L., Maeda, F., Zaidel, E., Mazziotta, J., & Iacoboni, M. (2002). Lateralization in motor facilitation during action observation: A tms study. *Experimental Brain Research*, 144(1), 127-131.
- Aziz-Zadeh, L., Wilson, S. M., Rizzolatti, G., & Iacoboni, M. (2006). Congruent embodied representations for visually presented actions and linguistic phrases describing actions. *Current Biology*, 16(18), 1818-1823.
- Badre, D., & Wagner, A. (2002). Semantic retrieval, mnemonic control, and prefrontal cortex. *Behavioral and Cognitive Neuroscience Reviews*, 1(3), 206.
- Badre, D., & Wagner, A. (2007). Left ventrolateral prefrontal cortex and the cognitive control of memory. *Neuropsychologia*, 45(13), 2883-2901.
- Bak, T. H., & Hodges, J. R. (2004). The effects of motor neurone disease on language: Further evidence. *Brain and language*, 89(2), 354-361.
- Bak, T. H., O'Donovan, D. G., Xuereb, J. H., Boniface, S., & Hodges, J. R. (2001). Selective impairment of verb processing associated with pathological changes in brodmann areas 44 and 45 in the motor neurone disease-dementia-aphasia syndrome. *Brain*, 124(1), 103.
- Barbas, H., & Pandya, D. (1987). Architecture and frontal cortical connections of the premotor cortex (area 6) in the rhesus monkey. *The Journal of comparative neurology*, 256(2), 211-228.
- Barsalou, L. (1999). Perceptual symbol systems. *Behavioral & Brain Sciences*, 22(4), 577-609; discussion 610-560.
- Barsalou, L. (2008). Grounded cognition. *Annual Review of Psychology*, 59, 617-645.

- Barsalou, L. W., Kyle Simmons, W., Barbey, A. K., & Wilson, C. D. (2003). Grounding conceptual knowledge in modality-specific systems. *Trends in cognitive sciences*, 7(2), 84-91.
- Battaglini, P., Muzur, A., Galletti, C., Skrap, M., Brovelli, A., & Fattori, P. (2002). Effects of lesions to area v6a in monkeys. *Experimental Brain Research*, 144(3), 419-422.
- Battaglini, P., Muzur, A., & Skrap, M. (2003). Visuomotor deficits and fast recovery after area v6a lesion in monkeys. *Behavioural Brain Research*, 139(1-2), 115-122.
- Baumgaertner, A., Weiller, C., & Buchel, C. (2002). Event-related fmri reveals cortical sites involved in contextual sentence integration. *NeuroImage*, 16(3PA), 736-745.
- Beauchamp, M., Lee, K., Haxby, J., & Martin, A. (2002). Parallel visual motion processing streams for manipulable objects and human movements. *Neuron*, 34(1), 149-159.
- Beilock, S., Lyons, I., Mattarella-Micke, A., Nusbaum, H., & Small, S. (2008). Sports experience changes the neural processing of action language. *Proceedings of the National Academy of Sciences*, 105(36), 13269.
- Berner, J., Schönfeldt-Lecuona, C., & Nowak, D. (2007). Sensorimotor memory for fingertip forces during object lifting: The role of the primary motor cortex. *Neuropsychologia*, 45(8), 1931-1938.
- Beurze, S., De Lange, F., Toni, I., & Medendorp, W. (2007). Integration of target and effector information in the human brain during reach planning. *Journal of Neurophysiology*, 97(1), 188.
- Beurze, S., De Lange, F., Toni, I., & Medendorp, W. (2009). Spatial and effector processing in the human parietofrontal network for reaches and saccades. *Journal of Neurophysiology*, 101(6), 3053.
- Binkofski, F., Buccino, G., Stephan, K., Rizzolatti, G., Seitz, R., & Freund, H. (1999). A parieto-premotor network for object manipulation: Evidence from neuroimaging. *Experimental Brain Research*, 128(1), 210-213.
- Binkofski, F., Dohle, C., Posse, S., Stephan, K., Hefter, H., Seitz, R., et al. (1998). Human anterior intraparietal area subserves prehension: A combined lesion and functional mri activation study. *Neurology*, 50(5), 1253.
- Boronat, C. B., Buxbaum, L. J., Coslett, H. B., Tang, K., Saffran, E. M., Kimberg, D. Y., et al. (2005). Distinctions between manipulation and function knowledge of objects: Evidence from functional magnetic resonance imaging. *Cognitive Brain Research*, 23(2-3), 361-373.
- Borreggine, K., & Kaschak, M. (2006). The action-sentence compatibility effect: It's all in the timing. *Cognitive Science: A Multidisciplinary Journal*, 30(6), 1097-1112.
- Borroni, P., Montagna, M., Cerri, G., & Baldissera, F. (2005). Cyclic time course of motor excitability modulation during the observation of a cyclic hand movement. *Brain research*, 1065(1-2), 115-124.
- Boulenger, V., Hauk, O., & Pulvermüller, F. (2008). Grasping ideas with the motor system: Semantic somatotopy in idiom comprehension. *Cerebral Cortex*.
- Boulenger, V., Roy, A. C., Paulignan, Y., Deprez, V., Jeannerod, M., & Nazir, T. A. (2006). Cross-talk between language processes and overt motor behavior in the

- first 200 msec of processing. *Journal of cognitive neuroscience*, 18(10), 1607-1615.
- Boussaoud, D. (2001). Attention versus intention in the primate premotor cortex. *NeuroImage*, 14(1), S40-S45.
- Brass, M., Bekkering, H., & Prinz, W. (2001). Movement observation affects movement execution in a simple response task. *Acta Psychologica*, 106(1-2), 3-22.
- Brass, M., Bekkering, H., Wohlschläger, A., & Prinz, W. (2000). Compatibility between observed and executed finger movements: Comparing symbolic, spatial, and imitative cues. *Brain and Cognition*, 44(2), 124-143.
- Brighina, F., La Bua, V., Oliveri, M., Piazza, A., & Fierro, B. (2000). Magnetic stimulation study during observation of motor tasks. *Journal of the neurological sciences*, 174(2), 122-126.
- Bub, D., & Masson, M. (2009). Grasping beer mugs: On the dynamics of alignment effects induced by handled objects. *Journal of Experimental Psychology: Human Perception and Performance*, 36(2), 341-358.
- Bub, D., Masson, M., & Cree, G. S. (2008). Evocation of functional and volumetric gestural knowledge by objects and words. *Cognition*, 106(1), 27-58.
- Buccino, G., Binkofski, F., Fink, G., Fadiga, L., Fogassi, L., Gallese, V., et al. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: An fmri study. *European Journal of Neuroscience*, 13(2), 400-404.
- Buccino, G., Lui, F., Canessa, N., Patteri, I., Lagravinese, G., Benuzzi, F., et al. (2004). Neural circuits involved in the recognition of actions performed by nonconspicuous: An fmri study. *Journal of cognitive neuroscience*, 16(1), 114-126.
- Buccino, G., Riggio, L., Melli, G., Binkofski, F., Gallese, V., & Rizzolatti, G. (2005). Listening to action-related sentences modulates the activity of the motor system: A combined tms and behavioral study. *Cognitive Brain Research*, 24(3), 355-363.
- Buccino, G., Vogt, S., Ritzl, A., Fink, G., Zilles, K., Freund, H., et al. (2004a). Neural circuits underlying imitation learning of hand actions: An event-related fmri study. *Neuron*, 42(2), 323-334.
- Buccino, G., Vogt, S., Ritzl, A., Fink, G., Zilles, K., Freund, H., et al. (2004b). Neural circuits underlying imitation learning of hand actions: An event-related fmri study. *Neuron*, 42(2), 323-334.
- Busan, P., Barbera, C., Semenic, M., Monti, F., Pizzolato, G., Pelamatti, G., et al. (2009). Effect of transcranial magnetic stimulation (tms) on parietal and premotor cortex during planning of reaching movements. *PLoS One*, 4(2).
- Buxbaum, L., & Coslett, H. (1997). Subtypes of optic ataxia: Reframing the disconnection account. *Neurocase*, 3(3), 159-166.
- Calvo-Merino, B., Glaser, D. E., Grezes, 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.
- Caminiti, R., Ferraina, S., & Johnson, P. (1996). The sources of visual information to the primate frontal lobe: A novel role for the superior parietal lobule. *Cerebral Cortex*, 6(3), 319.

- Candidi, M. (2007). Virtual lesion of ventral premotor cortex impairs visual perception of biomechanically possible but not impossible actions. *Social neuroscience*, 99999(1), 1-13.
- Candidi, M., Leone-Fernandez, B., Barber, H. A., Carreiras, M., & Aglioti, S. M. (2010). Hands on the future: Facilitation of cortico-spinal hand-representation when reading the future tense of hand-related action verbs. *European Journal of Neuroscience*, 32(4), 677-683.
- Caplan, D., & Waters, G. (1999). Verbal working memory capacity and language comprehension. *Behavioral and Brain Science*, 22, 114-126.
- Castiello, U., Lusher, D., Mari, M., Edwards, M., & Humphreys, G. W. (2002). Observing a human or a robotic hand grasping an object: Differential motor priming effects. *Common mechanisms in perception and action: Attention and performance XIX*, 315-333.
- Chao, L. L., & Martin, A. (2000). Representation of manipulable man-made objects in the dorsal stream. *NeuroImage*, 12(4), 478-484.
- Cheng, Y., Meltzoff, A., & Decety, J. (2007). Motivation modulates the activity of the human mirror-neuron system. *Cerebral Cortex*, 17(8), 1979.
- Chiarello, C., Shears, C., & Lund, K. (1999). Imageability and distributional typicality measures of nouns and verbs in contemporary english. *Behavior research methods, instruments, & computers: a journal of the Psychonomic Society, Inc*, 31(4), 603.
- Chouinard, P., Leonard, G., & Paus, T. (2005). Role of the primary motor and dorsal premotor cortices in the anticipation of forces during object lifting. *Journal of Neuroscience*, 25(9), 2277.
- Cisek, P., Crammond, D., & Kalaska, J. (2003). Neural activity in primary motor and dorsal premotor cortex in reaching tasks with the contralateral versus ipsilateral arm. *Journal of Neurophysiology*, 89(2), 922-942.
- Cisek, P., & Kalaska, J. (2004). Neural correlates of mental rehearsal in dorsal premotor cortex. *Nature*, 431(7011), 993-996.
- Clark, S., Tremblay, F., & Ste-Marie, D. (2004). Differential modulation of corticospinal excitability during observation, mental imagery and imitation of hand actions. *Neuropsychologia*, 42(1), 105-112.
- Cole, K., & Rotella, D. (2002). Old age impairs the use of arbitrary visual cues for predictive control of fingertip forces during grasp. *Experimental Brain Research*, 143(1), 35-41.
- Connolly, J., Andersen, R., & Goodale, M. (2003). Fmri evidence for a 'parietal reach region' in the human brain. *Experimental Brain Research*, 153(2), 140-145.
- Connolly, J. D., Goodale, M. A., Cant, J. S., & Munoz, D. P. (2007). Effector-specific fields for motor preparation in the human frontal cortex. *NeuroImage*, 34(3), 1209-1219.
- Costantini, M., Galati, G., Ferretti, A., Caulo, M., Tartaro, A., Romani, G. L., et al. (2005). Neural systems underlying observation of humanly impossible movements: An fmri study. *Cerebral Cortex*, 15(11), 1761-1767.
- Craigheo, L., Bello, A., Fadiga, L., & Rizzolatti, G. (2002). Hand action preparation influences the responses to hand pictures. *Neuropsychologia*, 40(5), 492-502.

- Craighero, L., Fadiga, L., Rizzolatti, G., & Umiltà, C. (1999). Action for perception: A motor-visual attentional effect. *Journal of Experimental Psychology Human Perception and Performance*, 25(6), 1673-1692.
- Craighero, L., Fadiga, L., Umiltà, C., & Rizzolatti, G. (1996). Evidence for visuomotor priming effect. *Neuroreport*, 8(1), 347.
- Cramer, S. C., Welsskoff, R. M., Schaechter, J. D., Nelles, G., Foley, M., Finklestein, S. P., et al. (2002). Motor cortex activation is related to force of squeezing. *Human brain mapping*, 16(4), 197-205.
- Creem-Regehr, S., Dilda, V., Vicchirilli, A., Federer, F., & Lee, J. (2007). The influence of complex action knowledge on representations of novel graspable objects: Evidence from functional magnetic resonance imaging. *Journal of the International Neuropsychological Society*, 13(06), 1009-1020.
- Cross, E., Hamilton, A., & Grafton, S. (2006). Building a motor simulation de novo: Observation of dance by dancers. *NeuroImage*, 31(3), 1257-1267.
- Cross, E., Kraemer, D., Hamilton, A., Kelley, W., & Grafton, S. (2009). Sensitivity of the action observation network to physical and observational learning. *Cerebral Cortex*, 19(2), 315.
- Culham, J., Valyear, K., & Stiglick, A. (2004). Fmri activation in grasp-related regions during naming of tools and other graspable objects. *Journal of Vision*, 4(8), 410.
- Dafotakis, M., Sparing, R., Eickhoff, S., Fink, G., & Nowak, D. (2008). On the role of the ventral premotor cortex and anterior intraparietal area for predictive and reactive scaling of grip force. *Brain research*, 1228, 73-80.
- Dai, T., Liu, J., Sahgal, V., Brown, R., & Yue, G. (2001). Relationship between muscle output and functional mri-measured brain activation. *Experimental Brain Research*, 140(3), 290-300.
- Damasio, A. (1989). The brain binds entities and events by multiregional activation from convergence zones. *Neural Computation*, 1(1), 123-132.
- Damasio, A., & Meyer, K. (2008). Behind the looking-glass. *Nature*, 454(7201), 167.
- Danckert, J., Goldberg, L., & Broderick, C. (2009). Damage to superior parietal cortex impairs pointing in the sagittal plane. *Experimental Brain Research*, 195(2), 183-191.
- Daniele, A., Giustolisi, L., Silveri, M. C., Colosimo, C., & Gainotti, G. (1994). Evidence for a possible neuroanatomical basis for lexical processing of nouns and verbs. *Neuropsychologia*, 32(11), 1325-1341.
- Dassonville, P., Zhu, X., Ugurbil, K., Kim, S., & Ashe, J. (1997). Functional activation in motor cortex reflects the direction and the degree of handedness. *Proceedings of the National Academy of Sciences*, 94(25), 14015.
- Davare, M., Andres, M., Cosnard, G., Thonnard, J., & Olivier, E. (2006). Dissociating the role of ventral and dorsal premotor cortex in precision grasping. *Journal of Neuroscience*, 26(8), 2260.
- de C Hamilton, A. F., Wolpert, D. M., Frith, U., & Grafton, S. (2006). Where does your own action influence your perception of another person's action in the brain? *NeuroImage*, 29(2), 524-535.
- de C. Hamilton, A. F., & Grafton, S. (2009). Repetition suppression for performed hand gestures revealed by fmri. *Human brain mapping*.

- De Zubicaray, G., Postle, N., McMahon, K., Meredith, M., & Ashton, R. (2010). Mirror neurons, the representation of word meaning, and the foot of the third left frontal convolution. *Brain and language*, 112(1), 77-84.
- Deiber (1996). Cerebra structures participating in motor preparation in humans: A positron emission tomography study. *Journal of Neurophysiology*, 75(1), 233-247.
- Deiber, M., Iba ez, V., Honda, M., Sadato, N., Raman, R., & Hallett, M. (1998). Cerebral processes related to visuomotor imagery and generation of simple finger movements studied with positron emission tomography* 1. *NeuroImage*, 7(2), 73-85.
- Desai, R. H., Binder, J. R., Conant, L. L., & Seidenberg, M. S. (2009). Activation of sensory-motor areas in sentence comprehension. *Cerebral Cortex*.
- Dettmers, C., Fink, G., Lemon, R., Stephan, K., Passingham, R., Silbersweig, D., et al. (1995). Relation between cerebral activity and force in the motor areas of the human brain. *Journal of Neurophysiology*, 74(2), 802.
- Dinstein, I., Gardner, J. L., Jazayeri, M., & Heeger, D. J. (2008). Executed and observed movements have different distributed representations in human aips. *Journal of Neuroscience*, 28(44), 11231.
- Eastough, D., & Edwards, M. G. (2007). Movement kinematics in prehension are affected by grasping objects of different mass. *Experimental Brain Research*, 176(1), 193-198.
- Edwards, M. G., Humphreys, G. W., & Castiello, U. (2003). Motor facilitation following action observation: A behavioural study in prehensile action. *Brain and Cognition*, 53(3), 495-502.
- Ehrsson, H., Geyer, S., & Naito, E. (2003). Imagery of voluntary movement of fingers, toes, and tongue activates corresponding body-part-specific motor representations. *Journal of Neurophysiology*, 90(5), 3304.
- Evangelidou, M., Raos, V., Galletti, C., & Savaki, H. (2009). Functional imaging of the parietal cortex during action execution and observation. *Cerebral Cortex*, 19(3), 624.
- Evarts, E. (1968). Relation of pyramidal tract activity to force exerted during voluntary movement. *Journal of Neurophysiology*, 31(1), 14.
- Evarts, E., Fromm, C., Kroller, J., & Jennings, V. (1983). Motor cortex control of finely graded forces. *Journal of Neurophysiology*, 49(5), 1199.
- Fadiga, L., Buccino, G., Craighero, L., Fogassi, L., Gallese, V., & Pavesi, G. (1998). Corticospinal excitability is specifically modulated by motor imagery: A magnetic stimulation study. *Neuropsychologia*, 37(2), 147-158.
- Fadiga, L., Craighero, L., & Olivier, E. (2005). Human motor cortex excitability during the perception of others' action. *Current Opinion in Neurobiology*, 15(2), 213-218.
- Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: A magnetic stimulation study. *Journal of Neurophysiology*, 73(6), 2608-2611.
- Fagioli, S., Hommel, B., & Schubotz, R. (2007). Intentional control of attention: Action planning primes action-related stimulus dimensions. *Psychological research*, 71(1), 22-29.

- Fattori, P., Breveglieri, R., Amoroso, K., & Galletti, C. (2004). Evidence for both reaching and grasping activity in the medial parieto-occipital cortex of the macaque. *European Journal of Neuroscience*, *20*(9), 2457-2466.
- Fattori, P., Raos, V., Breveglieri, R., Bosco, A., Marzocchi, N., & Galletti, C. (2001). The dorsomedial pathway is not just for reaching: Grasping neurons in the medial parieto-occipital cortex of the macaque monkey. *Journal of Neuroscience*, *30*(1), 342.
- Ferro, J. (1984). Transient inaccuracy in reaching caused by a posterior parietal lobe lesion. *Journal of Neurology, Neurosurgery & Psychiatry*, *47*(9), 1016.
- Fiebach, C., Rissman, J., & D'Esposito, M. (2006). Modulation of inferotemporal cortex activation during verbal working memory maintenance. *Neuron*, *51*(2), 251-261.
- Filimon, F., Nelson, J., Hagler, D., & Sereno, M. (2007). Human cortical representations for reaching: Mirror neurons for execution, observation, and imagery. *NeuroImage*, *37*(4), 1315-1328.
- Fodor, J. (1981). *Representations*: Harvester Press.
- Fodor, J. (2001). *The mind doesn't work that way*: MIT press Cambridge, MA.
- Fogassi, L., Ferrari, P. F., Gesierich, B., Rozzi, S., Chersi, F., & Rizzolatti, G. (2005). Parietal lobe: From action organization to intention understanding. *Science*, *308*(5722), 662-667.
- Fogassi, L., Gallese, V., Buccino, G., Craighero, L., Fadiga, L., & Rizzolatti, G. (2001). Cortical mechanism for the visual guidance of hand grasping movements in the monkey: A reversible inactivation study. *Brain: a journal of neurology*, *124*(Pt 3), 571.
- Fogassi, L., Gallese, V., Fadiga, L., & Rizzolatti, G. (1998). *Neurons responding to the sight of goal-directed hand/arm actions in the parietal area pf (7b) of the macaque monkey*. Paper presented at the *Society of Neuroscience Abstracts*.
- Fogassi, L., & Luppino, G. (2005). Motor functions of the parietal lobe. *Current Opinion in Neurobiology*, *15*(6), 626-631.
- Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, *119*(2), 593.
- Gallese, V., Fogassi, L., Fadiga, L., & Rizzolatti, G. (2002). Action representation and the inferior parietal lobule. *Attention and Performance*, *19*, 247-266.
- Gallese, V., & Lakoff, G. (2005). The brain's concepts: The role of the sensory-motor system in conceptual knowledge. *Cognitive Neuropsychology*, *1*(1), 1-1.
- Gallese, V., Murata, A., Kaseda, M., Niki, N., & Sakata, H. (1994). Deficit of hand preshaping after muscimol injection in monkey parietal cortex. *NeuroReport-International Journal for Rapid Communications of Research in Neuroscience*, *5*(12), 1525-1529.
- Gangitano, M., Mottaghy, F., & Pascual-Leone, A. (2001). Phase-specific modulation of cortical motor output during movement observation. *Neuroreport*, *12*(7), 1489.
- Gangitano, M., Mottaghy, F., & Pascual-Leone, A. (2004). Modulation of premotor mirror neuron activity during observation of unpredictable grasping movements. *European Journal of Neuroscience*, *20*(8), 2193-2202.
- Gazzola, V., Aziz-Zadeh, L., & Keysers, C. (2006). Empathy and the somatotopic auditory mirror system in humans. *Current Biology*, *16*(18), 1824-1829.

- Gazzola, V., & Keysers, C. (2009). The observation and execution of actions share motor and somatosensory voxels in all tested subjects: Single-subject analyses of unsmoothed fmri data. *Cerebral Cortex*, *19*(6), 1239.
- Gennari, S. P., MacDonald, M. C., Postle, B. R., & Seidenberg, M. S. (2007). Context-dependent interpretation of words: Evidence for interactive neural processes. *NeuroImage*, *35*(3), 1278-1286.
- Gentilucci, M. (2003). Object motor representation and language. *Experimental Brain Research*, *153*(2), 260-265.
- Gentilucci, M., & Gangitano, M. (1998). Influence of automatic word reading on motor control. *European Journal of Neuroscience*, *10*(2), 752-756.
- Gentilucci, M., Gangitano, M., Benuzzi, F., Bertolani, L., & Daprati, E. (2000). Language and motor control. *Experimental Brain Research*, *133*(4), 468-490.
- Gerardin, E., Sirigu, A., Lehericy, S., Poline, J., Gaymard, B., Marsault, C., et al. (2000). Partially overlapping neural networks for real and imagined hand movements. *Cerebral Cortex*, *10*(11), 1093.
- Gerfo, E., Oliveri, M., Torriero, S., Salerno, S., Koch, G., & Caltagirone, C. (2008). The influence of rtms over prefrontal and motor areas in a morphological task: Grammatical vs. Semantic effects. *Neuropsychologia*, *46*(2), 764-770.
- Glenberg, A. (1997). What memory is for: Creating meaning in the service of action. *Behavioral and brain sciences*, *20*(01), 41-50.
- Glenberg, A., & Kaschak, M. P. (2002). Grounding language in action. *Psychonomic bulletin & review*, *9*(3), 558-565.
- 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., Graham, J., & Dixon, P. (2004). Grasping the meaning of words. *Experimental Brain Research*, *154*(1), 103-108.
- Godschalk, M., Mitz, A. R., Duin, B., & Burga, H. (1995). Somatotopy of monkey premotor cortex examined with microstimulation. *Neuroscience Research*, *23*(3), 269-279.
- Goldberg, G. (2010). Supplementary motor area structure and function: Review and hypotheses. *Behavioral and Brain Sciences*, *8*(04), 567-588.
- Gordon, A., Forssberg, H., Johansson, R., & Westling, G. (1991). Visual size cues in the programming of manipulative forces during precision grip. *Experimental Brain Research*, *83*(3), 477-482.
- Gordon, A., Westling, G., Cole, K., & Johansson, R. (1993). Memory representations underlying motor commands used during manipulation of common and novel objects. *Journal of Neurophysiology*, *69*(6), 1789.
- Grabowski, T., Damasio, H., & Damasio, A. (1998). Premotor and prefrontal correlates of category-related lexical retrieval. *NeuroImage*, *7*(3), 232-243.
- Grafton, S., Arbib, M., Fadiga, L., & Rizzolatti, G. (1996). Localization of grasp representations in humans by positron emission tomography. *Experimental Brain Research*, *112*(1), 103-111.
- Grafton, S., Fadiga, L., Arbib, M., & Rizzolatti, G. (1997). Premotor cortex activation during observation and naming of familiar tools. *NeuroImage*, *6*(4), 231-236.
- Grefkes, C., Ritzl, A., Zilles, K., & Fink, G. (2004). Human medial intraparietal cortex subserves visuomotor coordinate transformation. *NeuroImage*, *23*(4), 1494-1506.

- Grezes, 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.
- Haaland, K. Y., Harrington, D. L., & Knight, R. T. (2000). Neural representations of skilled movement. *Brain, 123*(11), 2306.
- Hamilton, A., Wolpert, D., & Frith, U. (2004). Your own action influences how you perceive another person's action. *Current Biology, 14*(6), 493-498.
- Hamilton, A., Wolpert, D., Frith, U., & Grafton, S. (2006). Where does your own action influence your perception of another person's action in the brain? *NeuroImage, 29*(2), 524-535.
- Hanakawa, T., Honda, M., Zito, G., Dimyan, M., & Hallett, M. (2006). Brain activity during visuomotor behavior triggered by arbitrary and spatially constrained cues: An fmri study in humans. *Experimental Brain Research, 172*(2), 275-282.
- Hari, R., Forss, N., Avikainen, S., Kirveskari, E., Salenius, S., & Rizzolatti, G. (1998). Activation of human primary motor cortex during action observation: A neuromagnetic study. *Proceedings of the National Academy of Sciences of the United States of America, 95*(25), 15061.
- Hashimoto, R., & Sakai, K. (2002). Specialization in the left prefrontal cortex for sentence comprehension. *Neuron, 35*(3), 589-597.
- Haslinger, B., Erhard, P., Altenmüller, E., Schroeder, U., Boecker, H., & Ceballos-Baumann, A. (2005). Transmodal sensorimotor networks during action observation in professional pianists. *Journal of cognitive neuroscience, 17*(2), 282-293.
- Hauk, O., Johnsrude, I., & Pulvermüller, F. (2004). Somatotopic representation of action words in human motor and premotor cortex. *Neuron, 41*(2), 301-307.
- Hauk, O., Shtyrov, Y., & Pulvermüller, F. (2006). The sound of actions as reflected by mismatch negativity: Rapid activation of cortical sensory-motor networks by sounds associated with finger and tongue movements. *European Journal of Neuroscience, 23*(3), 811-821.
- Hebb, D. O. (1949). *The organization of behavior: A neuropsychological theory*: Wiley.
- Hendrix, C., Mason, C., & Ebner, T. (2009). Signaling of grasp dimension and grasp force in dorsal premotor cortex and primary motor cortex neurons during reach to grasp in the monkey. *Journal of Neurophysiology, 102*(1), 132.
- Hepp-Reymond, M., Hüsler, E., Maier, M., & Qi, H. (1994). Force-related neuronal activity in two regions of the primate ventral premotor cortex. *Canadian Journal of Physiology and Pharmacology, 72*(5), 571-579.
- Hepp-Reymond, M., Kirkpatrick-Tanner, M., Gabernet, L., Qi, H., & Weber, B. (1999). Context-dependent force coding in motor and premotor cortical areas. *Experimental Brain Research, 128*(1), 123-133.
- Heyes, C. (2001). Causes and consequences of imitation. *Trends in cognitive sciences, 5*(6), 253-261.
- Hommel, B., Müsseler, J., Aschersleben, G., & Prinz, W. (2002). The theory of event coding (tec): A framework for perception and action planning. *Behavioral and brain sciences, 24*(05), 849-878.

- Horenstein, C., Lowe, M., Koenig, K., & Phillips, M. (2009). Comparison of unilateral and bilateral complex finger tapping-related activation in premotor and primary motor cortex. *Human brain mapping, 30*(4), 1397-1412.
- Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J., & Rizzolatti, G. (2005). Grasping the intentions of others with one's own mirror neuron system. *PLoS Biol, 3*(3), e79.
- Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science, 286*(5449), 2526.
- Jacobs, A., & Shiffrar, M. (2005). Walking perception by walking observers. *Journal of Experimental Psychology, 31*(1), 157-169.
- James, K., & Maouene, J. (2009). Auditory verb perception recruits motor systems in the developing brain: An fmri investigation. *Developmental Science, 12*(6), F26-F34.
- Järveläinen, J., Schürmann, M., & Hari, R. (2004). Activation of the human primary motor cortex during observation of tool use. *NeuroImage, 23*(1), 187-192.
- Jeannerod, M. (2001). Neural simulation of action: A unifying mechanism for motor cognition. *NeuroImage, 14*(1), 103-109.
- Jeannerod, M., & Decety, J. (1995). Mental motor imagery: A window into the representational stages of action. *Current Opinion in Neurobiology, 5*(6), 727-732.
- Jefferies, E., & Lambon Ralph, M. (2006). Semantic impairment in stroke aphasia versus semantic dementia: A case-series comparison. *Brain, 129*(8), 2132.
- Jenkinson, M., Bannister, P., Brady, M., & Smith, S. (2002). Improved optimization for the robust and accurate linear registration and motion correction of brain images. *NeuroImage, 17*(2), 825-841.
- Jenkinson, M., & Smith, S. (2001). A global optimisation method for robust affine registration of brain images. *Medical image analysis, 5*(2), 143-156.
- Johnson-Frey, S. H., Newman-Norlund, R., & Grafton, S. (2005). A distributed left hemisphere network active during planning of everyday tool use skills. *Cerebral Cortex, 15*(6), 681-695.
- Johnson, P., Ferraina, S., Bianchi, L., & Caminiti, R. (1996). Cortical networks for visual reaching: Physiological and anatomical organization of frontal and parietal lobe arm regions. *Cerebral Cortex, 6*(2), 102.
- Kable, J. W., Lease-Spellmeyer, J., & Chatterjee, A. (2002). Neural substrates of action event knowledge. *Journal of cognitive neuroscience, 14*(5), 795-805.
- Kamide, Y., Altmann, G. T. M., & Haywood, S. L. (2003). The time-course of prediction in incremental sentence processing: Evidence from anticipatory eye movements. *Journal of Memory and Language, 49*(1), 133-156.
- Karnath, H., & Perenin, M. (2005). Cortical control of visually guided reaching: Evidence from patients with optic ataxia. *Cerebral Cortex, 15*(10), 1561.
- Keisker, B., Hepp-Reymond, M., Blickenstorfer, A., Meyer, M., & Kollias, S. (2009). Differential force scaling of fine-graded power grip force in the sensorimotor network. *Human brain mapping, 30*(8), 2453-2465.
- Kellenbach, M., 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.

- Kemmerer, D., & Tranel, D. (2003). A double dissociation between the meanings of action verbs and locative prepositions. *Neurocase*, 9(5), 421-435.
- Kermadi, I., Liu, Y., & Rouiller, E. (2000). Do bimanual motor actions involve the dorsal premotor (pmd), cingulate (cma) and posterior parietal (ppc) cortices? Comparison with primary and supplementary motor cortical areas. *Somatosensory and Motor Research*, 17(3), 255-271.
- Keysers, C., Kohler, E., Umiltà, M., Nanetti, L., Fogassi, L., & Gallese, V. (2003). Audiovisual mirror neurons and action recognition. *Experimental Brain Research*, 153(4), 628-636.
- Keysers, C., & Perrett, D. I. (2004). Demystifying social cognition: A hebbian perspective. *Trends in cognitive sciences*, 8(11), 501-507.
- 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.
- Klatzky, R. L., Pellegrino, J. W., McCloskey, B. P., & Doherty, S. (1989). Can you squeeze a tomato? The role of motor representations in semantic sensibility judgments. *Journal of memory and language(Print)*, 28(1), 56-77.
- Kohler, E., Keysers, C., Umiltà, M., Fogassi, L., Gallese, V., & Rizzolatti, G. (2002). Hearing sounds, understanding actions: Action representation in mirror neurons. *Science*, 297(5582), 846.
- Kroliczak, G., McAdam, T. D., Quinlan, D. J., & Culham, J. C. (2008). The human dorsal stream adapts to real actions and 3d shape processing: A functional magnetic resonance imaging study. *Journal of Neurophysiology*, 100(5), 2627.
- Kurata, K. (1989). Distribution of neurons with set-and movement-related activity before hand and foot movements in the premotor cortex of rhesus monkeys. *Experimental Brain Research*, 77(2), 245-256.
- Kurata, K., & Hoffman, D. (1994). Differential effects of muscimol microinjection into dorsal and ventral aspects of the premotor cortex of monkeys. *Journal of Neurophysiology*, 71(3), 1151.
- Lahav, A., Saltzman, E., & Schlaug, G. (2007). Action representation of sound: Audiomotor recognition network while listening to newly acquired actions. *Journal of Neuroscience*, 27(2), 308.
- Lambon Ralph, M., Pobric, G., & Jefferies, E. (2009). Conceptual knowledge is underpinned by the temporal pole bilaterally: Convergent evidence from rtms. *Cerebral Cortex*, 19(4), 832.
- Lewis, J. W. (2006). Cortical networks related to human use of tools. *The Neuroscientist*, 12(3), 211.
- Lewis, J. W., & Van Essen, D. C. (2000). Corticocortical connections of visual, sensorimotor, and multimodal processing areas in the parietal lobe of the macaque monkey. *The Journal of comparative neurology*, 428(1), 112-137.
- Leyton, A. S. F., & Sherrington, C. S. (1917). Observations on the excitable cortex of the chimpanzee, orang-utan, and gorilla. *Experimental Physiology*, 11(2), 135-222.
- Lotze, M., Montoya, P., Erb, M., Hülsmann, E., Flor, H., Klose, U., et al. (1999). Activation of cortical and cerebellar motor areas during executed and imagined

- hand movements: An fmri study. *Journal of cognitive neuroscience*, 11(5), 491-501.
- Luppino, G., Murata, A., Govoni, P., & Matelli, M. (1999). Largely segregated parietofrontal connections linking rostral intraparietal cortex (areas aip and vip) and the ventral premotor cortex (areas f5 and f4). *Experimental Brain Research*, 128(1), 181-187.
- 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*.
- Maier, M., Bennett, K., Hepp-Reymond, M., & Lemon, R. (1993). Contribution of the monkey corticomotoneuronal system to the control of force in precision grip. *Journal of Neurophysiology*, 69(3), 772.
- Marconi, B., Genovesio, A., Battaglia-Mayer, A., Ferraina, S., Squatrito, S., Molinari, M., et al. (2001). Eye-hand coordination during reaching. I. Anatomical relationships between parietal and frontal cortex. *Cerebral Cortex*, 11(6), 513.
- Martin, A., & Chao, L. L. (2001). Semantic memory and the brain: Structure and processes. *Current Opinion in Neurobiology*, 11(2), 194-201.
- Martin, A., Haxby, J. V., Lalonde, F. M., Wiggs, C. L., & Ungerleider, L. G. (1995). Discrete cortical regions associated with knowledge of color and knowledge of action. *Science*, 270(5233), 102.
- Martin, A., Wiggs, C. L., Ungerleider, L. G., & Haxby, J. V. (1996). Neural correlates of category-specific knowledge. *Nature*, 379(6566), 649-652.
- Masson, M., Bub, D., & Newton-Taylor, M. (2008). Language-based access to gestural components of conceptual knowledge. *The Quarterly Journal of Experimental Psychology*, 61(6), 869-882.
- Masson, M., Bub, D., & Warren, C. M. (2008). Kicking calculators: Contribution of embodied representations to sentence comprehension. *Journal of Memory and Language*, 59(3), 256-265.
- Matelli, M., Camarda, R., Glickstein, M., & Rizzolatti, G. (1986). Afferent and efferent projections of the inferior area 6 in the macaque monkey. *Journal of comparative neurology*(1911), 251(3), 281-298.
- McGeoch, P. D., Brang, D., & Ramachandran, V. S. (2007). Apraxia, metaphor and mirror neurons. *Medical Hypotheses*, 69(6), 1165-1168.
- Medendorp, W., Goltz, H., Crawford, J., & Vilis, T. (2005). Integration of target and effector information in human posterior parietal cortex for the planning of action. *Journal of Neurophysiology*, 93(2), 954.
- Miall, R., Stanley, J., Todhunter, S., Levick, C., Lindo, S., & Miall, J. (2006). Performing hand actions assists the visual discrimination of similar hand postures. *Neuropsychologia*, 44(6), 966-976.
- Molnar-Szakacs, I., Iacoboni, M., Koski, L., & Mazziotta, J. (2005). Functional segregation within pars opercularis of the inferior frontal gyrus: Evidence from fmri studies of imitation and action observation. *Cerebral Cortex*, 15(7), 986.
- Monsell, S. (1991). The nature and locus of word frequency effects in reading. *Basic processes in reading: Visual word recognition*, 148-197.
- Morin, O., & Grèzes, J. (2008). What is "Mirror" In the premotor cortex? A review. *Neurophysiol Clin*, 38(3), 189-195.

- Muesseler, J., & Hommel, B. (1997). Blindness to response-compatible stimuli. *Journal of Experimental Psychology Human Perception and Performance*, 23, 861-872.
- Murata, A., Fadiga, L., Fogassi, L., Gallese, V., Raos, V., & Rizzolatti, G. (1997). Object representation in the ventral premotor cortex (area f5) of the monkey. *Journal of Neurophysiology*, 78(4), 2226.
- Murata, A., Gallese, V., Luppino, G., Kaseda, M., & Sakata, H. (2000). Selectivity for the shape, size, and orientation of objects for grasping in neurons of monkey parietal area aip. *Journal of Neurophysiology*, 83(5), 2580-2601.
- Myung, J., Blumstein, S. E., & Sedivy, J. C. (2006). Playing on the typewriter, typing on the piano: Manipulation knowledge of objects. *Cognition*, 98(3), 223-243.
- Nakayama, Y., Yamagata, T., Tanji, J., & Hoshi, E. (2008). Transformation of a virtual action plan into a motor plan in the premotor cortex. *Journal of Neuroscience*, 28(41), 10287.
- Neininger, B., & Pulvermüller, F. (2003). Word-category specific deficits after lesions in the right hemisphere. *Neuropsychologia*, 41(1), 53-70.
- Newell, A., & Simon, H. (1972). *Human problem solving*: Prentice-Hall Englewood Cliffs, NJ.
- Nishitani, N., & Hari, R. (2000). Temporal dynamics of cortical representation for action. *Proceedings of the National Academy of Sciences of the United States of America*, 97(2), 913.
- Nishitani, N., & Hari, R. (2002). Viewing lip forms cortical dynamics. *Neuron*, 36(6), 1211-1220.
- Nowak, D., Voss, M., Ying-Zu Huang, D., & Rothwell, J. (2005). High-frequency repetitive transcranial magnetic stimulation over the hand area of the primary motor cortex disturbs predictive grip force scaling. *European Journal of Neuroscience*, 22(9), 2392-2396.
- Oldfield, R. (1971). The assessment and analysis of handedness: The edinburgh inventory. *Neuropsychologia*, 9(1), 97-113.
- Oliveri, M., Finocchiaro, C., Shapiro, K., Gangitano, M., Caramazza, A., & Pascual-Leone, A. (2004). All talk and no action: A transcranial magnetic stimulation study of motor cortex activation during action word production. *Journal of cognitive neuroscience*, 16(3), 374-381.
- Papeo, L., Vallesi, A., Isaja, A., & Rumiati, R. I. (2009). Effects of tms on different stages of motor and non-motor verb processing in the primary motor cortex. *PLoS One*, 4(2).
- Passingham, R. (1988). Premotor cortex and preparation for movement. *Experimental Brain Research*, 70(3), 590-596.
- Patuzzo, S., Fiaschi, A., & Manganotti, P. (2003). Modulation of motor cortex excitability in the left hemisphere during action observation: A single-and paired-pulse transcranial magnetic stimulation study of self-and non-self-action observation. *Neuropsychologia*, 41(9), 1272-1278.
- Pecher, D., & Zwaan, R. A. (2005). *Grounding cognition: The role of perception and action in memory, language, and thinking*: Cambridge University Press.
- Penfield, W., & Rasmussen, T. (1952). The cerebral cortex of man. 2 e ed. *New York: The Mac Millan Co.*

- Petrides, M. (1997). Visuo-motor conditional associative learning after frontal and temporal lesions in the human brain. *Neuropsychologia*, 35(7), 989-997.
- Petrides, M., & Pandya, D. N. (1984). Projections to the frontal cortex from the posterior parietal region in the rhesus monkey. *Journal of comparative neurology(1911)*, 228(1), 105-116.
- Phillips, J., & Ward, R. (2002). Sr correspondence effects of irrelevant visual affordance: Time course and specificity of response activation. *Visual cognition*, 9(4), 540-558.
- Phillips, J. A., Humphreys, G. W., Noppeney, U., & Price, C. J. (2002). The neural substrates of action retrieval: An examination of semantic and visual routes to action. *Visual cognition*, 9(4), 662-685.
- Picard, N., & Strick, P. (2001). Imaging the premotor areas. *Current Opinion in Neurobiology*, 11(6), 663-672.
- Pizzamiglio, L., Aprile, T., Spitoni, G., Pitzalis, S., Bates, E., D'Amico, S., et al. (2005). Separate neural systems for processing action-or non-action-related sounds. *NeuroImage*, 24(3), 852-861.
- Porro, C., Francescato, M., Cettolo, V., Diamond, M., Baraldi, P., Zuiani, C., et al. (1996). Primary motor and sensory cortex activation during motor performance and motor imagery: A functional magnetic resonance imaging study.
- Postle, N., McMahan, K. L., Ashton, R., Meredith, M., & de Zubicaray, G. I. (2008). Action word meaning representations in cytoarchitectonically defined primary and premotor cortices. *NeuroImage*, 43(3), 634-644.
- Preuss, T. M., & Kaas, H. (1996). Movement representation in the dorsal and ventral premotor areas of owl monkeys: A microstimulation study. *The Journal of comparative neurology*, 371, 649-676.
- Pujol, J., Deus, J., Losilla, J. M., & Capdevila, A. (1999). Cerebral lateralization of language in normal left-handed people studied by functional mri. *Neurology*, 52(5), 1038-1038.
- Pulvermuller, F. (1999). Words in the brain's language. *Behavioral & Brain Sciences*, 22(2), 253-279.
- Pulvermuller, 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.
- Pulvermuller, F., Shtyrov, Y., & Ilmoniemi, R. (2005). Brain signatures of meaning access in action word recognition. *Journal of cognitive neuroscience*, 17(6), 884-892.
- Pylyshyn, Z. (1984). *Computation and cognition*: Mit Press Cambridge, MA.
- Raos, V., Evangelidou, M., & Savaki, H. (2007). Mental simulation of action in the service of action perception. *Journal of Neuroscience*, 27(46), 12675.
- Raposo, A., Moss, H. E., Stamatakis, E. A., & Tyler, L. K. (2009). Modulation of motor and premotor cortices by actions, action words and action sentences. *Neuropsychologia*, 47(2), 388-396.
- Rayner, K., Warren, T., Juhasz, B. J., & Liversedge, S. P. (2004). The effect of plausibility on eye movements in reading. *Journal of experimental psychology. Learning, memory, and cognition*, 30(6), 1290.

- Repp, B. H., & Knoblich, G. (2007). Action can affect auditory perception. *Psychological Science, 18*(1), 6-7.
- Richter, W., Andersen, P. M., Georgopoulos, A. P., & Kim, S. G. (1997). Sequential activity in human motor areas during a delayed cued finger movement task studied by time-resolved fmri. *Neuroreport, 8*(5), 1257.
- Rizzolatti, G., Camarda, R., Fogassi, L., Gentilucci, M., Luppino, G., & Matelli, M. (1988). Functional organization of inferior area 6 in the macaque monkey. *Experimental Brain Research, 71*(3), 491-507.
- Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annu. Rev. Neurosci, 27*, 169-192.
- Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research, 3*(2), 131-141.
- Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat Rev Neurosci, 2*(9), 661-670.
- Rizzolatti, G., & Luppino, G. (2001). The cortical motor system. *Neuron, 31*(6), 889-901.
- Rizzolatti, G., & Matelli, M. (2003). Two different streams form the dorsal visual system: Anatomy and functions. *Experimental Brain Research, 153*(2), 146-157.
- Roth, M., Decety, J., Raybaudi, M., Massarelli, R., Delon-Martin, C., Segebarth, C., et al. (1996). Possible involvement of primary motor cortex in mentally simulated movement: A functional magnetic resonance imaging study. *Neuroreport, 7*(7), 1280.
- Rueschemeyer, S., Lindemann, O., van Elk, M., & Bekkering, H. (2009). Embodied cognition: The interplay between automatic resonance and selection-for-action mechanisms. *European Journal of Social Psychology, 39*(7), 1180-1187.
- Rueschemeyer, S., van Rooij, D., Lindemann, O., Willems, R., & Bekkering, H. (2010). The function of words: Distinct neural correlates for words denoting differently manipulable objects. *Journal of cognitive neuroscience, 22*(8), 1844-1851.
- Sabsevitz, D. S., Medler, D. A., Seidenberg, M., & Binder, J. R. (2005). Modulation of the semantic system by word imageability. *NeuroImage, 27*(1), 188-200.
- Sakata, H., Taira, M., Murata, A., & Mine, S. (1995). Neural mechanisms of visual guidance of hand action in the parietal cortex of the monkey. *Cerebral Cortex, 5*(5), 429-438.
- Sasaki, K., & Gamba, H. (1986). Effects of premotor cortex cooling upon visually initiated hand movements in the monkey. *Brain research, 374*(2), 278-286.
- Sato, M., Mengarelli, M., Riggio, L., Gallese, V., & Buccino, G. (2008). Task related modulation of the motor system during language processing. *Brain and language, 105*(2), 83-90.
- Schabrun, S., Ridding, M., & Miles, T. (2008). Role of the primary motor and sensory cortex in precision grasping: A transcranial magnetic stimulation study. *European Journal of Neuroscience, 27*(3), 750-756.
- Schneider, T., Engel, A., & Debener, S. (2008). Multisensory identification of natural objects in a two-way crossmodal priming paradigm. *Experimental Psychology (formerly" Zeitschrift für Experimentelle Psychologie")*, 55(2), 121-132.

- Schumacher, E. H., Cole, M.W., & D'Esposito, M (2007). Selection and maintenance of stimulus–response rules during preparation and performance of a spatial choice-reaction task. *Brain research*, 113677 - 87.
- Scorolli, C., Borghi, A. M., & Glenberg, A. (2009). Language-induced motor activity in bi-manual object lifting. *Experimental Brain Research*, 193(1), 43-53.
- Shapiro, K., & Caramazza, A. (2003). The representation of grammatical categories in the brain. *Trends in cognitive sciences*, 7(5), 201-206.
- Simon, S., Meunier, M., Piettre, L., Berardi, A., Segebarth, C., & Boussaoud, D. (2002). Spatial attention and memory versus motor preparation: Premotor cortex involvement as revealed by fmri. *Journal of Neurophysiology*, 88(4), 2047.
- Simon, S. R., Meunier, M., Piettre, L., Berardi, A.M., Segebarth, C. M., Boussaoud, D. (2001). Spatial attention and memory versus motor preparation: Premotor cortex involvement as revealed by fmri. *Journal of Neurophysiology*, 88(4), 2047-2057.
- Smith, S. M., & Nichols, T. E. (2009). Threshold-free cluster enhancement: Addressing problems of smoothing, threshold dependence and localisation in cluster inference. *NeuroImage*, 44(1), 83-98.
- Strafella, A., & Paus, T. (2000). Modulation of cortical excitability during action observation: A transcranial magnetic stimulation study. *Neuroreport*, 11(10), 2289.
- Strain, E., Patterson, K., & Seidenberg, M. S. (1995). Semantic effects in single-word naming. *Journal of experimental psychology. Learning, memory, and cognition*, 21(5), 1140.
- Symes, E., Ellis, R., & Tucker, M. (2007). Visual object affordances: Object orientation. *Acta Psychologica*, 124(2), 238-255.
- Taira, M., Mine, S., Georgopoulos, A. P., Murata, A., & Sakata, H. (1990). Parietal cortex neurons of the monkey related to the visual guidance of hand movement. *Experimental Brain Research*, 83(1), 29-36.
- Tanji, J., Okano, K., & Sato, K. (1988). Neuronal activity in cortical motor areas related to ipsilateral, contralateral, and bilateral digit movements of the monkey. *Journal of Neurophysiology*, 60(1), 325.
- Tanne-Gariepy, J., Rouiller, E. M., & Boussaoud, D. (2002). Parietal inputs to dorsal versus ventral premotor areas in the macaque monkey: Evidence for largely segregated visuomotor pathways. *Experimental Brain Research*, 145(1), 91-103.
- Taylor, L. J. (2008). Motor resonance and linguistic focus. *The Quarterly Journal of Experimental Psychology*, 99999(1), 1-1.
- Taylor, L. J., Lev-Ari, S., & Zwaan, R. A. (2008). Inferences about action engage action systems. *Brain and language*, 107(1), 62-67.
- Taylor, L. J., & Zwaan, R. A. (2008). Motor resonance and linguistic focus. *The Quarterly Journal of Experimental Psychology*, 99999(1), 1-1.
- Tettamanti, M., Buccino, G., Saccuman, M. C., Gallese, V., Danna, M., Scifo, P., et al. (2005). Listening to action-related sentences activates fronto-parietal motor circuits. *Journal of cognitive neuroscience*, 17(2), 273-281.
- Thach, W. (1978). Correlation of neural discharge with pattern and force of muscular activity, joint position, and direction of intended next movement in motor cortex and cerebellum. *Journal of Neurophysiology*, 41(3), 654.

- Thoenissen, D., Zilles, K., & Toni, I. (2002). Differential involvement of parietal and precentral regions in movement preparation and motor intention. *Journal of Neuroscience*, 22(20), 9024.
- Thompson-Schill, S. L., Bedny, M., & Goldberg, R. F. (2005). The frontal lobes and the regulation of mental activity. *Current Opinion in Neurobiology*, 15(2), 219-224.
- Thompson-Schill, S. L., D'Esposito, M., Aguirre, G. K., & Farah, M. J. (1997). Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation (Vol. 94, pp. 14792-14797): National Acad Sciences.
- Tipper, S., Paul, M., & Hayes, A. (2006). Vision-for-action: The effects of object property discrimination and action state on affordance compatibility effects. *Psychonomic bulletin & review*, 13(3), 493.
- Tkach, D., Reimer, J., & Hatsopoulos, N. (2007). Congruent activity during action and action observation in motor cortex. *Journal of Neuroscience*, 27(48), 13241.
- Tomasino, B., Fink, G., Sparing, R., Dafotakis, M., & Weiss, P. (2008). Action verbs and the primary motor cortex: A comparative tms study of silent reading, frequency judgments, and motor imagery. *Neuropsychologia*, 46(7), 1915-1926.
- Toni, I., Shah, N., Fink, G., Thoenissen, D., Passingham, R., & Zilles, K. (2002a). Multiple movement representations in the human brain: An event-related fmri study. *Journal of cognitive neuroscience*, 14(5), 769-784.
- Toni, I., Shah, N. J., Fink, G. R., Thoenissen, D., Passingham, R. E., & Zilles, K. (2002b). Multiple movement representations in the human brain: An event-related fmri study. *Journal of cognitive neuroscience*, 14(5), 769-784.
- Traxler, M. J., & Pickering, M. J. (1996). Plausibility and the processing of unbounded dependencies: An eye-tracking study. *Journal of Memory and Language*, 35(3), 454-475.
- Tucker, M., & Ellis, R. (1998). On the relations between seen objects and components of potential actions. *Journal of Experimental Psychology-Human Perception and Performance*, 24(3), 830-846.
- Tucker, M., & Ellis, R. (2004). Action priming by briefly presented objects. *Acta Psychologica*, 116(2), 185-203.
- Tunik, E., Frey, S., & Grafton, S. (2005). Virtual lesions of the anterior intraparietal area disrupt goal-dependent on-line adjustments of grasp. *Nature neuroscience*, 8(4), 505-511.
- Ulrich, R., & Miller, J. (1994). Effects of truncation on reaction time analysis. *Journal of experimental psychology. General*, 123(1), 34-80.
- Umiltà, M., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C., et al. (2001). I know what you are doing a neurophysiological study. *Neuron*, 31(1), 155-165.
- Urgesi, C., Candidi, M., Fabbro, F., Romani, M., & Aglioti, S. (2006). Motor facilitation during action observation: Topographic mapping of the target muscle and influence of the onlooker's posture. *European Journal of Neuroscience*, 23(9), 2522-2530.
- Vainio, L., Ellis, R., & Tucker, M. (2007). The role of visual attention in action priming. *The Quarterly Journal of Experimental Psychology*, 60(2), 241-261.
- Vallet, G., Brunel, L., & Versace, R. (2010). The perceptual nature of the cross-modal priming effect. *Experimental Psychology*, 57(5), 376-382.

- van Dam, W., Rueschemeyer, S., & Bekkering, H. (2010). How specifically are action verbs represented in the neural motor system: An fmri study. *NeuroImage*.
- Wannier, T., Maier, M., & Hepp-Reymond, M. (1991). Contrasting properties of monkey somatosensory and motor cortex neurons activated during the control of force in precision grip. *Journal of Neurophysiology*, 65(3), 572.
- Warrington, E. K., & McCarthy, R. A. (1987). Categories of knowledge: Further fractionations and an attempted integration. *Brain*, 110(5), 1273.
- Warrington, E. K., & Shallice, T. (1984). Category specific semantic impairments. *Brain*, 107(3), 829.
- Werner, W., Bauswein, E., & Fromm, C. (1991). Static firing rates of premotor and primary motor cortical neurons associated with torque and joint position. *Experimental Brain Research*, 86(2), 293-302.
- Willems, R., Hagoort, P., & Casasanto, D. (2010). Body-specific representations of action verbs. *Psychological Science*, 21(1), 67.
- Willems, R. M., Labruna, L., D'Esposito, M., Ivry, R., & Casasanto, D. (2011). A functional role for the motor system in language understanding: Evidence from theta burst tms. *Psychological Science*(In Press).
- Wise, R. J. S., Howard, D., Mummery, C. J., Fletcher, P., Leff, A., Bichel, C., et al. (2000). Noun imageability and the temporal lobes. *Neuropsychologia*, 38(7), 985-994.
- Wohlschläger, A. (1998). Mental and manual rotation. *Journal of experimental psychology. Human perception and performance*, 24(2), 397.
- Wohlschläger, A. (2000). Visual motion priming by invisible actions. *Vision Research*, 40(8), 925-930.
- Wohlschläger, A. (2001). Mental object rotation and the planning of hand movements. *Perception & psychophysics*, 63(4), 709.
- Worsley, K., Evans, A., Marrett, S., & Neelin, P. (1992). A three-dimensional statistical analysis for cbf activation studies in human brain. *Journal of Cerebral Blood Flow and Metabolism*, 12, 900-900.
- Wuhr, P., & Müsseler, J. (2001). Time course of the blindness to response-compatible stimuli. *Journal of Experimental Psychology*, 27(5), 1260-1270.
- Xiao, J., Padoa-Schioppa, C., & Bizzi, E. (2006). Neuronal correlates of movement dynamics in the dorsal and ventral premotor area in the monkey. *Experimental Brain Research*, 168(1), 106-119.
- Zwaan, R. A., & Taylor, L. J. (2006). Seeing, acting, understanding: Motor resonance in language comprehension. *Journal of Experimental Psychology General*, 135(1), 1.
- Zwicker, J., Grosjean, M., & Prinz, W. (2007). Seeing while moving: Measuring the online influence of action on perception. *The Quarterly Journal of Experimental Psychology*, 60(8), 1063-1071.